TITLE:

Phylogenetic relationship of a fossil macaque (*Macaca cf. robusta*) from the Korean Peninsula to extant species of macaques based on zygomaxillary morphology

AUTHOR(S):

Ito, Tsuyoshi; Lee, Yung-jo; Nishimura, Takeshi D.; Tanaka, Mikiko; Woo, Jong-yoon; Takai, Masanaru

CITATION:

Ito, Tsuyoshi ...[et al]. Phylogenetic relationship of a fossil macaque (*Macaca cf. robusta*) from the Korean Peninsula to extant species of macaques based on zygomaxillary morphology. *Journal of Human Evolution* 2018, 119: 1-13

ISSUE DATE:

2018-06

URL:

<http://hdl.handle.net/2433/243881>

RIGHT:

© 2018. This manuscript version is made available under the CC-BY-NC-ND 4.0 license <http://creativecommons.org/licenses/by-nc-nd/4.0/>; この論文は出版社版ではありません。引用の際には出版社版をご確認ご利用ください。; This is not the published version. Please cite only the published version.

1

2 **Phylogenetic relationship of a fossil macaque (*Macaca cf. robusta*) from the Korean**3 **Peninsula to extant species of macaques based on zygomaxillary morphology**

4

5 Tsuyoshi Ito¹, Yung-jo Lee², Takeshi D. Nishimura¹, Mikiko Tanaka¹, Jong-yoon Woo²,6 Masanaru Takai¹

7

8 ¹Department of Evolution and Phylogeny, Primate Research Institute, Kyoto University,

9 Inuyama, Aichi 484-8506, Japan

10 ²Institute of Korean Prehistory, 2559, Yongam-dong, Sangdang-gu, Cheongju, Chungbuk

11 28763, Korea

12

13 * Corresponding author: Tsuyoshi Ito

14 Telephone: +81-568-63-0523, Fax: +81-568-61-5775

15 E-mail: ito.tsuyoshi.3a@kyoto-u.ac.jp

16

17 Keywords: Biogeography; Computed tomography; East Asia; *Macaca*; Phylogentic
18 morphometrics

19

20 **Abstract**

21 Little is known about the biogeographical and evolutionary histories of macaques
22 (*Macaca* spp.) in East Asia because the phylogenetic positions of fossil species remain
23 unclear. Here we examined the zygomaxillary remains of a fossil macaque (*M. cf. robusta*)
24 from the Durubong Cave Complex, South Korea, that dates back to the late Middle to Late
25 Pleistocene, to infer its phylogenetic relationship to extant species. We took 195 fixed- and
26 semi-landmarks from the zygomaxillary regions of the fossil specimen and from 147
27 specimens belonging to 14 extant species. We then conducted a generalized Procrustes
28 analysis followed by a multivariate statistical analysis to evaluate the phenetic affinities of
29 the fossil to the extant species and reconstructed the most parsimonious phylogenetic tree
30 using a phylogenetic morphometric approach. We found that the fossil was most similar to

M. fuscata (Japanese macaque) in the zygomaxillary morphospace although it was at the limit of the range of variation for this species. The second closest in the morphospace was the continental *M. mulatta* (rhesus macaque). Parsimonious reconstruction confirmed that the fossil was most closely related to *M. fuscata*, even after controlling for the effects of allometry. These findings suggest that in the late Middle to Late Pleistocene, close relatives of *M. fuscata* that looked like the extant species were distributed on the Korean Peninsula, where no species of macaques are found today. Thus, some morphological characteristics of *M. fuscata* may have developed before its ancestor dispersed into the Japanese archipelago.

1. Introduction

The genus *Macaca* consists of approximately 20 extant species and occupies a wider range of climates and habitats than any other genus of nonhuman primates (Fleagle, 2013). Consequently, macaques have attracted much attention as an analogy to understand how humans left tropical regions and adapted to various other environments (Rae et al., 2003; Márquez and Laitman, 2008; Hanya et al., 2011; Karen J, 2011; Tsuji et al., 2013; Ito et al., 2015). Furthermore, some East Asian species, particularly *M. mulatta* (rhesus macaque) and *M. fuscata* (Japanese macaque or snow monkey), are often used in biological laboratory

studies (Sibal and Samson, 2001). To better understand these cold-adapted and well-studied species, we need to understand their biogeographic and evolutionary histories, particularly at the northern limit of their distribution in East Asia.

The phylogeny of extant species of macaques has been well studied, with most molecular phylogenetic studies (Tosi et al., 2000; Li et al., 2009; Jiang et al., 2016), except mitochondrial studies (Morales and Melnick, 1998; Liedigk et al., 2014), supporting the classification of Delson (1980). Delson's classification subdivides macaques into four phylogenetic groups: *fascicularis*, *sinica*, *silenus*, and *sylvanus* groups. A molecular phylogenetic study by Jiang et al. (2016) suggested that the African *sylvanus* group first diverged ca. 5.5 million years ago (Mya), the *silenus* group diverged ca. 4.5 Mya, and the *fascicularis* and *sinica* groups diverged ca. 3.5 Mya.

The most recently diverged groups (i.e., *fascicularis* and *sinica* groups) are distributed in East Asia and partly overlap each other (Fooden, 1988, 2006). The *fascicularis* group consists of four extant species, including *M. fuscata* and *M. mulatta*, which are found in temperate regions: *M. fuscata* is distributed in the Japanese archipelago, which is at the northernmost limit of extant nonhuman primates (Fooden and Aimi, 2005), while *M. mulatta* is widely distributed from Afghanistan to southern China (Fooden, 2000). The *sinica* group

consists of at least five (Sinha et al., 2005; possibly six or seven; Chakraborty et al., 2007; Li et al., 2015; Fan et al., 2016) extant species, with some of the large-bodied species, such as *M. thibetana*, *M. assamensis*, and *M. leucogenys*, distributed in high-altitude areas in southern China (Fooden, 1982, 1983; Li et al., 2015). Thus, both phylogenetic groups inhabit relatively cold environments in East Asia. However, no species currently inhabit northern China and the Korean Peninsula, isolating *M. fuscata* from the other continental species.

However, some excavations of Pleistocene fossil macaques have been reported from northern China and the Korean Peninsula (Schlosser, 1924; Young, 1934; Zhang et al., 1986; Pan and Jablonski, 1987; Park and Lee, 1998; Takai et al., 2008). The first record of a fossil macaque from East Asia was *M. anderssoni*, which was described from a nearly complete face excavated from the Early Pleistocene sediment of Mianchi, Henan Province, China (Schlosser, 1924). A decade later, another species, *M. robusta*, was described from a partial maxilla excavated from the Middle Pleistocene sediment of Choukoutien, Beijing, China (Young, 1934). Since then, nearly all of the fossil specimens that have been discovered in northern China or the Korean Peninsula from the Early to Middle Pleistocene have been referred to as one of these two fossil species. Although *M. anderssoni* has a larger dental size than *M. robusta*, it is sometimes considered a junior synonym of the latter (Simons, 1970;

Delson, 1980; but see Fooden, 1990). These fossils are believed to fill the biogeographical gap in the current distribution of macaques, which will potentially elucidate their evolutionary histories. However, the phylogenetic relationships of these fossils and extant species remain controversial (Delson, 1977, 1980; Jablonski and Pan, 1988; Fooden, 1990; Pan and Yanzhang, 1995; Park and Lee, 1998; Ito et al., 2014b), particularly with regard to whether they are phylogenetically related to members of the *sinica* group or the *fascicularis* group.

The fossil records from the Korean Peninsula is key to understanding the evolution of *M. fuscata* in particular. Some fossil macaques have been reported from the Middle and Late Pleistocene sediments of several localities in the Korean Peninsula (Park and Lee, 1998; Fooden and Aimi, 2005; Lee and Woo, 2005; Lee, 2006; Lee and Takai, 2012; Lee et al., 2013). Most of these fossils are isolated teeth or partial fragments of skeletons, but the fossil specimen excavated by the Chungbuk National University Museum Team from the Durubong (=Turupong) Cave Complex, Cheongju City, Chungbuk Province, South Korea, is a well-preserved zygomaxillary region (Fig. 1). This was identified as *M. cf. robusta* by Park and Lee (1998), who reported that its morphology was intermediate between *M. robusta* and *M. fuscata* but more similar to *M. robusta* with regard to tooth size. Lee and Takai (2012) stated that the upper molars of the Korean fossils were relatively large, making them comparable

with those of *M. anderssoni*, while the lower molars were relatively small compared with other fossil and extant macaques. Furthermore, they also stated that most of the Korean fossils retain some accessory cusps (distoconules, interconulus, 6th cusp, and 7th cusp), which are frequently found in the molars of *M. fuscata* (Lee and Takai, 2012). Fooden and Aimi (2005) demonstrated that measurements of the Korean fossil molars were within the range of variation shown by *M. fuscata*. Together, these findings imply that the Korean fossils may be related to the ancestors of *M. fuscata* or the other fossil species, namely *M. anderssoni* and/or *M. robusta*; and that more than one lineage may have been distributed in the Korean Peninsula during the Middle to Late Pleistocene. However, most previous studies have based their conclusions on tooth morphology alone, and no phylogenetic assessment of the fossil species in comparison with the various extant species of macaques has been conducted to date.

In this study, we compared the morphology of the zygomaxillary region in the Korean fossil specimen that was discovered in the Durubong Cave Complex with that of extant species of macaques. This is the most well-preserved fossil macaque specimen in Korea. Zygomaxillary morphology is likely to be informative for the reconstruction of phylogenetic relationships, because zygomaxillary shape can be partially differentiated among the four phylogenetic groups in macaques (Ito et al., 2014a) and has some phylogenetic signal (Ito et

al., 2014a). First, we evaluated the pattern of zygomaxillary variation in extant species and estimated the evolutionary and phylogenetic significance of this variation. We then assigned the fossil to the morphospace of the extant species and performed a cladistic analysis to infer the evolutionary and phylogenetic relationships of this fossil to the extant species. To do this, we used semi-landmark-based geometric morphometrics to capture the surface topography of the zygomaxillary region, because anatomically defined landmarks were limited on the fossil. Moreover, we examined the nasal cavity morphology using computed tomography (CT), because it has been reported that this reflects phylogenetic relationships (Ito et al., 2014b; Nishimura et al., 2014; Ito and Nishimura, 2016). Based on the findings of these analyses, we discuss the biogeographic and evolutionary histories of East Asian macaques.

2. Materials and methods

2.1. Molecular phylogeny

The phylogeny that was used for the phylogenetic comparative analyses was estimated using 11 mitochondrial and 53 nuclear DNA sequences (Supplementary Online Material [SOM] Table S1). The DNA sequences were obtained from the 10KTrees webserver (Arnold et al., 2010; <http://10ktrees.fas.harvard.edu/Primates/>) and Perelman et al. (2011). The

sequences were aligned using MAFFT version 7 (Kato and Standley, 2013) and then concatenated using SequenceMatrix software (<http://gaurav.github.io/taxondna/>). BEAST 2 software (Bouckaert et al., 2014) was used for phylogenetic inference using a site model that was estimated by the Bayesian approach with the bModelTest package (Bouckaert, 2015). Markov Chain Monte Carlo simulations were performed for 10,000,000,000 generations with a sampling frequency of 100,000. Five species belonging to the subtribe Papionina (*Cercocebus torquatus*, *Lophocebus aterrimus*, *Mandrillus sphinx*, *Papio hamadryas*, and *Theropithecus gelada*) were used as an outgroup. The maximum clade credibility tree was chosen after removing a 10% burn-in using TreeAnnotator version 2.4.7 (SOM Fig. S1).

2.2. Cranial sample

For the fossil specimen, we used the zygomaxillary specimen of a fossil macaque stored at the Chungbuk Natural History Museum, Chungbuk, South Korea (2 $\uparrow$ □-12-2169; Fig. 1), which has been partially broken and repaired. The fully erupted third molars and relatively large canines indicate that this individual was an adult male. This specimen originated from the Durubong (=Turupong) Cave Complex, Cheongju City, Chungbuk Province, South Korea. The faunal composition of Durubong Cave Complex (*Ursus arctosi*, *Crocota ultima*, *Dicerorhinus* cf. *choukoutiensis*, and *M.* cf. *robusta*) suggests that this specimen dates back

to the late Middle Pleistocene to the Late Pleistocene period (Park and Lee, 1998), while the faunal complex together with the results of pollen analyses suggests that this was a warm (interglacial or interstadial) period (Lee and Woo, 2005).

For the extant samples, we used the dry crania with almost-erupted or fully erupted third molars from 147 adult males belonging to 14 extant species (Table 1). These specimens are stored at eight institutes in Japan and USA, which are listed in SOM Table S2. Sulawesi macaques were not included in the sample because of their unusual cranial morphology (Albrecht, 1978). The samples consisted of wild ($n = 80$), captive ($n = 35$), and unknown-origin specimens ($n = 32$), but any pathological specimens, which showed evidence of severe alveolar pyorrhea and/or unusual deflection of muzzles, were not included in the samples. ANOVA showed that the differences in zygomaxillary shape among wild, captive, and unknown-origin specimens were significant in some cases, but were much smaller compared with interspecies differences (SOM Table S3).

2.3. CT examinations

CT images were acquired for the fossil specimen and 134 specimens of extant species. The zygomaxillary fragment of the Korean fossil specimen (2 $\uparrow$ □ -12-2169) was scanned

using a helical scanner (HiSpeed; GE Medical Systems Inc., Waukesha, WI, USA) at the veterinary medical center of Chungbuk National University, Chungbuk, South Korea, with a pixel size of 0.1 mm and a slice thickness of 1.0 mm. The original volume data were then reconstructed to give a slice thickness of 0.3 mm. CT scans of the extant species were obtained previously (Ito and Nishimura, 2016) and are available at the Digital Morphology Museum, Kyoto University (<http://dmm.pri.kyoto-u.ac.jp>), with the exception of specimens that were not permitted for release due to copyright restrictions (SOM Table S2), or from MorphoSource (<http://www.morphosource.org>).

The internal structure of the maxilla was observed using Amira 5.5. In particular, we investigated the degree of lateral expansion of the nasal cavity and the maxillary thickness, which are considered to reflect phylogenetic relationships in macaques (Ito et al., 2014b).

2.4. Geometric morphometrics

Three-dimensional (3D) surface models of the face were obtained from the Smithsonian 3D collection of primates (<http://humanorigins.si.edu/evidence/3d-collection/primate>) or constructed from the serial CT images using Amira 5.5 software (FEI Visualization Sciences Group, Bordeaux, France). Details of the 3D surface modeling were described in a previous

paper (Ito and Nishimura, 2016). Small superficial holes, if any, were manually filled using Amira 5.5 or Rapidform XOS3 64. Where the left side of the face was broken, the 3D surface model was horizontally flipped using MeshLab software (<http://www.meshlab.net>). Because the repair of the fossil specimen was slightly imperfect (i.e., the joins of fragments were not smooth; Fig. 1), we slightly re-repaired the fossil specimen virtually using Amira 5.5 software so that the joins of fragments were smooth and the repaired specimen had a more natural appearance (Fig. 2).

In total, 195 landmarks were taken on the 3D surface models (left side of the face) using Stratovan Checkpoint software (Stratovan Corporation, Sacramento, CA, USA; Fig. 3). This included 22 anatomically defined landmarks, 42 semi-landmarks on curves, and 131 semi-landmarks on the surface (SOM Table S4). Missing landmarks (16 landmarks in nine specimens) were estimated by deforming the configurations of the weighted average of the complete dataset for the same species using a thin-plate spline (TPS) interpolation calculated from the available landmarks. The semi-landmarks were slid on curves or surfaces so that the bending energy of TPS deformation was minimal (Gunz et al., 2005). These procedures were performed using the package “Morpho” version 2.5.1 (Schlager, 2017) in R software version 3.4.1 (R Core Team, 2017). Following sliding, the semi-landmarks were treated in the same

197 way as the homologous landmarks in subsequent analyses.

198 All of the final coordinates were subjected to generalized Procrustes analysis (GPA),
199 which registered the landmark configurations across all individuals to produce Procrustes
200 coordinates. The centroid size was simultaneously calculated as the square root of the sum of
201 the square distances of all landmarks from their centroid. To evaluate non-allometric
202 variations, we also produced size-adjusted shape components by calculating the residuals of
203 the multiple regression of Procrustes coordinates on natural-logarithmically transformed
204 centroid size (lnCS) using MorphoJ version 1.06d (Klingenberg, 2011), wherein 16.2% of
205 the shape variance was explained by lnCS ($p < 0.0001$).

206 We then calculated species mean values. To do this, GPA was conducted for each
207 species, and the mean shapes of the 15 operational taxonomic units (the 14 extant species and
208 the fossil specimen) were then subjected to another GPA. A size-adjusted shape component
209 was then calculated in the same way as mentioned above but on a species mean basis, wherein
210 27.2% of the shape variance was explained by lnCS ($p = 0.0012$).

211 The individual values were used in the phenetic analyses, while the species mean values
212 were used in the phylogenetic comparative and cladistic analyses. Each of these analyses was

213 conducted twice using the raw and size-adjusted shape data.

214 2.5. *Phenetic analyses*

215 The phenetic affinity of the fossil specimen was evaluated to assign it to the
216 morphospace of the extant species. To detect shape vectors that exhibited interspecies
217 differences, between-group principal component analyses (bgPCAs) were performed. The
218 bgPCA is the projection of data onto the principal components of the group means
219 (Mitteroecker and Bookstein, 2011). In this study, the species means for extant species were
220 included in the calculation of the covariance matrix, following which the individuals of extant
221 species and the fossil specimens were projected onto the bgPCA axes. This step was
222 performed using the “plotTangentSpace” function of the “geomorph” package with some
223 modifications. Shape changes along the bgPC axes were visualized using R, Amira 5.5, and
224 Rapidform XOS3 64.

225 Procrustes distances were calculated from the fossil specimen to all extant individuals
226 to quantify its phenetic affinity to extant species using the R package “shapes” version 1.2.0
227 (Dryden, 2016).

228 *2.6. Phylogenetic comparative analyses*

229 Phylogenetic comparative analyses were performed to evaluate the phylogenetic
230 significance and evolutionary polarity of zygomaxillary shape. A phylomorphospace
231 (Sidlauskas, 2008) was obtained to reconstruct the evolutionary changes in zygomaxillary
232 shape along the tree using the “plotGMPhyloMorphoSpace” function of the “geomorph”
233 package with some modifications. A phylomorphospace is a PCA of the species mean values
234 and the inferred ancestral shapes, with the phylogeny mapped onto the plane of the PCs. This
235 was produced using only the extant species (and the inferred ancestral nodes), following
236 which the fossil specimen was extrapolated into the PC axes. The phylogenetic signal in
237 zygomaxillary shape was evaluated using the “physignal” function of the “geomorph”
238 package. The significance of the phylogenetic signal was then tested using permutation
239 procedures with 9,999 iterations.

240 *2.7. Cladistic analyses*

241 A phylogenetic morphometric approach (Catalano et al., 2010; Goloboff and Catalano,
242 2011) was used to estimate the phylogenetic relationship between the fossil specimen and the
243 extant species examined. This approach parsimoniously detects the ancestral points that

244 minimize the distance between the ancestor and descendant points along the tree and has been
245 shown to have a better performance than other landmark-based cladistic approaches
246 (Catalano and Torres, 2016). We performed the cladistic analyses using the species mean
247 values of the Procrustes coordinates with the Windows GUI version of TNT 1.5 software
248 (Goloboff et al., 2008; Goloboff and Catalano, 2016), setting *M. sylvanus* as an outgroup and
249 searching for the best tree with and without monophyly constraints. Considering previous
250 molecular phylogenetic studies of Alu elements (Li et al., 2009; Jiang et al., 2016), the
251 constraints were forced as follows: [(arc, ass, thi), (rad, sin)], ([fus, mul, cyc], fas)], (leo, sil,
252 sib, nem); the fossil was allowed to move freely (for abbreviations, see Table 1). Landmark
253 optimization was set as six grid cells and one nesting with iterations. A traditional search was
254 conducted, which consisted of Wagner trees with 10 replications followed by tree bisection
255 reconnection. Resampling was performed to evaluate phylogenetic uncertainty, wherein
256 symmetric resampling with 33% change probability was conducted, and the frequency
257 difference (GC values; Goloboff, 2003) was calculated.

3. Results

3.1. Internal structures

The internal structures of the maxilla in the extant species are shown in Figure 4. The large-bodied species of the *sinica* group, namely *M. arctoides*, *M. assamensis*, and *M. thibetana*, often exhibited a laterally expanded nasal cavity with thin maxillary walls, which was well represented at the M¹ level (this corresponds approximately to the level at which the nasal cavity shows a maximum width). By contrast, other species, including members of the *fascicularis*, *silenus*, and *sylvanus* groups, usually had limited lateral expansion of the nasal cavity and a relatively thick maxillary wall.

In the fossil specimen, the lateral and upper walls of the nasal cavity were broken (Fig. 5). Nevertheless, based on the surrounding structures, it appeared that the nasal cavity was not as greatly expanded laterally as those of the large-bodied species of the *sinica* group, and the maxillary walls were relatively thick.

3.2. Phenetic affinities of zygomaxillary shape

The bgPCA for the raw shape data showed allometric and non-allometric variations in the zygomaxillary shape (Fig. 6). bgPC1 and bgPC2 accounted for 47.2% and 18.0% of the

total interspecies variance, respectively; bgPC1 was positively correlated with lnCS ($r = 0.70$, $p < 0.001$), whereas bgPC2 was not ($r = 0.10$, $p = 0.238$). Individuals with more positive bgPC1 scores (and thus larger lnCS) tended to have muzzles that were longer, superior-inferiorly shorter, and narrower, had a more prominent canine alveolus, and were more ventrally oriented at the anterior portion (Fig. 7). The intercept of this allometric trajectory was significantly different among the species groups (ANCOVA, $p = 0.010$; the *sylvanus* group was excluded from this analysis due to its small sample size), but their distributions highly overlapped each other. Individuals with more positive bgPC2 scores tended to have less prognathic and higher muzzles, with a wider posterior portion compared with the anterior portion. The *fascicularis* and *sylvanus* groups had high bgPC2 scores compared with the other two groups, although their distributions also considerably overlapped.

The bgPCA for the size-adjusted shape data exhibited non-allometric variations (Fig. 6), with bgPC1 and bgPC2 accounting for 27.2% and 16.4% of this interspecies variance, respectively. In contrast to the bgPCA for the raw shape data, bgPCA for the size-adjusted shape data did not show a variation in facial elongation (Fig. 7). A more positive bgPC1 score was associated with a more inferior deflection of the anterior portion of the muzzle against the posterior portion. The shape changes, as well as interspecies group differences along the

bgPC2 axis, were almost identical to those shown for bgPC2 of the raw shape data, but in the opposite direction.

For the fossil specimen, lnCS and bgPC1 were approximately intermediate among the macaques (Fig. 6). The bgPC2 showed that the fossil specimen had a less prognathic and higher muzzle, and the posterior portion of the muzzle was wider than the anterior portion, making it similar to members of the *fascicularis* and *sylvanus* groups. In particular, the fossil specimen was closest to or within the ranges of variation for *M. fuscata* and *M. mulatta*, as seen in the scatterplots of lnCS and bgPC scores. Figure 8 shows the Procrustes distances from the fossil specimen to each of the examined individuals of extant species. For both the raw and size-adjusted shape data, the fossil specimen was the most similar to *M. fuscata* and the least similar to species of the *silenus* group. The other species were positioned intermediate between these two extremes, but *M. thibetana* was similar to the fossil when size was adjusted.

3.3. Phylogenetic comparisons

A moderate phylogenetic signal was detected in the raw shape data ($K = 0.42$, $p = 0.0163$) but was marginally significant in the size-adjusted shape data ($K = 0.36$, $p = 0.0627$).

The phylomorphospace demonstrated evolutionary changes in the zygomaxillary shape (Fig. 9). For the raw shape data, PC1 and PC2 accounted for 50.4% and 17.5% of the variance, respectively, and PC1 was positively correlated with lnCS ($r = 0.79$, $p = 0.0009$), whereas PC2 was not ($r = 0.06$, $p = 0.831$). Shape changes along these PC axes showed similar patterns to the bgPCA of the raw shape data (SOM Fig. S2). For the size-adjusted shape data, PC1 and PC2 accounted for 27.7% and 26.4% of the variance, respectively. More positive PC1 scores were associated with a more prominent canine alveolus and with the anterior portion of the muzzles being deflected more inferiorly against the posterior portion. Shape changes along PC2 were almost identical to those shown in the raw shape data, but in the opposite direction.

The fossil specimen was positioned near the branch of *M. fuscata* for both the raw and size-adjusted shape data (Fig. 9). The clade that included *M. fuscata*, *M. mulatta*, and *M. cyclopis*, as well as *M. sylvanus*, deviated from the ancestral nodes in phylomorphospace. Although the degree of deviation was limited compared with the two lineages, *M. thibetana* also approached the derived fields of the phylomorphospace, particularly when size was adjusted. Such deviations indicated that these lineages independently acquired similar derived features (i.e., a less prognathic and higher muzzle, whose posterior portion was narrower than

the anterior portion).

3.4. Cladistic analyses

Cladistic analyses were performed based on the 3D landmark data from the zygomaxillary region (Fig. 10). The unconstrained models reconstructed trees whose topologies were quite different from the molecular phylogenetic trees (Li et al., 2009; SOM Fig. S1), indicating that there is some homoplasy in the zygomaxillary morphology. The best tree scores, which indicate the sum of the differences between the shapes of the ancestor and descendants for all tree branches (Goloboff and Catalano, 2016), were 3.21664 and 3.41040 for the raw and size-adjusted shape data, respectively. When the analyses were repeated with monophyly constraints, which searched for the most parsimonious scenario within the constraints, the best tree scores were 3.70956 and 3.85731 for the raw and size-adjusted shape data, respectively. In all four cases, the phylogenetic proximity between the fossil specimen and *M. fuscata* was supported.

4. Discussion

4.1. Patterns of zygomaxillary variation in extant species

We observed allometric variations in zygomaxillary shape among the extant species

examined. As commonly found in papionin crania (Singleton, 2002; Frost et al., 2003; Gilbert and Grine, 2010; Ito et al., 2014a), we confirmed that larger individuals tended to have more elongated and inferiorly deflected muzzles. Such allometric shape components should be interpreted with care in phylogenetic studies because they can obscure phylogenetic signal. For example, although bgPC1 showed that an elongated and inferiorly deflected muzzle is characteristic of members of the *silenus* group, this feature is actually just a scaled-up version of that found in small-bodied taxa. Similarly, the shape components that were represented by PC1 of the phylomorphospace were also allometric and therefore problematic. Although allometric shape components are potentially phylogenetically informative (Gilbert and Rossie, 2007; Gilbert et al., 2009), we were unable to detect clear differences in allometric vectors among the four phylogenetic groups. Furthermore, although size itself may provide some phylogenetic information, it is inappropriate to rely on a single trait (i.e., size) when inferring phylogenetic relationships (see Pearson et al., 2015).

Non-allometric shape components were observed in two ways. First, bgPC2 and PC2 of phylomorphospace based on the raw shape data were independent of size, which can be interpreted as non-allometric. Second, the size-adjusted shape components, which were the residuals of a multiple regression of raw Procrustes shape components on lnCS (Monteiro,

1999; Drake and Klingenberg, 2008; Klingenberg, 2011), were free from allometric associations, although they had also partially lost some phylogenetic information in the process (see Gilbert, 2011). These non-allometric shape components did not include facial elongation but could be characterized by the degrees of height and prognathism of the muzzle, as well as some localized shape changes in the zygomaxillary region.

The phylogenetic significance and evolutionary polarity of zygomaxillary shape were evaluated. The phylomorphospace suggested that a higher and less prognathic muzzle was a derived condition in macaques as shown in PC2, and this was observed in the clade that includes *M. fuscata*, *M. mulatta*, and *M. cyclopis* of the *fascicularis* group, as well as *M. thibetana* and *M. sylvanus*. These lineages all inhabit relatively cold environments, and therefore this shape change may reflect parallel adaptive evolution to a cold environment, although further testing is required to verify this hypothesis. The degree of change along this PC2 axis, however, varies among lineages; *M. fuscata* is located at the extreme end of this axis (and thus has the highest and least prognathic muzzle), followed by *M. sylvanus*, close relatives of *M. fuscata* (*M. mulatta* and *M. cyclopis*), and *M. thibetana*. The difference in the degree of the shape change among phylogenetic groups could be explained by phylogenetic constraints, as suggested by the finding that some phylogenetic signal is detected in the

zygomaxillary shape, although it is marginally significant for size-adjusted shape data.

In addition, previous studies have indicated that variations in the nasal cavity can be explained by phylogeny but not by allometry (Ito et al., 2014b; Ito and Nishimura, 2016). Here, the most notable characteristics are a laterally expanded nasal cavity and thin lateral maxillary walls at the anterior portion of the muzzle, which are often seen in the three large-bodied species of the *sinica* group (*M. arctoides*, *M. assamensis*, and *M. thibetana*). These internal features are considered to be derived traits in macaques (Ito et al., 2009; Ito et al., 2014b). Certainly, nasal cavity morphology also varies in relation to ecological adaptation and developmental plasticity. For example, in modern humans, individuals in colder environments tend to have a narrower nasal cavity (Noback et al., 2011), while in Japanese macaques, individuals in colder environments tend to have a larger cross-sectional area of the cavity (Rae et al., 2003); such clinal variations are generally considered to be a consequence of adaptation to climate. Additionally, cold environment-reared rats have smaller nasal cavities than a corresponding control group, which reflects developmental plasticity (Rae et al., 2006). Nevertheless, it is difficult to explain, solely by such environmental factors, why an expanded nasal cavity is often found in the three-large-bodied species of the *sinica* group but is barely observed in other cold environment-inhabiting species such as *M. sylvanus* and

M. fuscata. Therefore, the derived traits of internal structures that are found in members of the *sinica* group as well as those of zygomaxillary shape that are typically found in members of the *fascicularis* and *sylvanus* groups are considered to be informative for estimating the phylogenetic relationships of a fossil specimen.

4.2. Characteristics of the Korean fossil specimen and their phylogenetic significance

The Korean fossil specimen was most similar to *M. fuscata* in several characteristics. However, it must be remembered that a phenetic affinity does not necessarily reflect phylogenetic relatedness. The nasal cavity of the Korean fossil specimen exhibited moderate lateral expansion, making it similar to members of the *fascicularis* group and some of the other groups. However, this is not considered to be a derived character (Ito et al., 2014b) and so cannot be used to imply their phylogenetic relatedness. The Korean fossil specimen also had a somewhat similar level of facial elongation to some other species, such as *M. fuscata*. However, since this feature is largely associated with size, its reliability for phylogenetic interpretation is also questionable. The long-standing controversies around the phylogenetic relationships of fossil macaques (Delson, 1977, 1980; Jablonski and Pan, 1988; Fooden, 1990; Pan and Yanzhang, 1995; Park and Lee, 1998; Ito et al., 2014b) could be partly ascribed to the use of such confusing characteristics.

The Korean fossil specimen has a vertically high and less prognathic muzzle, which is the same as the clade that includes *M. mulatta*, *M. cyclopis*, and *M. fuscata*, as well as *M. sylvanus*. This shape component is independent of allometry and is probably a derived condition in macaques. It is not likely that the Korean fossil is closely related to the African species *M. sylvanus*. Among the three species of the clade, the Korean fossil was most similar to *M. fuscata*, followed by *M. mulatta*, with features that lay within the range of intraspecific variation for each. Furthermore, cladistic analyses also confirmed phylogenetic relatedness between the Korean fossil specimen and *M. fuscata*. Although *M. thibetana* is similar to the Korean fossil, particularly for the size-adjusted shape data, the degree of similarity is limited compared with *M. fuscata*. Therefore, it is reasonable to consider that the Korean fossil specimen is phylogenetically related to the clade that includes *M. mulatta*, *M. cyclopis*, and *M. fuscata*, particularly to *M. fuscata*.

It should be noted here that this finding does not necessarily suggest a phylogenetic closeness between members of the *fascicularis* group and the Chinese fossil species, namely *M. robusta* and *M. anderssoni*. Although the fossil macaques discovered from the Korean Peninsula are sometimes referred to as *M. robusta* (Park and Lee, 1998; Lee and Woo, 2005), some or all of them may be actually unrelated to this fossil species. Further studies are

expected to elucidate the phylogenetic relationships among the fossil specimens in East Asia.

4.3. Biogeographical and evolutionary implications

The present study suggests that the Korean fossil specimen is phylogenetically related to the *fascicularis*, rather than the *sinica*, group of macaques. Delson (1980) and Ito et al. (2014b) suggested that the proto-members of the *sinica* group, for example, *M. anderssoni*, were largely distributed in northern China in the Early Pleistocene and that members of this group may have retreated southward and been replaced by latecomers, that is, members of the *fascicularis* group, likely by the Middle Pleistocene (Delson, 1980; Ito et al., 2014b). This scenario is congruent with the present inference that the macaques living on the Korean Peninsula in the late Middle to Late Pleistocene were related to the *fascicularis* group.

The late Middle to Late Pleistocene period is likely later than the divergence time between *M. fuscata* and *M. mulatta*, which is considered to be ca. 0.4–1.4 Mya based on molecular studies and fossil evidence from Japan (Fooden and Aimi, 2005; Fooden, 2006; Chu et al., 2007; Jiang et al., 2016). Therefore, the Korean macaque is not the direct ancestor of *M. fuscata* but rather belongs to a collateral line that diverged from the main line of *M. fuscata*, *M. mulatta*, or the common ancestral lineage of the two species. They are probably

remnants that had been retained in the Korean Peninsula. Alternatively, the Korean macaque may be a subpopulation of Japanese macaques that had returned from the Japanese archipelago. In light of the parsimony principle, the former scenario is more probable. In either case, the Korean lineage could have become extinct due to an inability to escape the Korean Peninsula during the Late Pleistocene glacial period.

The zygomaxillary shape of the Korean fossil specimen is intermediate between *M. fuscata* and *M. mulatta* but more similar to the former. It has previously been suggested that the distinct morphological characteristics of *M. fuscata* developed after its dispersal into the Japanese archipelago (Fooden, 2006). However, assuming that the Korean macaque is not the lineage that has returned from the Japanese archipelago, it follows that the morphological evolution of these features started before this dispersal. These findings fill in some of the biogeographical and evolutionary gaps between *M. fuscata* and continental lineages, potentially shedding light on cold adaptation in primates.

4.4. Limitations of this study

This study has several important limitations, particularly related to sample composition. First, the sample size is small for both extant ($n = 2\text{--}53/\text{species}$) and fossil species ($n = 1$).

This limitation risks an underestimation of intraspecific variation and reduces the reliability of species mean value estimation (Cardini and Elton, 2007; Schillaci and Schillaci, 2009). Second, the sample includes not only wild-caught specimens but also captive and unknown-origin specimens. We demonstrated that the morphological differences among specimen sources were small compared with interspecies differences, but were significant in some cases. Therefore, our interpretation of the results, which mainly suggested a phylogenetic closeness between the Korean lineage and *M. fuscata*, is not necessarily conclusive. In particular, *M. thibetana* should remain a candidate for being the sister taxon of the Korean lineage, because *M. thibetana* is somewhat similar to the Korean fossil in terms of zygomaxillary shape, particularly when size is adjusted. Further studies with a larger sample size, which ideally include only wild-caught specimens, will clarify our findings.

5. Conclusion

This study investigated the zygomaxillary morphology of the fossil macaque from the Middle to Late Pleistocene of the Korean Peninsula compared with living macaque species. We found that the Korean fossil is the most similar in zygomaxillary morphology to *M. fuscata*, followed by *M. mulatta*, and is phylogenetically related to the clade that includes *M.*

mulatta, *M. cyclopis*, and *M. fuscata* (particularly to *M. fuscata*). This finding, unlike traditional scenarios, suggests that the morphological characteristics of *M. fuscata* could have been formed before this group dispersed to the Japanese archipelago, potentially shedding light on how primates adapted to a cold environment.

Acknowledgments

We would like to convey our gratitude to JY Seong, SY Lee, BI Yun, KW Lee, and the staff of the Chungbuk Natural History Museum and the Institute of Korean Prehistory for their help with accessing the fossil specimens and for providing information about them, and C. Dongwoo and Y. Lee for their assistance with CT scanning of the specimens. We also thank Tet. Hayashi, Ter. Hayashi, S. Yachimori, E. Ashida, D. Shimizu, T. Takano, Y. Shintaku, H. Taru, H. Hirotani, H. Takahashi, N. Shigehara, and many field workers for collecting/preserving the remains of macaques and/or permitting us to access the collections that they manage. We thank N. Ogihara, S. Kondo, M. Nakatsukasa, Thaung Htike, Zin-Maung-Maung-Thein, and W. Yano for their help with CT scanning of extant species and N. Egi for her help with the 3D surface modeling. We thank three anonymous reviewers and editors for their constructive comments on our previous version of this manuscript, which

considerably improved the clarity of this paper. We thank the Smithsonian's Division of Mammals (Dr. Kristofer Helgen) and Human Origins Program (Dr. Matt Tocheri) for the scans of USNM specimens used in this research (<http://humanorigins.si.edu/evidence/3d-collection/primate>). These scans were acquired through the generous support of the Smithsonian 2.0 Fund and the Smithsonian's Collections Care and Preservation Fund. Lynn Copes, Lynn Lucas, and the MCZ provided access to these scans, originally appearing in Copes and Kimbel (2016) and Copes et al. (2016), funding for the collection of which was provided by NSF DDIG #0925793, and a Wenner-Gren Foundation Dissertation Grant #8102 (both to Lynn Copes). These scans were downloaded from MorphoSource.org, a web-accessible archive for 3D digital data housed by Duke University. This study was funded by the Fujiwara Natural History Foundation (to TI), the Keihanshin Consortium for Fostering the Next Generation of Global Leaders in Research (K-CONNEX) (to TI), and JSPS grants-in-aid for Scientific Research (Grant 26650171 to TDN).

References

Albrecht, G.H., 1978. The Craniofacial Morphology of the Sulawesi Macaques: Multivariate Approaches to Biological Problems. Contributions to Primatology 13,. Karger, Basel.

- 505 Arnold, C., Matthews, L.J., Nunn, C.L., 2010. The 10 k Trees Website: A new online resource
506 for primate phylogeny. *Evolutionary Anthropology* 19, 114-118.
- 507 Bouckaert, R., Heled, J., Kuhnert, D., Vaughan, T., Wu, C.H., Xie, D., Suchard, M.A., Rambaut,
508 A., Drummond, A.J., 2014. BEAST 2: a software platform for Bayesian evolutionary
509 analysis. *PLoS Computational Biology* 10, e1003537.
- 510 Bouckaert, R., 2015. bModelTest: Bayesian site model selection for nucleotide data. *bioRxiv*,
511 020792.
- 512 Cardini, A., Elton, S., 2007. Sample size and sampling error in geometric morphometric studies
513 of size and shape. *Zoomorphology* 126, 121-134.
- 514 Catalano, S.A., Goloboff, P.A., Giannini, N.P., 2010. Phylogenetic morphometrics (I): the use
515 of landmark data in a phylogenetic framework. *Cladistics* 26, 539-549.
- 516 Catalano, S.A., Torres, A., 2016. Phylogenetic inference based on landmark data in 41
517 empirical data sets. *Zoological Scripta* 46, 1-11.
- 518 Chakraborty, D., Ramakrishnan, U., Panor, J., Mishra, C., Sinha, A., 2007. Phylogenetic
519 relationships and morphometric affinities of the Arunachal macaque *Macaca munzala*, a
520 newly described primate from Arunachal Pradesh, northeastern India. *Molecular*
521 *Phylogenetics and Evolution* 44, 838-849.

- 522 Chu, J.H., Lin, Y.S., Wu, H.Y., 2007. Evolution and dispersal of three closely related macaque
523 species, *Macaca mulatta*, *M. cyclopis*, and *M. fuscata*, in the eastern Asia. Molecular
524 Phylogenetics and Evolution 43, 418-429.
- 525 Copes, L.E., Kimbel, W.H., 2016. Cranial vault thickness in primates: *Homo erectus* does not
526 have uniquely thick vault bones. Journal of Human Evolution 90, 120-134.
- 527 Copes, L.E., Lucas, L.M., Thostenson, J.O., Hoekstra, H.E., Boyer, D.M., 2016. A collection
528 of non-human primate computed tomography scans housed in MorphoSource, a repository
529 for 3D data. Scientific Data 3, 160001.
- 530 Delson, E., 1977. Vertebrate paleontology, especially of nonhuman primates, in China. In:
531 Howells, W.W., Tsuchitani, P.J. (Eds.), Paleoanthropology in the People's Republic of
532 China. National Academy of Science, Washington, D.C., pp. 40-65.
- 533 Delson, E., 1980. Fossil macaques, phyletic relationships and a scenario of deployment. In:
534 Lindburg, D.G. (Ed.), The Macaques: Studies in Ecology, Behavior and Evolution.
535 Nostrand-Reinhold, New York, pp. 10-30.
- 536 Drake, A.G., Klingenberg, C.P., 2008. The pace of morphological change: historical
537 transformation of skull shape in St Bernard dogs. Proceedings of the Royal Society of
538 London B: Biological Sciences 275, 71-76.

- 539 Dryden, I.L., 2016. shapes: Statistical Shape Analysis. R package version 1.1-13. [https://cran.r-](https://cran.r-project.org/package=shapes)
- 540 [project.org/package=shapes](https://cran.r-project.org/package=shapes).
- 541 Fan, P., Liu, Y., Zhang, Z., Zhao, C., Li, C., Liu, W., Liu, Z., Li, M., 2016. Phylogenetic position
- 542 of the white-cheeked macaque (*Macaca leucogenys*), a newly described primate from
- 543 Southeastern Tibet. *Molecular Phylogenetics and Evolution* 107, 80-89.
- 544 Fleagle, J.G., 2013. *Primate Adaptation and Evolution*. 3rd edn. Academic Press, San Diego.
- 545 Fooden, J., 1982. Taxonomy and evolution of the *sinica* group of macaques: 3. Species and
- 546 subspecies accounts of *Macaca assamensis*. *Fieldiana Zoology* 10, 1-52.
- 547 Fooden, J., 1983. Taxonomy and evolution of the *sinica* group of macaques: 4. Species account
- 548 of *Macaca thibetana*. *Fieldiana Zoology* 17, 1-20.
- 549 Fooden, J., 1988. Taxonomy and evolution of the *sinica* group of macaques: 6. Interspecific
- 550 comparisons and synthesis. *Fieldiana Zoology* 45, 1-44.
- 551 Fooden, J., 1990. The bear macaques, *Macaca arctoides*: a systematic review. *Journal of*
- 552 *Human Evolution* 19, 607-686.
- 553 Fooden, J., 2000. Systematic review of the rhesus macaques, *Macaca mulatta* (Zimmermann,
- 554 1780). *Fieldiana Zoology* 96, 1-180.
- 555 Fooden, J., Aimi, M., 2005. Systematic review of Japanese macaques, *Macaca fuscata* (Gray,

- 556 1870). *Fieldiana Zoology* 104, 1-198.
- 557 Fooden, J., 2006. Comparative review of *fascicularis*-group species of macaques (Primates:
- 558 *Macaca*). *Fieldiana Zoology* 107, 1-44.
- 559 Frost, S.R., Marcus, L.F., Bookstein, F.L., Reddy, D.P., Delson, E., 2003. Cranial allometry,
- 560 phylogeography, and systematics of large-bodied papionins (primates: Cercopithecinae)
- 561 inferred from geometric morphometric analysis of landmark data. *Anatomical Record*
- 562 275A, 1048-1072.
- 563 Gilbert, C.C., 2011. Phylogenetic analysis of the African papionin basicranium using 3-D
- 564 geometric morphometrics: the need for improved methods to account for allometric effects.
- 565 *American Journal of Physical Anthropology* 144, 60-71.
- 566 Gilbert, C.C., Grine, F.E., 2010. Morphometric variation in the papionin muzzle and the
- 567 biochronology of the South African Plio-Pleistocene karst cave deposits. *American*
- 568 *Journal of Physical Anthropology* 141, 418-429.
- 569 Gilbert, C.C., Rossie, J.B., 2007. Congruence of molecules and morphology using a narrow
- 570 allometric approach. *Proceedings of the National Academy of Sciences of the United*
- 571 *States of America* 104, 11910-11914.
- 572 Gilbert, C.C., Frost, S.R., Strait, D.S., 2009. Allometry, sexual dimorphism, and phylogeny: a

- 573 cladistic analysis of extant African papionins using craniodental data. *Journal of Human*
574 *Evolution* 57, 298-320.
- 575 Goloboff, P., 2003. Improvements to resampling measures of group support. *Cladistics* 19, 324-
576 332.
- 577 Goloboff, P.A., Catalano, S.A., 2011. Phylogenetic morphometrics (II): algorithms for
578 landmark optimization. *Cladistics* 27, 42-51.
- 579 Goloboff, P.A., Catalano, S.A., 2016. TNT version 1.5, including a full implementation of
580 phylogenetic morphometrics. *Cladistics* 32, 221-238.
- 581 Goloboff, P.A., Farris, J.S., Nixon, K.C., 2008. TNT, a free program for phylogenetic analysis.
582 *Cladistics* 24, 774-786.
- 583 Gunz, P., Mitteroecker, P., Bookstein, F.L., 2005. Semilandmarks in three dimensions. In: Slice,
584 D.E. (Ed.), *Modern Morphometrics in Physical Anthropology*. Kluwer Academic
585 Publishers, New York, pp. 73-98.
- 586 Hanya, G., Menard, N., Qarro, M., Ibn Tattou, M., Fuse, M., Vallet, D., Yamada, A., Go, M.,
587 Takafumi, H., Tsujino, R., Agetsuma, N., Wada, K., 2011. Dietary adaptations of
588 temperate primates: comparisons of Japanese and Barbary macaques. *Primates* 52, 187-
589 198.

- 590 Ito, T., Nishimura, T.D., 2016. Enigmatic diversity of the maxillary sinus in macaques and its
591 possible role as a spatial compromise in craniofacial modifications. *Evolutionary Biology*
592 43, 414-426.
- 593 Ito, T., Nishimura, T.D., Senut, B., Koppe, T., Treil, J., Takai, M., 2009. Reappraisal of *Macaca*
594 *speciosa subfossilis* from the late Pleistocene of northern Vietnam based on the analysis
595 of cranial anatomy. *International Journal of Primatology* 30, 646-661.
- 596 Ito, T., Nishimura, T., Takai, M., 2014a. Ecogeographical and phylogenetic effects on
597 craniofacial variation in macaques. *American Journal of Physical Anthropology* 154, 27-
598 41.
- 599 Ito, T., Nishimura, T.D., Ebbestad, J.O.R., Takai, M., 2014b. Computed tomography
600 examination of the face of *Macaca anderssoni* (Early Pleistocene, Henan, northern China):
601 implications for the biogeographic history of Asian macaques. *Journal of Human*
602 *Evolution* 72, 64-80.
- 603 Ito, T., Nishimura, T.D., Hamada, Y., Takai, M., 2015. Contribution of the maxillary sinus to
604 the modularity and variability of nasal cavity shape in Japanese macaques. *Primates* 56,
605 11-19.
- 606 Jablonski, N.G., Pan, Y., 1988. The evolution and palaeobiogeography of monkeys in China.

- 607 In: Whyte, P., Aigner, J., Jablonski, N.G., Taylor, G., Walker, D., Wang, P.X. (Eds.), The
608 Palaeoenvironment of East Asia from the Mid-Tertiary. Centre of Asian Studies, Hong
609 Kong, pp. 849-867.
- 610 Jiang, J., Yu, J., Li, J., Li, P., Fan, Z., Niu, L., Deng, J., Yue, B., 2016. Mitochondrial genome
611 and nuclear markers provide new insight into the evolutionary history of macaques. PLoS
612 ONE 11, e0154665.
- 613 Karen J, W., 2011. Climatic and altitudinal influences on variation in *Macaca* limb morphology.
614 Anatomy Research International 2011, 1-18.
- 615 Katoh, K., Standley, D.M., 2013. MAFFT multiple sequence alignment software version 7:
616 improvements in performance and usability. Molecular Biology and Evolution 30, 772-
617 780.
- 618 Klingenberg, C.R., 2011. MorphoJ: an integrated software package for geometric
619 morphometrics. Molecular Ecology Resources 11, 353-357.
- 620 Lee, Y.-J. (Ed.), 2006. The Paleolithic Culture of Jungwon Region, Korea. Institute for
621 Jungwon Culture, Chungbuk National University, Cheongju [Korean with English
622 abstracts].
- 623 Lee, Y.-J., Takai, M., 2012. The Middle to Late Pleistocene macaque fossils from central Korea.

- 624 In: Drozdov, N.I., Lee, Y.-J., Woo, J.-Y. (Eds.), The 17th International Symposium:
625 Suyanggae and Her Neighbors in Kurtak. Institute of Korean Prehistory and Krasnoyarsk
626 State Pedagogical University, Cheongju, pp. 116–119.
- 627 Lee, Y.-J., Woo, J.-Y. (Eds.), 2005. Paleolithic Sites of the Jungwon Region, Korea. Chungbuk
628 National History Museum, Chungbuk [Korean with English abstracts].
- 629 Lee, Y.-J., Woo, J.-Y., Lee, S.-W., Byeong-Il, Y., Park, J.-Y., 2013. Progress Report of Gunang
630 Cave Site, Danyang (IV) – 2011 Year Excavation (5th). Institute of Korean Prehistory
631 Danyang County-Research Report 38 [Korean with English abstract].
- 632 Li, C., Zhao, C., Fan, P.F., 2015. White - cheeked macaque (*Macaca leucogenys*): A new
633 macaque species from Modog, southeastern Tibet. American Journal of Primatology 77,
634 753-766.
- 635 Li, J., Han, K., Xing, J., Kim, H.S., Rogers, J., Ryder, O.A., Disotell, T., Yue, B., Batzer, M.A.,
636 2009. Phylogeny of the macaques (Cercopithecidae: *Macaca*) based on Alu elements.
637 Gene 448, 242-249.
- 638 Liedigk, R., Roos, C., Brameier, M., Zinner, D., 2014. Mitogenomics of the Old World monkey
639 tribe Papionini. BMC Evolutionary Biology 14, 176.
- 640 Márquez, S., Laitman, J.T., 2008. Climatic effects on the nasal complex: a CT imaging,

- 641 comparative anatomical, and morphometric investigation of *Macaca mulatta* and *Macaca*
642 *fascicularis*. Anatomical Record 291, 1420-1445.
- 643 Mitteroecker, P., Bookstein, F., 2011. Linear discrimination, ordination, and the visualization
644 of selection gradients in modern morphometrics. Evolutionary Biology 38, 100-114.
- 645 Monteiro, L.R., 1999. Multivariate regression models and geometric morphometrics: the search
646 for causal factors in the analysis of shape. Systematic Biology 48, 192-199.
- 647 Morales, J.C., Melnick, D.J., 1998. Phylogenetic relationships of the macaques
648 (Cercopithecidae: *Macaca*), as revealed by high resolution restriction site mapping of
649 mitochondrial ribosomal genes. Journal of Human Evolution 34, 1-23.
- 650 Nishimura, T.D., Ito, T., Yano, W., Ebbestad, J.O.R., Takai, M., 2014. Nasal architecture in
651 *Procynocephalus wimani* (Early Pleistocene, China) and implications for its phyletic
652 relationship with *Paradolichopithecus*. Anthropological Science 122, 101-113.
- 653 Noback, M.L., Harvati, K., Spoor, F., 2011. Climate-related variation of the human nasal cavity.
654 American Journal of Physical Anthropology 145, 599-614.
- 655 Pan, R., Yanzhang, P., 1995. Body size of *Macaca anderssoni* and its offspring. Human
656 Evolution 10, 283-287.
- 657 Pan, Y.R., Jablonski, N.G., 1987. The age and geographical distribution of fossil cercopithecids

- 658 in China. *Human Evolution* 2, 59-69.
- 659 Park, S., Lee, Y., 1998. Pleistocene faunal remains from Saekul/Chonyokul at Turupong cave
- 660 complex with special emphasis on the large mammalian fossils. In: Xu, Q., Lee, Y. (Eds.),
- 661 International Symposium for the Celebration of Chinese Academician Jia Lanpo's 90th
- 662 Birthday: Suyanggae and Her Neighbours. Science Press, Beijing, pp. 55-70.
- 663 Pearson, A., Groves, C., Cardini, A., 2015. The 'temporal effect' in hominids: Reinvestigating
- 664 the nature of support for a chimp-human clade in bone morphology. *Journal of Human*
- 665 *Evolution* 88, 146-159.
- 666 Perelman, P., Johnson, W.E., Roos, C., Seuánez, H.N., Horvath, J.E., Moreira, M.A., Kessing,
- 667 B., Pontius, J., Roelke, M., Rumpler, Y., 2011. A molecular phylogeny of living primates.
- 668 *PLoS Genetetics* 7, e1001342.
- 669 R Core Team, 2017. R: A language and environment for statistical computing, R foundation
- 670 for Statistical Computing, Vienna.
- 671 Rae, T.C., Hill, R.A., Hamada, Y., Koppe, T., 2003. Clinal variation of sinus volume in
- 672 Japanese macaques (*Macaca fuscata*). *American Journal of Primatology* 59, 153-158.
- 673 Rae, T.C., Vidarsdottir, U.S., Jeffery, N., Steegmann, A.T., 2006. Developmental response to
- 674 cold stress in cranial morphology of *Rattus*: implications for the interpretation of climatic

- 675 adaptation in fossil hominins. *Proceedings of the Royal Society of London B: Biological*
676 *Sciences* 273, 2605-2610.
- 677 Schillaci, M.A., Schillaci, M.E., 2009. Estimating the probability that the sample mean is within
678 a desired fraction of the standard deviation of the true mean. *Journal of Human Evolution*
679 56, 134-138.
- 680 Schlager, S., 2017. Morpho and Rvcg – Shape Analysis in R. In: Zheng, G., Li, S., Szekely, G.
681 (Eds.), *Statistical Shape and Deformation Analysis*. Academic Press, New York, pp. 217-
682 256.
- 683 Schlosser, M., 1924. Fossil primates from China. *Palaeontologia Sinica Series C* 1, 1-16.
- 684 Sibal, L.R., Samson, K.J., 2001. Nonhuman primates: a critical role in current disease research.
685 *ILAR Journal* 42, 74-84.
- 686 Sidlauskas, B., 2008. Continuous and arrested morphological diversification in sister clades of
687 characiform fishes: a phylomorphospace approach. *Evolution* 62, 3135-3156.
- 688 Simons, E.L., 1970. The deployment and history of Old World monkeys (Cercopithecidae,
689 Primates). In: Napier, J.R., Napier, P.H. (Eds.), *Old World Monkeys: Evolution,*
690 *Systematics, and Behavior*. Academic Press, New York, pp. 97-137.
- 691 Singleton, M., 2002. Patterns of cranial shape variation in the Papionini (Primates:

- 692 Cercopithecinae). Journal of Human Evolution 42, 547-578.
- 693 Sinha, A., Datta, A., Madhusudan, M.D., Mishra, C., 2005. *Macaca munzala*: A new species
694 from Western Arunachal Pradesh, Northeastern India. International Journal of
695 Primatology 26, 977-989.
- 696 Takai, M., Maschenko, E.N., Nishimura, T.D., Anezaki, T., Suzuki, T., 2008. Phylogenetic
697 relationships and biogeographic history of *Paradolichopithecus suskini* Trofimov 1977, a
698 large-bodied cercopithecus monkey from the Pliocene of Eurasia. Quaternary International
699 179, 108-119.
- 700 Tosi, A.J., Morales, J.C., Melnick, D.J., 2000. Comparison of Y chromosome and mtDNA
701 phylogenies leads to unique inferences of macaque evolutionary history. Molecular
702 Phylogenetics and Evolution 17, 133-144.
- 703 Tsuji, Y., Hanya, G., Grueter, C.C., 2013. Feeding strategies of primates in temperate and alpine
704 forests: comparison of Asian macaques and colobines. Primates 54, 201-215.
- 705 Young, C.C., 1934. On the Insectivora, Chiroptera, Rodentia and Primates other than
706 *Sinanthropus* from locality 1 at Choukoutien. Palaeontologia Sinica Series C 8, 1-139.
- 707 Zhang, Z., Wei, H., Xu, Z., 1986. Mammalian fossils. In: City, M.o.L.P.a.M.o.B. (Ed.),
708 Miaohoushan: A Site of Early Paleolithic in Benxi Country, Liaoning. Wenwu Press,

709 Beijing, pp. 35–66 (in Chinese).

710

711

712 **Figure legends**

713 **Figure 1.** The zygomaxillary specimen (2 π □ -12-2169) from the Durubong Cave Complex
714 (Site 2), South Korea. (a) Left lateral view, (b) right lateral view, (c) occlusal view, and
715 (d) dorsal view. The scale is in centimeters.

716 **Figure 2.** (a) Original surface model and (b) corrected surface model of the Durubong specimen.
717 The arrows denote fixing of the orientation of fragments (green and blue regions) and
718 filling of gaps in the main body (red region).

719 **Figure 3.** Landmarks used in this study. (a) Frontal view, (b) dorsal view, (c) left lateral view,
720 and (d) occlusal view. Anatomically defined landmarks: red; curve semi-landmarks:
721 blue; and surface semi-landmarks: green (see also SOM Table S4).

722 **Figure 4.** Coronal computed tomography (CT) images at the level of M¹ in extant macaques.
723 (a–d) Species of the *sinica* group. Arrows denote the degree of lateral

expansion/constriction of the nasal cavity and the thickness of the lateral bony wall of the maxilla. The scale is in centimeters. An asterisk denotes the maxillary sinus.

Figure 5. Coronal computed tomography (CT) image (bottom left) and corresponding line-drawn diagram at the level of M¹ (bottom right) in the Durubong fossil macaque specimen (2 $\uparrow$ □-12-2169). Upper image illustrates where the cross-section is located. The areas filled in gray and the dots on the line diagram indicate the bony structure and plaster, respectively. Arrows denote the limited expansion of the nasal cavity and the thick lateral bony wall of the maxilla. The scale is in centimeters.

Figure 6. Relationships between bgPC scores and the lnCS of the zygomaxillary region in the fossil macaque specimen and extant macaque species. (a) bgPC1 based on the raw shape data vs. lnCS, (b) bgPC2 based on the raw shape data vs. lnCS, (c) bgPC2 vs. bgPC1 based on the raw shape data, and (d) bgPC2 vs. bgPC1 based on the size-adjusted shape data. Red (dashed-dotted lines), *sinica* group; green (dashed lines), *fascicularis* group; blue (dotted lines), *silenus* group; yellow (solid lines), *sylvanus* group; black, the fossil specimen (2 $\uparrow$ □-12-2169).

Figure 7. Zygomaxillary shape changes along the bgPC axes. (a) Image of the fossil specimen

showing the locations of the polygons illustrated in this figure. (b) bgPC1 and (c) bgPC2 based on the raw shape data. (d) bgPC1 and (e) bgPC2 based on the size-adjusted shape data. The upper row represents the lateral views of the zygomaxillary region, while the lower column represents the dorsal views. The negative (left, blue) and positive (right, red) extremes, and their superimposition (middle) are shown.

Figure 8. Procrustes distances from the fossil macaque specimen (*Macaca cf. robusta*) to all examined individuals of extant species of macaques based on (a) the raw shape data and (b) the size-adjusted shape data. Color indicates the species group (see the legend of Fig. 6).

Figure 9. Phylomorphospace of (a) the raw shape data and (b) the size-adjusted shape data. Color indicates the species group (see the legend of Fig. 6). Gray-filled circles indicate the most recent common ancestor of all macaques.

Figure 10. Parsimonious phylogenetic trees inferred from the three-dimensional landmark data from the zygomaxillary region of the fossil macaque specimen (2 π □ -12-2169) and extant species of macaques based on (a) the raw shape data with a monophyly constraint, (b) the size-adjusted shape data with a monophyly constraint, (c) the raw shape data

756 without a monophyly constraint, and (d) the size-adjusted shape data without a
757 monophyly constraint. Numbers near the nodes indicate GC support value when the
758 landmarks were resampled. Asterisk indicates the fossil specimen.
759

b

b

c

d

京都大学
KYOTO UNIVERSITY

A Self-archived copy in

Kyoto University Research Information Repository
<https://repository.kulib.kyoto-u.ac.jp>

京都大学学術情報リポジトリ

KURENAI 紅
Kyoto University Research Information Repository

a

b

c

d

e

sylvanus gr.

syl

silenus gr.

nem

sib

sil

leo

fascicularis
gr.

fas

cyc

mul

fus

sin

rad

thi

ass

arc

sinica gr.

b

syl

nem

sib

sil

leo

fas

cyc

mul

fus

sin

rad

thi

ass

arc

Table 1 The sample used in this study.

Species group	Species	Abbreviation	<i>n</i>
<i>sinica</i> group	<i>M. arctoides</i>	arc	9
	<i>M. assamensis</i>	ass	10
	<i>M. thibetana</i>	thi	5
	<i>M. radiata</i>	rad	8
	<i>M. sinica</i>	sin	2
<i>fascicularis</i> group	<i>M. fuscata</i>	fus	53
	<i>M. mulatta</i>	mul	11
	<i>M. cyclopis</i>	cyc	10
	<i>M. fascicularis</i>	fas	11
<i>silenus</i> group	<i>M. leonina</i>	leo	2
	<i>M. silenus</i>	sil	4
	<i>M. siberu</i>	sib	9
	<i>M. nemestrina</i>	nem	8
<i>sylvanus</i> group	<i>M. sylvanus</i>	syl	5

unknown	<i>M. cf. robusta</i>	rob	1
---------	-----------------------	-----	---

Table S2 Specimens used in this study.

Species	Institute ^a	Catalog number	ID for analysis	Data source ^b	Doi	Origin
<i>M. arctoides</i>	DKY	1473	DKY_1473	PRI CT		unknown
	JMC	3111	JMC_3111	PRI CT		captive
	NMNH	256825	NMNH_256825	Smithsonian 3D collection		wild
	PRI	1871	PRI_1871	KAS CT		captive
	PRI	2793	PRI_2793	PRI CT		captive
	PRI	291	PRI_291	PRI CT		captive
	PRI	4227	PRI_4227	KAS CT		unknown
	PRI	5846	PRI_5846	PRI CT		captive
	PRI	6434	PRI_6434	PRI CT		unknown
<i>M. assamensis</i>	PRI	1893	PRI_1893	PRI CT		wild
	PRI	2178	PRI_2178	KAS CT		unknown
	PRI	2208	PRI_2208	PRI CT		unknown
	PRI	2302	PRI_2302	PRI CT		unknown
	PRI	2303	PRI_2303	PRI CT		unknown
	PRI	3057	PRI_3057	PRI CT		captive
	PRI	4498	PRI_4498	PRI CT		unknown
	PRI	5015	PRI_5015	PRI CT		unknown
	PRI	5230	PRI_5230	KAS CT		unknown
	PRI	5342	PRI_5342	PRI CT		unknown

<i>M. cyclopis</i>	DKY	1688	DKY_1688	PRI CT	unknown
	NMNH	296795	NMNH_296795	Smithsonian 3D collection	wild
	PRI	1358	PRI_1358	PRI CT	unknown
	PRI	4201	PRI_4201	PRI CT	captive
	PRI	4233	PRI_4233	PRI CT	unknown
	PRI	4486	PRI_4486	PRI CT	wild
	PRI	528	PRI_528	PRI CT	captive
	PRI	5847	PRI_5847	PRI CT	unknown
	PRI	6431	PRI_6431	PRI CT	captive
	PRI	9520	PRI_9520	PRI CT	unknown
<i>M. fascicularis</i>	DKY	995	DKY_995	PRI CT	unknown
	NMNH	121511	NMNH_121511	Smithsonian 3D collection	wild
	NMNH	317191	NMNH_317191	Smithsonian 3D collection	wild
	NMNH	573504	NMNH_573504	Smithsonian 3D collection	wild
	PRI	3046	PRI_3046	PRI CT	unknown
	PRI	4434	PRI_4434	KAS CT	unknown
	PRI	4477	PRI_4477	PRI CT	unknown
	PRI	4478	PRI_4478	PRI CT	unknown
	PRI	4703	PRI_4703	PRI CT	unknown
	PRI	5225	PRI_5225	PRI CT	captive
	PRI	6680	PRI_6680	PRI CT	captive

<i>M. fuscata</i>	HMCZ	37709	HMCZ_37709	MorphoSource	doi:10.17602/M2/M3043	wild
	HNCC	03-10	HNCC_03-10	PRI CT		wild
	HNCC	04-14	HNCC_04-14	PRI CT		wild
	HNCC	04-60	HNCC_04-60	PRI CT		wild
	HNCC	05-16	HNCC_05-16	PRI CT		wild
	HNCC	05-17	HNCC_05-17	PRI CT		wild
	HNCC	05-43	HNCC_05-43	PRI CT		wild
	HNCC	06-23	HNCC_06-23	PRI CT		wild
	HNCC	06-40	HNCC_06-40	PRI CT		wild
	HNCC	06-59	HNCC_06-59	PRI CT		wild
	HNCC	06-60	HNCC_06-60	PRI CT		wild
	PRI	1571	PRI_1571	PRI CT		wild
	PRI	2168	PRI_2168	PRI CT		wild
	PRI	2586	PRI_2586	PRI CT		wild
	PRI	3452	PRI_3452	PRI CT		wild
	PRI	4076	PRI_4076	PRI CT		wild
	PRI	4113	PRI_4113	PRI CT		wild
	PRI	4335	PRI_4335	PRI CT		wild
	PRI	4338	PRI_4338	PRI CT		wild
	PRI	4341	PRI_4341	PRI CT		wild
	PRI	5868	PRI_5868	PRI CT		wild

PRI	6162	PRI_6162	PRI CT	wild
PRI	6470	PRI_6470	PRI CT	wild
PRI	6474	PRI_6474	PRI CT	wild
PRI	6498	PRI_6498	PRI CT	wild
PRI	6504	PRI_6504	PRI CT	wild
PRI	6833	PRI_6833	PRI CT	wild
PRI	7317	PRI_7317	PRI CT	wild
PRI	7381	PRI_7381	PRI CT	wild
PRI	7382	PRI_7382	PRI CT	wild
PRI	7385	PRI_7385	PRI CT	wild
PRI	8644	PRI_8644	PRI CT	wild
PRI	8658	PRI_8658	PRI CT	wild
PRI	8873	PRI_8873	PRI CT	wild
PRI	8885	PRI_8885	PRI CT	wild
PRI	8886	PRI_8886	PRI CT	wild
PRI	8889	PRI_8889	PRI CT	wild
PRI	8892	PRI_8892	PRI CT	wild
PRI	8893	PRI_8893	PRI CT	wild
PRI	8914	PRI_8914	PRI CT	wild
PRI	8974	PRI_8974	PRI CT	wild
PRI	9328	PRI_9328	PRI CT	wild

	PRI	9332	PRI_9332	PRI CT		wild
	PRI	9340	PRI_9340	PRI CT		wild
	PRI	9361	PRI_9361	PRI CT		wild
	SNC	H22-170	SNC_H22-170	PRI CT		wild
	SNC	H23-077	SNC_H23-077	PRI CT		wild
	SNC	H23-285	SNC_H23-285	PRI CT		wild
	TPM	M1656	TPM_M1656	PRI CT		wild
	TPM	M1889	TPM_M1889	PRI CT		wild
	TPM	M3958	TPM_M3958	PRI CT		wild
	TPM	M529	TPM_M529	PRI CT		wild
	TPM	M659	TPM_M659	PRI CT		wild
<i>M. leonina</i>	AMNH	MO-11090	AMNH_MO-11090	MorphoSource		wild
	NMNH	241022	NMNH_241022	Smithsonian 3D collection		wild
<i>M. mulatta</i>	DKY	1682	DKY_1682	PRI CT		unknown
	HMCZ	26475	HMCZ_26475	MorphoSource	doi:10.17602/M2/M3052	wild
	KAS	41	KAS_0041	KAS CT		captive
	PRI	218	PRI_218	PRI CT		captive
	PRI	2200	PRI_2200	PRI CT		unknown
	PRI	223	PRI_223	PRI CT		captive
	PRI	224	PRI_224	PRI CT		captive
	PRI	242	PRI_242	PRI CT		captive

<i>M. nemestrina</i>	PRI	3523	PRI_3523	PRI CT	unknown
	PRI	4408	PRI_4408	PRI CT	captive
	PRI	580	PRI_580	PRI CT	captive
	DKY	2110	DKY_2110	PRI CT	unknown
	NMNH	123144	NMNH_123144	Smithsonian 3D collection	wild
	NMNH	154367	NMNH_154367	Smithsonian 3D collection	wild
	PRI	1849	PRI_1849	PRI CT	unknown
<i>M. radiata</i>	PRI	2299	PRI_2299	PRI CT	captive
	PRI	2454	PRI_2454	KAS CT	unknown
	PRI	3055	PRI_3055	KAS CT	unknown
	PRI	4225	PRI_4225	PRI CT	captive
	JMC	1483	JMC_1483	KAS CT	captive
	PRI	3052	PRI_3052	PRI CT	unknown
	PRI	6079	PRI_6079	PRI CT	captive
	PRI	6684	PRI_6684	PRI CT	captive
	PRI	6685	PRI_6685	PRI CT	captive
	PRI	6686	PRI_6686	PRI CT	captive
<i>M. siberu</i>	PRI	7140	PRI_7140	PRI CT	captive
	PRI	9532	PRI_9532	PRI CT	captive
	NMNH	546835	NMNH_546835	Smithsonian 3D collection	wild
	PRI	1324	PRI_1324	PRI CT	wild

<i>M. silenus</i>	PRI	1338	PRI_1338	PRI CT	wild
	PRI	1344	PRI_1344	PRI CT	wild
	PRI	1347	PRI_1347	PRI CT	wild
	PRI	5072	PRI_5072	PRI CT	wild
	PRI	5079	PRI_5079	PRI CT	wild
	PRI	5080	PRI_5080	PRI CT	wild
	PRI	5095	PRI_5095	PRI CT	wild
	JMC	2488	JMC_2488	PRI CT	captive
	JMC	4864	JMC_4864	PRI CT	captive
<i>M. sinica</i>	JMC	5740	JMC_5740	PRI CT	captive
	NMNH	574135	NMNH_574135	Smithsonian 3D collection	wild
	NMNH	15259	NMNH_15259	Smithsonian 3D collection	wild
<i>M. sylvanus</i>	PRI	1886	PRI_1886	PRI CT	wild
	JMC	1392	JMC_1392	PRI CT	captive
	JMC	4798	JMC_4798	KAS CT	captive
	JMC	5644	JMC_5644	KAS CT	captive
<i>M. thibetana</i>	JMC	6330	JMC_6330	PRI CT	captive
	NMNH	255979	NMNH_255979	Smithsonian 3D collection	wild
	AMNH	M-84472	AMNH_M-84472	MorphoSource	wild
	JMC	5722	JMC_5722	PRI CT	captive
	KPM	NF1001819	KPM_NF1001819	PRI CT	unknown

	NMNH	241163	NMNH_241163	Smithsonian 3D collection	wild
	PRI	4230	PRI_4230	KAS CT	unknown
Unknown (<i>M.</i> <i>cf. robusta</i>)	CNUM	2 $\overline{+}$ □-12-216	CNUM_2-12-2169	CNU CT	wild

^a CNUM, the Chungbuk National University Museum, Chungcheongbuk-do, Korea; PRI, the Primate Research Institute, Kyoto University, Inuyama, Japan; JMC, the Japan Monkey Centre, Inuyama, Japan; KPM, the Kanagawa Prefectural Museum of Natural History, Odawara, Japan; DKY, the Department of Anatomy (Macro), Dokkyo Medical University, Mibu, Japan; KAS, the Laboratory of Physical Anthropology, Graduate School of Science, Kyoto University, Kyoto, Japan; AMNH, the American Museum of Natural History, New York, USA; NMNH, the National Museum of Natural History, Washington DC, USA; HMCZ, the Harvard Museum of Comparative Zoology, Cambridge, USA.

^b PRI CT, the data scanned at the Primate Research Institute, Kyoto University, Inuyama, Japan; KAS CT, the data scanned at the the Laboratory of Physical Anthropology, Graduate School of Science, Kyoto University, Kyoto, Japan; CNU CT, the data scanned at the Chungbuk National University, Chungcheongbuk-do, Korea; the data downloaded from Smithsonian 3D collection (<http://humanorigins.si.edu/evidence/3d-collection/primate>); the data downloaded from MorphoSource (<http://morphosource.org>).

Table S3 Test for the differences in zygomaxillary shape among the different origins of specimens.

Response variable	Explanatory variable	R ²	SS	Df	F	P
<i>All (wild, captive, and unknown-origin specimens)</i>						
bgPC1 of raw shape data	Origin	0.009	0.001	2	0.59	0.556
	Species	0.488	0.138	14	8.92	< 0.001
	Residuals		0.145	131		
bgPC2 of raw shape data	Origin	0.007	0.001	2	0.47	0.628
	Species	0.626	0.136	14	15.69	< 0.001
	Residuals		0.081	131		
bgPC1 of size-adjusted shape data	Origin	0.044	0.005	2	3.02	0.052
	Species	0.303	0.045	14	4.07	< 0.001
	Residuals		0.103	131		
bgPC2 of size-adjusted shape data	Origin	0.039	0.002	2	2.63	0.076
	Species	0.670	0.124	14	18.96	< 0.001
	Residuals		0.061	131		
Procrustes coordinates of raw shape data	Origin	0.015	0.019	2	1.95	< 0.001
	Species	0.335	0.422	14	6.13	< 0.001
	Residuals		0.644	131		
Procrustes coordinates of size-adjusted shape data	Origin	0.021	0.021	2	2.44	< 0.001
	Species	0.304	0.314	14	5.15	< 0.001
	Residuals		0.571	131		

Subset (wild and captive specimens)

bgPC1 of raw shape data	Origin	0.001	0.000	1	0.11	0.739
	Species	0.579	0.125	14	9.81	< 0.001
	Residuals		0.091	100		
bgPC2 of raw shape data	Origin	0.001	0.000	1	0.08	0.778
	Species	0.712	0.125	14	17.68	< 0.001
	Residuals		0.051	100		
bgPC1 of size-adjusted shape data	Origin	0.046	0.003	1	4.83	0.030
	Species	0.377	0.038	14	4.31	< 0.001
	Residuals		0.063	100		
bgPC2 of size-adjusted shape data	Origin	0.025	0.001	1	2.59	0.111
	Species	0.732	0.116	14	19.49	< 0.001
	Residuals		0.043	100		
Procrustes coordinates of raw shape data	Origin	0.013	0.012	1	2.763	< 0.001
	Species	0.398	0.382	14	6.184	< 0.001
	Residuals		0.441	100		
Procrustes coordinates of size-adjusted shape data	Origin	0.017	0.013	1	3.344	< 0.001
	Species	0.360	0.280	14	5.037	< 0.001
	Residuals		0.397	100		

ANOVA (Type II) was performed for the bgPC scores and Procrustes coordinates, wherein origin of specimen (captive, wild, and unknown) and species were used as explanatory variables. This was done for all sample and for the subset of sample (wild and captive). For these analyses, "procD.lm" function of "geomorph" package and "etasq" function of "heplots" package in R were used.

Table S4 Landmarks used in this study.

Abbreviation	Definition
<i>Anatomically-defined landmarks</i>	
wpa	Point corresponding to largest width of piriform aperture.
ns	Nasospinale.
aif	Antero-sperior point of incisive foramen.
pif	Posterior-most point of incisive foramen.
lif	Lateral-most point of incisive foramen.
pr	Prosthion.
bia	Postero-labial point of lateral incisor alveolus.
lia	Postero-lingual point of lateral incisor alveolus.
bca	Antero-labial point of canine alveolus.
lca	Antero-lingual point of canine alveolus.
bp3	Labial P ³ : most mesial point on P ³ alveolus, projected labially onto alveolar margin.
lp3	Lingual P ³ : most mesial point on P ³ alveolus, projected lingually onto alveolar margin.
bp4	Labial P ⁴ : most mesial point on P ⁴ alveolus, projected labially onto alveolar margin.
lp4	Lingual P ⁴ : most mesial point on P ⁴ alveolus, projected lingually onto alveolar margin.
bm1	Labial M ¹ : contact point between P ⁴ and M ¹ , projected labially onto alveolar margin.
lm1	Lingual M ¹ : contact point between P ⁴ and M ¹ , projected lingually onto alveolar margin.
bm2	Labial M ² : contact point between M ¹ and M ² , projected labially onto alveolar margin.
lm2	Lingual M ² : contact point between M ¹ and M ² , projected lingually onto alveolar margin.

bm3	Labial M ³ : contact point between M ² and M ³ , projected labially onto alveolar margin.
lm3	Lingual M ³ : contact point between M ² and M ³ , projected lingually onto alveolar margin.
dm3	Distal M ³ : most posterior point on M ³ alveolus, projected labially onto alveolar margin.
gpf	Most posterior point on the margin of greater palatine foramen.

Semi-landmarks on curves

Eight points on the superior midline of nasal bone.

Six points on the superior midline of premaxilla, which is between ns and pr.

Seven points on the inferior midline of maxilla, which is from pif to approximately the meeting point of maxilla and palatine.

Five points on the lateral margin of nasal aperture, which is between wpa and ns.

Ten points on the inferior margin of orbital opening.

Seven points on the inferior margin of zygomatic process.

Semi-landmarks on surface

One-hundred and thirty-two points on the lateral side of zygomaxilla.

Some of these definitions are in accordance with Cardini et al. (2007) and Ito and Nishimura (2016).

Figure S1. Most likely phylogenetic tree from the BEAST2 analysis for macaques and outgroup taxa using mtDNA and nuclear sequences. Blue horizontal bars represent the posterior 95% CI for the node ages.

Figure S2. Shape changes along PC axes in the phylomorphospace. (a) PC1 and (b) PC2 based on the raw shape data. (c) PC1 and (d) PC2 based on the size-adjusted shape data. For more details, see the legend of Figure 6 in the main text.