

Maxillary morphology of chimpanzees: Captive versus wild environments

Hester Hanegraef¹  | Fred Spoor^{1,2} 

¹Centre for Human Evolution Research, Natural History Museum, London, UK

²Department of Human Origins, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany

Correspondence

Hester Hanegraef, Centre for Human Evolution Research, Natural History Museum, London, UK.
Email: h.hanegraef@nhm.ac.uk

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Abstract

Morphological studies typically avoid using osteological samples that derive from captive animals because it is assumed that their morphology is not representative of wild populations. Rearing environments indeed differ between wild and captive individuals. For example, mechanical properties of the diets provided to captive animals can be drastically different from the food present in their natural habitats, which could impact cranial morphology and dental health. Here, we examine morphological differences in the maxillae of wild versus captive chimpanzees (*Pan troglodytes*) given the prominence of this species in comparative samples used in human evolution research and the key role of the maxilla in such studies. Size and shape were analysed using three-dimensional geometric morphometric methods based on computed tomography scans of 94 wild and 30 captive specimens. Captive individuals have on average larger and more asymmetrical maxillae than wild chimpanzees, and significant differences are present in their maxillary shapes. A large proportion of these shape differences are attributable to static allometry, but wild and captive specimens still differ significantly from each other after allometric size adjustment of the shape data. Levels of shape variation are higher in the captive group, while the degree of size variation is likely similar in our two samples. Results are discussed in the context of ontogenetic growth trajectories, changes in dietary texture, an altered social environment, and generational differences. Additionally, sample simulations show that size and shape differences between chimpanzees and bonobos (*Pan paniscus*) are exaggerated when part of the wild sample is replaced with captive chimpanzees. Overall, this study confirms that maxillae of captive chimpanzees should not be included in morphological or taxonomic analyses when the objective is to characterise the species.

KEYWORDS

captivity, diet, geometric morphometrics, growth, maxilla, sexual dimorphism, variation

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1 | INTRODUCTION

Comparative samples in morphological studies ideally consist of non-captive specimens only because it is assumed that captive individuals are not representative of the wild morphology (Albrecht, 1982; O'Regan, 2001; O'Regan & Kitchener, 2005). Factors driving morphological changes among mammals in captivity have recently been reviewed (see Siciliano-Martina et al., 2021a). In short, morphological differences can result from evolutionary processes, such as directional or relaxed selection pressures (Bryant & Reed, 1999; Frankham et al., 1986; McPhee & McPhee, 2012; Schulte-Hostedde & Mastrodonato, 2015; Williams & Hoffman, 2009; Willoughby et al., 2015), as well as inbreeding and genetic drift caused by small population sizes and low numbers of founding members (Ballou et al., 2010; Frankham, 2008; Lacy, 1987; McPhee, 2004; Willoughby et al., 2015; Woodworth et al., 2002). Unusual phenotypes can also arise as a response to the unique environmental conditions in captivity, including limited enclosure sizes, different substrate compositions, and abnormal diets (Chirchir et al., 2022; Clubb & Mason, 2003; Curtis et al., 2018; Drake & Klingenberg, 2010; Harbers, Neaux, et al., 2020; Harbers, Zanolli, et al., 2020; Kroshko et al., 2016; Leigh, 1994; Morgan & Tromborg, 2007; Neaux et al., 2021; Perkins, 1992; Terranova & Coffman, 1997; Trut et al., 2009). However, sometimes it cannot be avoided to include captive individuals, for example, when the relevant specimens, such as a specific subspecies, are rarely sampled from the wild. In these cases, the impact of captivity needs to be assessed to understand whether and how morphological analyses may be affected. Similar questions have been explored previously with respect to the use of damaged and pathological specimens to increase sample sizes (Mitchell et al., 2021). Given the prominence of the common chimpanzee (*Pan troglodytes*) in comparative samples used in human evolution research and the key role of the maxilla in such studies (e.g., Bermúdez de Castro et al., 1997; Blumenschine et al., 2003; Constantino & Wood, 2004; Freidline et al., 2013; Grine, 1988; Haile-Selassie et al., 2015; Leakey et al., 2001, 2012; Lieberman et al., 1988; Rak, 1983, 1986; Rightmire, 1993; Spoor et al., 2010, 2015, 2016; Stringer, 1986; Stringer et al., 1984; Wood, 1992), we explore the differences in maxillary morphology between wild and captive samples of this extant species using geometric morphometric methods.

When wild and captive populations of primates have been compared, the latter were found to show faster dental and skeletal growth (Cheverud et al., 1992; Kelley & Schwartz, 2010; Kimura & Hamada, 1996; Machanda et al., 2015; Matsuzawa et al., 1990; Phillips-Conroy & Jolly, 1988; Turner et al., 2016; Zihlman et al., 2004, 2007, but see Smith & Boesch, 2011; Smith et al., 2010, 2013), reach sexual maturity earlier (Altmann et al., 1981; Haddow, 1952; Hamada et al., 1996; Pusey, 1978), and have a lower mortality rate (Hill et al., 2001). Most animals in captivity also live longer than their wild counterparts. In chimpanzees specifically, captive individuals are expected to live approximately 50 years (Dyke et al., 1995), whereas the life expectancy is only 13–30 years in the wild (Hill

et al., 2001), and field observations on social and behavioural development have shown that wild chimpanzees take up to 3 years longer to mature in comparison with captive individuals (Boesch & Boesch-Achermann, 2000; Zihlman et al., 2007). Firstly, the accelerated growth rates in captive individuals may be related to higher-quality diets and better health due to medical care (Altmann et al., 1981; Hamada et al., 1996; Kimura & Hamada, 1996; Mori, 1979; Phillips-Conroy & Jolly, 1988). For example, parasites in wild populations can influence nutritional status and lead to developmental delay (Smith & Boesch, 2011). Secondly, it has been suggested that the difference in tempo of physical growth is linked with less energy expenditure on thermoregulation and the absence of natural predators in captive environments (see O'Regan & Kitchener, 2005). Thirdly, the slower growth in wild individuals could also be explained as a strategy for nutrient-poor environments where metabolic needs are spread out over a longer immature period to reduce the risk of starvation and increase overall survival (Janson & van Schaik, 1993). Lastly, it has been argued that young individuals in wild environments can simply devote less energy to physical growth as the day-to-day life in these natural habitats demands more energy output for feeding, locomotion, and social activities than in captive environments (Turner et al., 2016; Zihlman et al., 2007).

The nature and magnitude of differences in cranial morphology between wild and captive specimens vary considerably across mammalian taxa (Siciliano-Martina et al., 2021a). As reviewed in Table 1, some studies report no change in skull size for wild and captive groups, while others observed either a decrease or an increase in captive animals. In this context, it is interesting to consider the maxilla, a central part of the facial morphology that reflects dietary, masticatory, and nasal functions. While some mammals exhibit broader maxillae in captivity, others have narrower dental arcades and palatal regions, or do not differ in palatal width compared to wild groups (see Table 1). Similarly, captive mammals can have either shorter or longer maxillae, or do not differ in muzzle length from their wild counterparts (see Table 1). Few studies mention changes in dental dimensions, except that captive lions and tigers have slightly smaller teeth than wild specimens (Cooper et al., 2023; Hollister, 1917) and that wild boar have larger third molars compared with captive individuals (Evin et al., 2015). Captive populations tend to have a higher prevalence of dental pathologies, abnormal tooth wear, and malocclusion, as well as increased tooth spacing (Clausen et al., 2007; Crossley & del Mar Miguélez, 2001; Fagan et al., 2001; Fitch & Fagan, 1982; Franz-Odenaal, 2004; Glatt et al., 2008; Groves, 1966; Haberstroh et al., 1984; Kaiser et al., 2009; Kapoor et al., 2016; Molnar & Ward, 1975; Siciliano-Martina et al., 2021b, 2022; Sutton, 1884; Taylor et al., 2014; Wenker et al., 1999). In contrast, a greater degree of tooth wear and tooth fracture frequency have been observed in wild populations of ring-tailed lemurs, likely reflecting the availability and use of different foods (Cuozzo et al., 2010), and in wild coyotes, potentially associated with a more mechanically challenging diet (Curtis et al., 2018). However, no differences were found in tooth wear pattern between wild and captive grey wolves (Gipson et al., 2000).

TABLE 1 Effect of captivity on cranial morphology of mammals.

	Species	References	Effect of captivity
Artiodactyla			
Equidae	<i>Equus africanus</i>	Groves (1966)	Skull smaller Palate width equal
Equidae	<i>Equus hemionus</i>	Groves (1966)	Skull smaller Palate width equal
Suidae	<i>Sus scrofa</i>	Neaux et al. (2021)	Cranium size equal
Carnivora			
Canidae	<i>Atelocynus microtis</i>	Siciliano-Martina et al. (2021b)	Palate width equal Rostrum length equal
Canidae	<i>Canis latrans</i>	Curtis et al. (2018)	Cranium size equal Palate width equal at canines Palate wider at fourth premolars Palate length equal
Canidae	<i>Canis latrans</i>	Siciliano-Martina et al. (2021b)	Palate width equal Rostrum length equal
Canidae	<i>Canis lupus</i>	Siciliano-Martina et al. (2021b)	Palate width equal Rostrum shorter
Canidae	<i>Canis lupus baileyi</i>	Siciliano-Martina et al. (2022)	Cranium smaller Palate narrower Rostrum longer
Canidae	<i>Canis rufus</i>	Siciliano-Martina et al. (2021b)	Palate width equal Rostrum shorter
Canidae	<i>Chrysocyon brachyurus</i>	Siciliano-Martina et al. (2021b)	Palate wider Rostrum shorter
Canidae	<i>Lycaon pictus</i>	Siciliano-Martina et al. (2021b)	Palate wider Rostrum shorter
Canidae	<i>Nyctereutes procyonoides</i>	Siciliano-Martina et al. (2021b)	Palate wider Rostrum shorter
Canidae	<i>Otocyon megalotis</i>	Siciliano-Martina et al. (2021b)	Palate width equal Rostrum length equal
Canidae	<i>Speothos venaticus</i>	Siciliano-Martina et al. (2021b)	Palate wider Rostrum shorter
Canidae	<i>Urocyon cinereoargenteus</i>	Siciliano-Martina et al. (2021b)	Palate wider Rostrum shorter
Canidae	<i>Vulpes lagopus</i>	Siciliano-Martina et al. (2021b)	Palate width equal Rostrum length equal
Canidae	<i>Vulpes macrotis</i>	Siciliano-Martina et al. (2021b)	Palate width equal Rostrum length equal
Canidae	<i>Vulpes velox</i>	Siciliano-Martina et al. (2021b)	Palate wider Rostrum shorter
Canidae	<i>Vulpes vulpes</i> ^a	Zatoń-Dobrowolska et al. (2018)	Cranium larger Palate width equal Palate length equal
Canidae	<i>Vulpes vulpes</i>	Siciliano-Martina et al. (2021b)	Palate wider Rostrum shorter
Canidae	<i>Vulpes zerda</i>	Siciliano-Martina et al. (2021b)	Palate width equal Rostrum length equal
Felidae	<i>Acinonyx jubatus</i>	Meachen et al. (2020)	Skull size equal Muzzle length equal
Felidae	<i>Panthera leo</i>	Hollister (1917, 1918)	Rostrum larger
Felidae	<i>Panthera leo</i>	Smuts et al. (1978)	Skull larger
Felidae	<i>Panthera leo</i>	O'Regan & Turner (2004)	Muzzle wider

(Continues)

TABLE 1 (Continued)

	Species	References	Effect of captivity
Felidae	<i>Panthera leo</i>	Zuccarelli (2004)	Palate wider at canines Palate width equal at cheek teeth Palate shorter
Felidae	<i>Panthera leo</i>	Hartstone-Rose et al. (2014)	Rostrum wider
Felidae	<i>Panthera leo</i>	Cooper et al. (2023)	Skull size equal Palate wider Palate longer
Felidae	<i>Panthera pardus</i>	O'Regan & Turner (2004)	Muzzle wider
Felidae	<i>Panthera tigris</i>	Hartstone-Rose et al. (2014)	Rostrum wider
Felidae	<i>Panthera tigris</i>	Cooper et al. (2023)	Skull size equal Palate wider Dental arcade longer
Mustelidae	<i>Mustela nigripes</i>	Wisely et al. (2002)	Skull smaller Tooth row shorter
Mustelidae	<i>Neogale vision</i> ^a	Lynch & Hayden (1995)	Cranium larger Dental arcade narrower Palate shorter
Mustelidae	<i>Neogale vision</i> ^a	Tamlin et al. (2009)	Skull larger Muzzle length equal
Mustelidae	<i>Neogale vision</i> ^a	Taraska et al. (2016)	Skull larger Dental arcade width equal Palate longer
Perissodactyla			
Rhinoceroidea	<i>Dicerorhinus sumatrensis</i>	Groves (1982)	Skull size equal (larger (or smaller
Rhinoceroidea	<i>Rhinoceros sondaicus</i>	Groves (1982)	Skull smaller
Rhinoceroidea	<i>Rhinoceros unicornis</i>	Groves (1982)	Skull smaller
Primates			
Cercopithecidae	<i>Macaca fuscata</i>	Geiger (2021)	Palate wider Rostrum longer
Rodentia			
Chinchillidae	<i>Chinchilla</i> sp.	Crossley & del Mar Miguélez (2001)	Tooth row longer

^aFarmed or domesticated animals.

Given that captivity affects the cranial morphology of mammals in different ways and no patterns can be detected within broader mammalian groups (see Table 1), the aim of this research was to assess whether and how the maxillary morphology of captive chimpanzees differs from that seen in wild populations and to evaluate whether their maxillae can be used in comparative samples without notably biasing morphological inferences about the species. Specifically, we will address the following questions:

1. Do captive specimens differ in maxillary size and shape from wild chimpanzees?
2. Can these differences be explained by static allometry?
3. Are age, sex, and generational differences linked with size and shape changes in captive chimpanzees?
4. Are captive maxillae more variable in size and shape than wild ones?
5. Are chimpanzee maxillae more asymmetric in captivity?
6. What is the impact of adding captive specimens to a sample?

2 | MATERIALS AND METHODS

Our sample comprises 94 wild chimpanzees and 30 captive specimens from various zoos, institutes, and sanctuaries that were either caught in the wild or born in captivity (Table S1). Additionally, 47 bonobos (*Pan paniscus*) were included for comparative purposes (Table S2). These specimens are housed in the Taï Collection, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany (MPITC); the Royal Museum for Central Africa, Tervuren, Belgium (RMCA); the National Museum of Natural History, Smithsonian Institution, Washington, District of Columbia, USA (USNM); the Naturmuseum Senckenberg, Frankfurt am Main, Germany (SMF); the Peabody Museum of Archaeology and Ethnology, Harvard University, Cambridge, Massachusetts, USA (PMAE); the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA (MCZ); and the Digital Morphology Museum, Kyoto University, Kyoto, Japan (DMM).

Sex attributions were taken from museum records when available or determined based on canine size and the development of cranial muscular markings and crests (Tables S1 and S2). All specimens are adults with their third molars in occlusion that show no maxillary pathologies. Three chimpanzee subspecies are included in this research, namely *Pan troglodytes troglodytes*, *Pan troglodytes schweinfurthii*, and *Pan troglodytes verus*, as well as some specimens with unknown subspecies status (Table S1). Two captive individuals (DMM KUPRI 371 and DMM KUPRI 1320) are hybrids, and five captive specimens (DMM KUPRI 371, DMM KUPRI 455, DMM KUPRI 515, DMM KUPRI 690, and DMM KUPRI 1320) are related (Figure S1).

Analyses are based on computed tomography (CT) scans, which were made available by the institutions listed above. Three-dimensional (3D) digital surface visualisations were extracted from the μ CT scans (isotropic voxel size: 0.09–0.25 mm) and medical CT scans (pixel size: 0.17–0.56 mm, slice interval: 0.2–1.0 mm, and slice thickness: 0.4–1.0 mm) using Avizo 7.1 (FEI Visualization Sciences Group, Berlin). In this process, high-resolution μ CT data were downsampled to approximately the pixel sizes of the medical CT scans.

The measurement protocol follows Hanegraef et al. (2022), with the size and shape of the maxillae captured by 68 3D landmarks (Table 2; Figure 1) that were placed on the surfaces and recorded using Avizo 7.1. These landmarks capture the relative position and size of the dental alveoli from the first incisor to the second molar, the midplane palate and subnasal area, the zygomatic root, and the inferior region of the nasal and orbital margins. Missing landmarks were estimated using bilateral symmetry or thin-plate spline interpolation (Gunz et al., 2009). All landmark data were then converted into shape variables using a generalised Procrustes analysis, which removes size, position, and orientation from the landmark dataset (Gower, 1975; Rohlf & Slice, 1990).

Size differences between captive and wild chimpanzees (question 1) were investigated based on the natural logarithms of centroid sizes, and a two-sample *t* test was used to determine statistical significance. A principal component analysis (PCA) was performed to examine maxillary shape differences between wild and captive individuals (question 1), and statistical significance was tested through multivariate regression (shape ~ group). Shape differences between captive and wild chimpanzees were visualised and then compared by superimposing their mean maxillary shapes, minimising the distance between postcanine alveolar landmarks as the most efficient way to characterise distinct morphologies (Hanegraef et al., 2022). Moreover, we obtained absolute and relative dimensions of the dental alveoli, averaging the left and right sides for each specimen, and statistical significance of differences between the wild and captive samples was examined with two-sample *t*-tests.

Static allometry (question 2) was investigated through multivariate regressions, both for size alone (shape ~ ln centroid size) and for the interaction with group differences (shape ~ ln centroid size \times group). Regression scores of the first model were plotted against the natural logarithms of centroid sizes to determine whether

wild and captive specimens are separated by size differences along the allometric trajectory. Moreover, allometrically adjusted shapes were obtained for each specimen by adding the residuals from the first model to the overall mean shape (Klingenberg, 2016). A PCA was then performed on the allometrically adjusted shapes, and statistical significance of the difference between the captive and wild samples was determined through multivariate regression (allometrically adjusted shape ~ group). Mean allometrically adjusted shapes of the wild and captive groups were also visualised to examine the maxillary shape differences that are independent of size.

Age (question 3) is known for 25 captive and 7 wild individuals (Table S1), although for the 16 first-generation captive specimens this is only an approximation given that their exact date of birth is not documented. Statistical significance of an apparent age trend relative to the PC1 scores of the shapes, the natural logarithms of centroid sizes, and the PC1 scores of the allometrically adjusted shapes was determined for the wild and captive groups using Pearson's product-moment correlation tests. Age is not available for the remainder of the sample, and therefore, the first and second molar wear stages of each specimen (Table S1), which provide a good estimation of relative ages within a sample (Dean et al., 1992; Lovejoy et al., 1985; Miles, 1963), were plotted against the PC1 score of their shape, their natural logarithm of centroid size, and the PC1 score of their allometrically adjusted shape to further investigate age trends.

To examine sexual dimorphism trends (question 3), the natural logarithms of centroid sizes of males and females were assessed separately for the wild and captive groups, and statistical significance of size differences was determined using two-sample *t* tests. Shape differences between males and females were investigated through a PCA, and multivariate regressions were performed separately for the wild and captive samples to determine statistical significance (shape ~ sex). The magnitudes of maxillary size, shape, and allometrically adjusted shape differences between wild and captive specimens were also investigated per sex by calculating the differences in natural logarithms of centroid sizes and the Procrustes distances for the shapes and allometrically adjusted shapes between all possible wild and captive specimen pairs separately for males and females, respectively. Two-sample *t*-tests were then performed to determine statistical significance. Additionally, size and shape differences between wild chimpanzees, first-generation captive specimens, and subsequent captive generations (question 3) were visually assessed.

The degree of size variation was examined for the wild and captive chimpanzees (question 4) based on the standard deviations of the natural logarithms of centroid sizes, and statistical significance was determined using a two-tailed *F*-test. Procrustes distances between all possible specimen pairs were computed for the wild and captive groups to investigate their degree of shape variation (question 4), and statistical significance was assessed based on a two-sample *t* test. Given the unequal sample sizes for the wild and captive groups, we randomly sampled with replacement 30 wild specimens 1000 times and then compared the degrees of size and shape variation in these wild subsamples with those of the 30 captive chimpanzees. Probabilities of statistical significance were obtained by calculating

TABLE 2 List of landmarks, with 1–62 bilateral points and 63–68 midsagittal points.

No.	Landmark definition
1–4	I ¹ , left: mesial, distal, labial, and lingual sides of the alveolar margin.
5–8	I ¹ , right: mesial, distal, labial, and lingual sides of the alveolar margin.
9–12	I ² , left: mesial, distal, labial, and lingual sides of the alveolar margin.
13–16	I ² , right: mesial, distal, labial, and lingual sides of the alveolar margin.
17–20	C, left: mesial, distal, labial, and lingual sides of the alveolar margin.
21–24	C, right: mesial, distal, labial, and lingual sides of the alveolar margin.
25–28	P ³ , left: mesial, distal, buccal, and lingual sides of the alveolar margin. ^a
29–32	P ³ , right: mesial, distal, buccal, and lingual sides of the alveolar margin. ^a
33–36	P ⁴ , left: mesial, distal, buccal, and lingual sides of the alveolar margin. ^a
37–40	P ⁴ , right: mesial, distal, buccal, and lingual sides of the alveolar margin. ^a
41–44	M ¹ , left: mesial, distal, buccal, and lingual sides of the alveolar margin. ^a
45–48	M ¹ , right: mesial, distal, buccal, and lingual sides of the alveolar margin. ^a
49–52	M ² , left: mesial, distal, buccal, and lingual sides of the alveolar margin. ^a
53–56	M ² , right: mesial, distal, buccal, and lingual sides of the alveolar margin. ^a
57–58	Anteroinferior take-off of zygomatic process, left–right: point most anterior, inferior, and medial on the root of the zygomatic process. ^b
59–60	Alare, left–right: most lateral point on the outer margin of the nasal aperture.
61–62	Orbitale, left–right: most inferior point of the orbital margin. ^c
63	Prosthion: most anterior point of the maxillary alveolar process in the midplane.
64	Nasospinale: point of intersection of the line uniting the inferiormost points on the margin of each nasal opening with the midplane.
65	Most posterior point of the nasoalveolar clivus at the opening of the incisive canal. ^d
66	Most posterior point on the palate at the opening of the incisive canal. ^d
67	Point at which the intermaxillary suture and a line connecting left and right distal M ¹ intersect.
68	Midline point of the posterior border of the palate. ^e

^aWhen two buccal and/or two lingual roots were present, two landmarks were placed buccally and/or two lingually at the most exposed position of each root and their average was used in the analyses.

^bBased on Spoor et al. (2010).

^cSometimes located on the zygomatic bone rather than the maxilla.

^dWhen the incisive canal was divided by a nasal septum, landmarks were placed for each opening and their average was used in the analyses.

^eLocated on the palatine bone rather than the maxilla but included based on the strongly integrated nature of the two forming the palate.

the percentage of these 1000 comparisons that show a significant difference between the wild and captive groups.

To assess asymmetry (question 5), symmetrised landmark configurations were obtained using reflected relabelling (Bookstein, 1991; Gunz et al., 2009; Mardia et al., 2000). The total magnitude of shape asymmetry in captive and wild maxillae was examined by first converting the unsymmetrised and symmetrised landmark configurations into shape variables using a single generalised Procrustes analysis and then calculating Procrustes distances between the unsymmetrised and symmetrised shapes for each specimen. A two-sample *t* test was subsequently performed to determine statistical significance between the wild and captive samples. Additionally, Euclidean distances were calculated for each landmark between the unsymmetrised and symmetrised configurations of each specimen. These distances were then averaged per landmark for the wild and captive groups to investigate whether any part of the maxilla is more susceptible to asymmetry.

This method to visualise the pattern of asymmetry was adapted from Wilson and Humphrey (2015). Lastly, the magnitudes of directional (side) and fluctuating (individual × side) asymmetry were determined for the wild and captive groups using the unsymmetrised shape variables.

To assess the potential impact of adding captive specimens to a wild sample (question 6), we replaced 12 random males and 18 random females in the wild sample with the 30 captive specimens 1000 times to obtain mixed samples with a similar sex ratio as the original wild sample. Size and shape differences as well as degrees of size and shape variation were compared between these mixed samples and the wild sample, and probabilities of statistical significance were obtained using the relevant tests as described above. We then investigated how replacing a random portion of the wild sample with the captive chimpanzees affects comparisons with bonobos. Size and shape differences between wild chimpanzees and bonobos and between the mixed samples and bonobos as well as

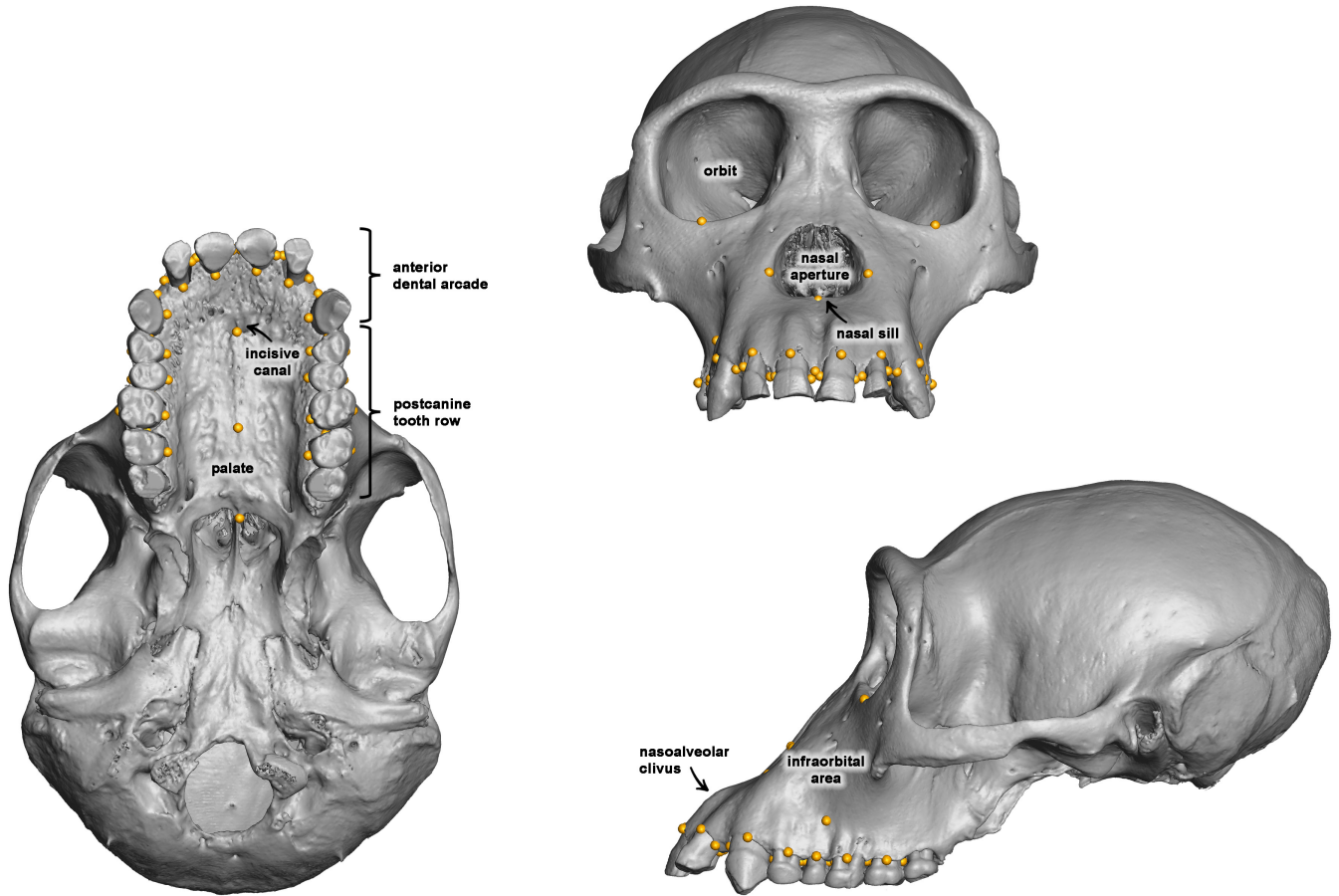


FIGURE 1 Position of landmarks used to capture the shape of the maxillae, shown for a chimpanzee skull (SMF PA-PC-360). Key morphological features are highlighted in the figure.

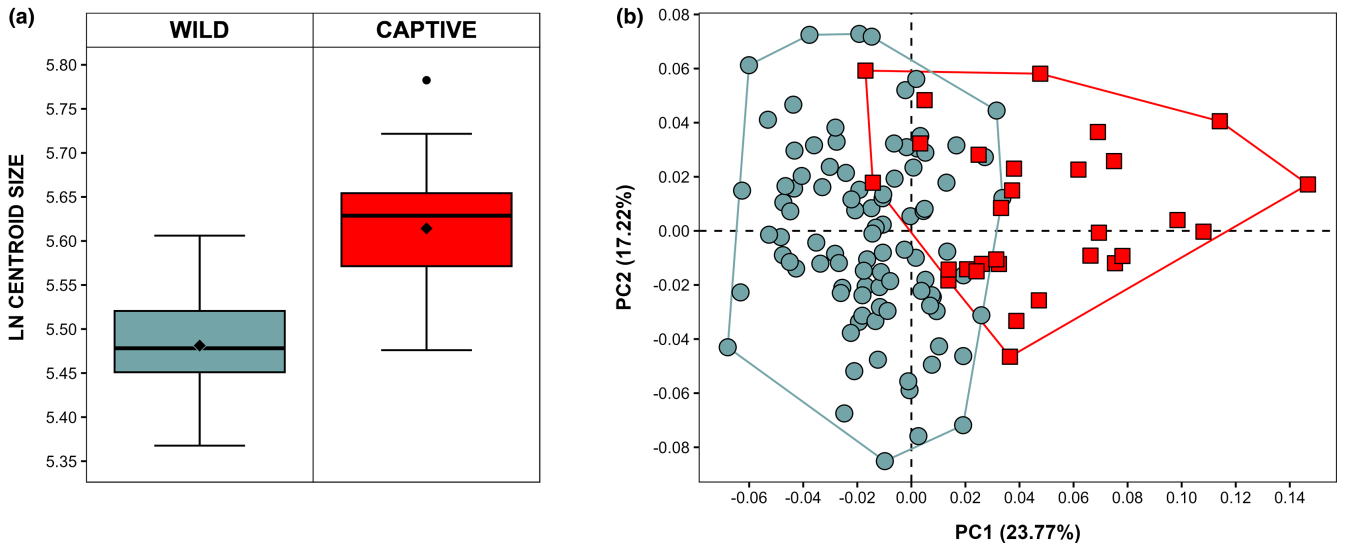


FIGURE 2 Boxplots of the natural logarithms of centroid sizes (a) showing the maxillary size differences between wild and captive chimpanzees, and plot of PC1 and PC2 (b) showing the maxillary shapes of wild (blue circles) and captive (red squares) chimpanzees.

the magnitudes of these differences were examined, and statistical significance was calculated using the appropriate tests as specified above. Additionally, we performed a PCA on a random mixed sample and the bonobos to examine how shape differences are affected

when including captive individuals in comparative analyses between chimpanzees and bonobos.

All statistical analyses and visualisations were performed in R 4.3.2 (R Core Team, 2023), with the specific packages and functions

provided in Table S3. A significance level of $p < 0.05$ was employed throughout. Any reference to significant results concerns statistically significant differences.

3 | RESULTS

3.1 | Size and shape differences (question 1)

Maxillae of captive chimpanzees are on average larger than those of wild populations (Figure 2a), and this size difference is significant ($t = 9.905$, $p < 0.001$). Their shapes are also significantly different ($SS = 0.095$, $F = 17.842$, $p < 0.001$), with captive chimpanzees having on average higher scores on PC1 and PC2 than wild specimens (Figure 2b). Maxillae of captive specimens are relatively lower inferosuperiorly, narrower bilaterally, and more prognathic than those of wild populations, with the infraorbital area inferosuperiorly, anteroposteriorly, and bilaterally compressed (Figure 3). The nasal aperture is located relatively more posterosuperiorly on the face of captive specimens, in association with a relatively longer and more prognathic subnasal segment in the midplane. The midplane palatal surface is inferiorly slightly convex in captive specimens and flat in wild populations. Captive chimpanzees show relatively more anterior projection of their dental arcades along with relatively larger diastemata. Dental alveoli are absolutely larger in captive individuals (Figure S2), yet there are few significant differences in relative alveolar dimensions compared with wild specimens, including a mesiodistally longer third premolar alveolus and mesiodistally shorter canine and first molar

alveoli, as well as buccolingually narrower third premolar and first molar alveoli (Figure S3).

3.2 | Static allometry (question 2)

Results of the multivariate regressions examining static allometry (Table S4) show that maxillary shape is significantly correlated with size ($SS = 0.105$, $F = 19.965$, $p < 0.001$), but that the interaction between size and group is not significant ($SS = 0.008$, $F = 1.540$, $p = 0.084$). Wild and captive chimpanzees thus share a common allometry (i.e., common slope of the allometric lines), but at any size, there is a shape difference between the groups which persists along the size axis (i.e., variable intercepts of the allometric lines). Wild and captive individuals are separated by size differences along the allometric trajectory (Figure 4a) and specimens show considerable overlap in shape space after allometric adjustment (Figure 4b), yet wild and captive chimpanzees still differ significantly from each other ($SS = 0.012$, $F = 2.281$, $p = 0.011$). Mean shape differences independent of size are less pronounced (Figure S4), but the same trends can be observed between the wild and captive groups as for the unadjusted shapes (Figure 3).

3.3 | Age, sex, and generational differences (question 3)

Age of captive individuals is positively correlated with the PC1 scores of their shapes ($r = 0.589$, $t = 3.498$, $p = 0.002$), with older specimens having on average higher scores and being furthest

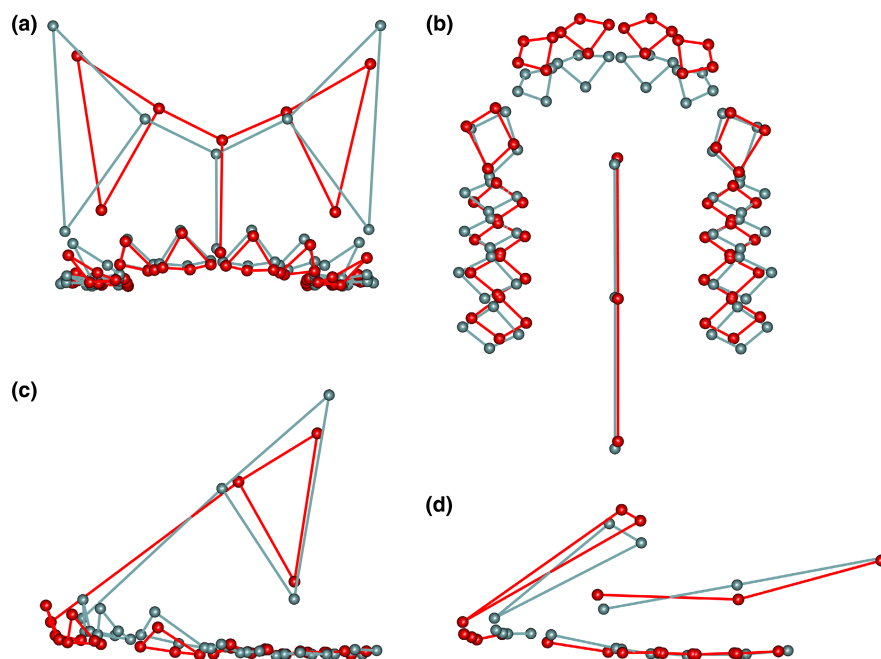


FIGURE 3 Differences between the mean maxillary shapes of wild (blue) and captive (red) chimpanzees in frontal (a), occlusal (b), lateral (c), and midplane (d) views. Shapes are rotated to minimise the distance between postcanine alveolar landmarks, and differences are magnified twice for better visualisation.

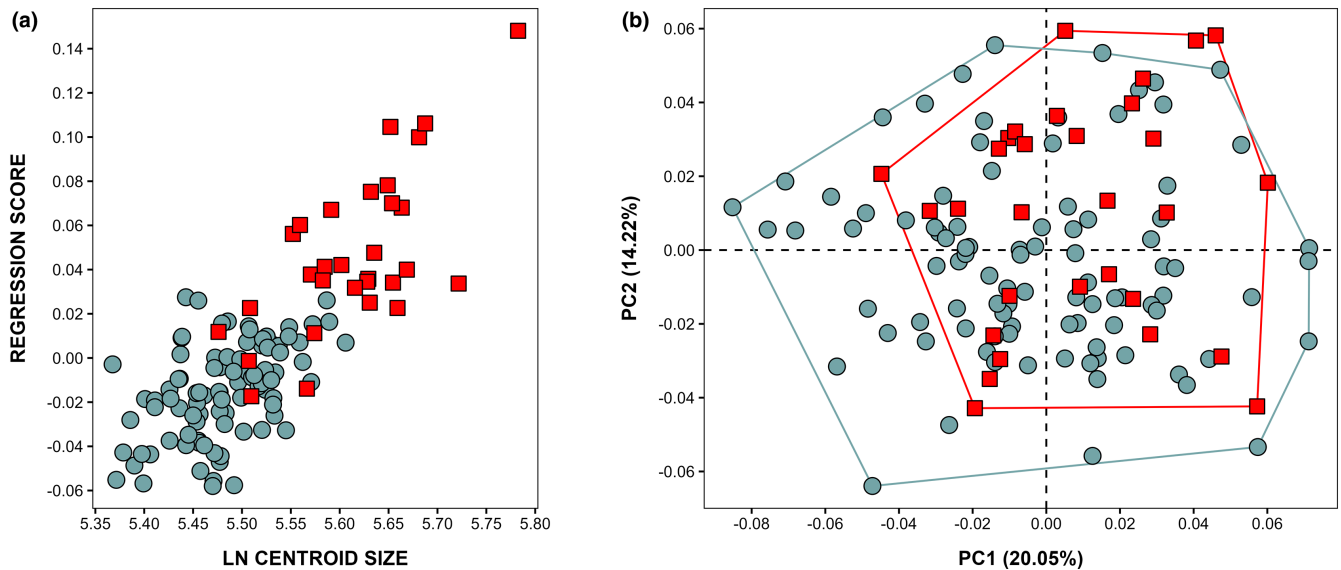


FIGURE 4 Natural logarithms of centroid sizes plotted against regression scores (a) showing the allometric trends for wild (blue circles) and captive (red squares) chimpanzees, and plot of PC1 and PC2 (b) showing the allometrically adjusted maxillary shapes of wild and captive chimpanzees.

removed from the wild sample (Figure 5a). In contrast, age is not correlated with PC1 score of the shapes for wild specimens ($r=0.310$, $t=0.728$, $p=0.499$), although this could be a consequence of the low sample size with known age and because none of these individuals are particularly old. Notably, captive specimens of a similar age as the wild individuals have higher PC1 scores (Figure 5a). When plotting wear stages of the first and second molars against PC1 scores of the shapes (Figure 5d,g, respectively), captive specimens have on average more positive PC1 scores with increasing dental wear stage and compared with wild individuals for each wear stage, suggesting some relationship between age, shape, and rearing environment. Similar trends are observed for the natural logarithms of centroid sizes, with captive specimens being on average larger with increasing age and dental wear stage and compared with wild individuals of a similar age or wear stage (Figure 5b,e,h). However, Pearson's product-moment correlation tests between size and age are not significant for either the wild ($r=0.254$, $t=0.588$, $p=0.582$) or captive ($r=0.255$, $t=1.262$, $p=0.219$) chimpanzees. Age and molar wear stages do not correlate with the PC1 scores of the allometrically adjusted shapes (Figure 5c,f,i), and the correlation tests are not significant for both wild ($r=0.399$, $t=0.972$, $p=0.376$) and captive ($r=0.076$, $t=0.367$, $p=0.717$) specimens with known age.

Males are significantly larger than females for the wild ($t=4.503$, $p<0.001$) and captive ($t=4.123$, $p<0.001$) groups (Figure 6a), and males have on average more positive scores on PC1 and PC2 than females in both samples (Figure 6b). There is considerable overlap between the sexes in shape space, yet differences are significant between wild males and females ($SS=0.021$, $F=4.320$, $p<0.001$), but not between captive males and females ($SS=0.009$, $F=1.517$, $p=0.102$). Additionally, wild and captive males are significantly more different from each other in size ($t=10.309$, $p<0.001$), shape ($t=7.562$, $p<0.001$), and allometrically adjusted shape ($t=6.944$, $p<0.001$) than are wild and captive females.

A morphological trend from wild chimpanzees to first-generation captive individuals to specimens from subsequent captive generations can be observed and comprises an increasingly larger size (Figure 7a) and a more distinct shape (Figure 7b). Note that the five related captive specimens do not plot particularly closer to each other in shape space than do the rest of the captive sample.

3.4 | Variability (question 4)

Degree of size variation does not differ between wild and captive chimpanzees when all specimens are considered, although statistical significance of the difference is only just above the $p<0.05$ threshold ($F=0.580$, $p=0.053$). In contrast, captive chimpanzees are more variable in maxillary shape ($t=9.279$, $p<0.001$) than the wild group. When comparing the 30 captive specimens with 30 randomly sampled wild individuals, the probability of a significantly larger degree of variation is only 24.1% for size, yet 99.4% for shape.

3.5 | Asymmetry (question 5)

Maxillae of captive specimens are overall more asymmetric than those of wild individuals, with the average Procrustes shape distance between unsymmetrised and symmetrised specimens significantly larger for captive chimpanzees ($t=5.080$, $p<0.001$). In both wild and captive individuals, the lateral nasal margin, labial canine alveolar margin, and especially the take-off of the zygomatic process and the inferior orbital margin are most affected by asymmetry (Figure S5). Although significant in both groups, directional asymmetry explains only 0.47% of the total shape variance in wild chimpanzees ($SS=0.004$, $F=4.989$, $p<0.001$), compared with 0.99% in captive specimens ($SS=0.004$, $F=2.108$, $p=0.028$). The degree of fluctuating asymmetry is also less

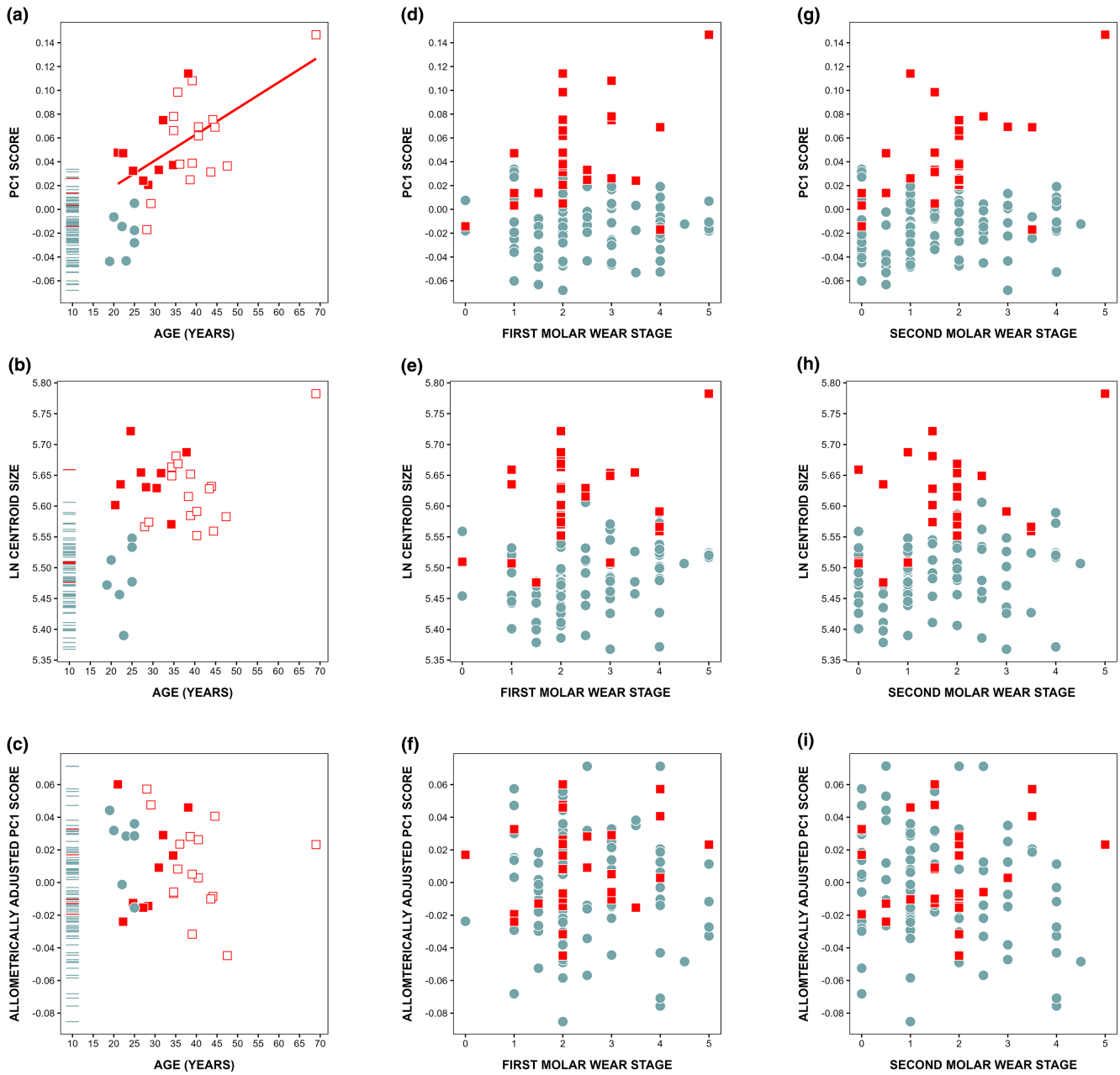


FIGURE 5 Age (a–c), first molar wear stage (d–f), and second molar wear stage (g–i) of wild (blue circles) and captive (red squares) chimpanzees plotted against PC1 scores of the shapes (a, d, g), natural logarithms of centroid sizes (b, e, h), and PC1 scores of the allometrically adjusted shapes (c, f, i). Captive specimens that were caught in the wild and have estimated ages are shown as open symbols, while those born in captivity or with known date of birth in the wild are shown as filled symbols.

in wild individuals than in the captive group, explaining 8.68% and 13.69% of the total shape variance, respectively.

3.6 | Impact of captive specimens (question 6)

When comparing the wild chimpanzees with mixed samples of wild and captive specimens, all 1000 mixed samples have on average significantly larger maxillae than the original wild sample ($t=3.542-5.329$, $p<0.001$), and their shapes are

always significantly different from each other ($SS=0.015-0.026$, $F=2.731-4.702$, $p<0.005$). Moreover, degrees of size ($F=0.342-0.442$, $p<0.001$) and shape ($t=17.101-28.702$, $p<0.001$) variation are significantly larger in the 1000 mixed samples compared with the original wild sample.

In comparison with bonobos, wild chimpanzees are on average significantly larger ($t=22.861$, $p<0.001$), as are the 1000 mixed samples ($t=20.121-23.378$, $p<0.001$), although the magnitude of size difference is always significantly larger in the latter comparisons than in the former ($t=21.435-31.523$, $p<0.001$). The larger

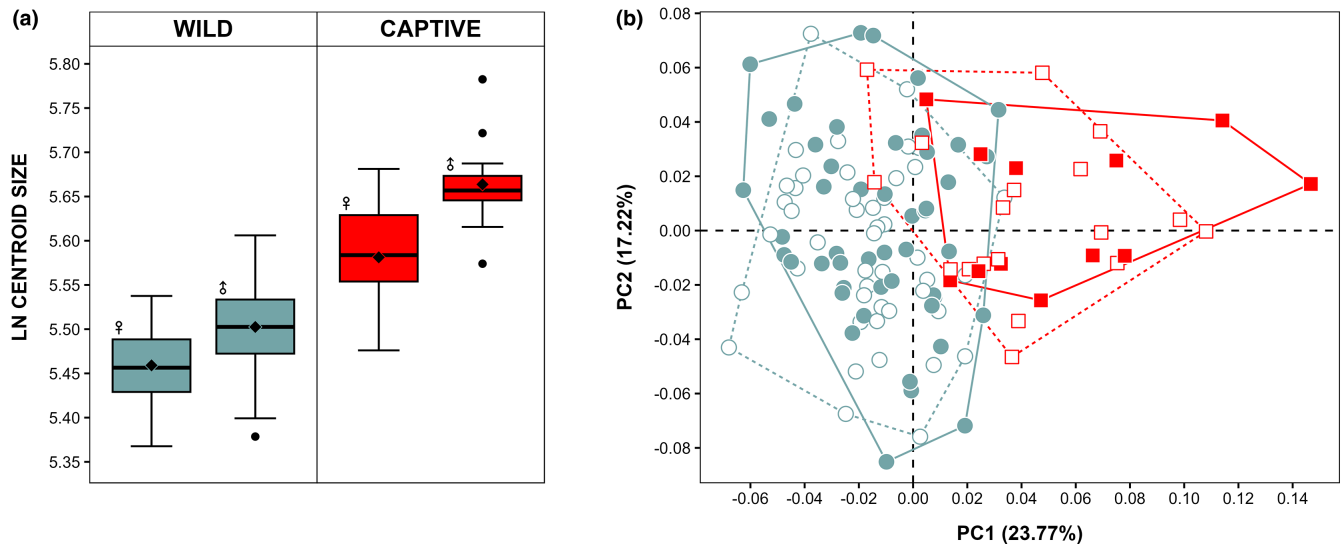


FIGURE 6 Boxplots of the natural logarithms of centroid sizes (a) showing the maxillary size differences between males and females of wild and captive chimpanzees, and plot of PC1 and PC2 (b) showing the maxillary shapes of males (closed symbols) and females (open symbols) of wild (blue circles) and captive (red squares) chimpanzees.

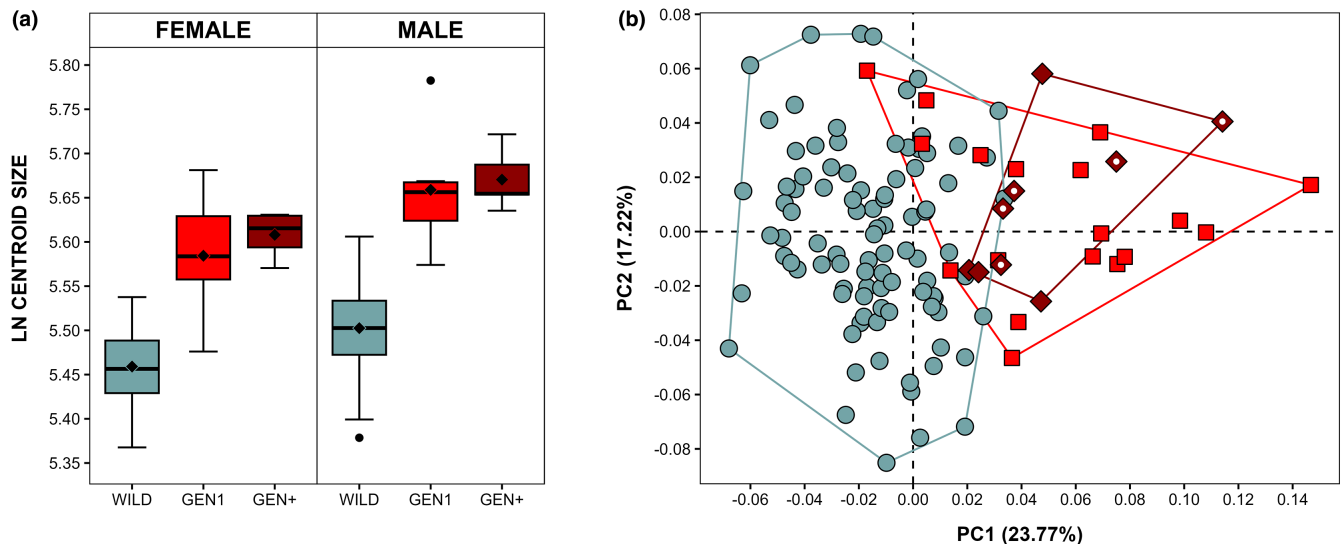


FIGURE 7 Boxplots of the natural logarithms of centroid sizes (a) showing the maxillary size differences between wild chimpanzees (WILD), first-generation captive specimens (GEN1), and subsequent captive generations (GEN+) per sex, and plot of PC1 and PC2 (b) showing the maxillary shapes of wild chimpanzees (blue circles), first-generation captive specimens (red squares), and subsequent captive generations (dark red diamonds). White dots mark related individuals.

magnitude of size difference is illustrated for a random mixed sample in Figure 8a. Similarly, shape differences between wild chimpanzees and bonobos are significant ($SS=0.046$, $F=9.215$, $p<0.001$), as are those between the 1000 mixed samples and bonobos ($SS=0.073-0.089$, $F=12.387-15.586$, $p<0.001$), but the magnitude of shape difference is again significantly larger in the latter comparisons than in the former ($t=23.416-35.125$, $p<0.001$). In the PC plot showing the maxillary shapes of a random mixed sample of chimpanzees and the bonobos, captive specimens are indeed further removed from bonobos than are wild chimpanzees and captive individuals show almost no overlap with bonobos on PC1 in contrast with wild specimens (Figure 8b).

4 | DISCUSSION

Researchers have long acknowledged that morphology, as well as behaviour and other traits, can drastically change in captive environments. In this study, we set out to assess the maxillary morphology of captive versus wild chimpanzees and found significant differences in both size and shape. A large proportion of the shape differences can be attributed to static allometry. Although it seems that captive maxillae become more distinct from the wild group with age, this is in fact simply a consequence of captive specimens growing larger, as no age trends could be detected for the allometrically adjusted shapes. It is thus of interest to examine growth patterns

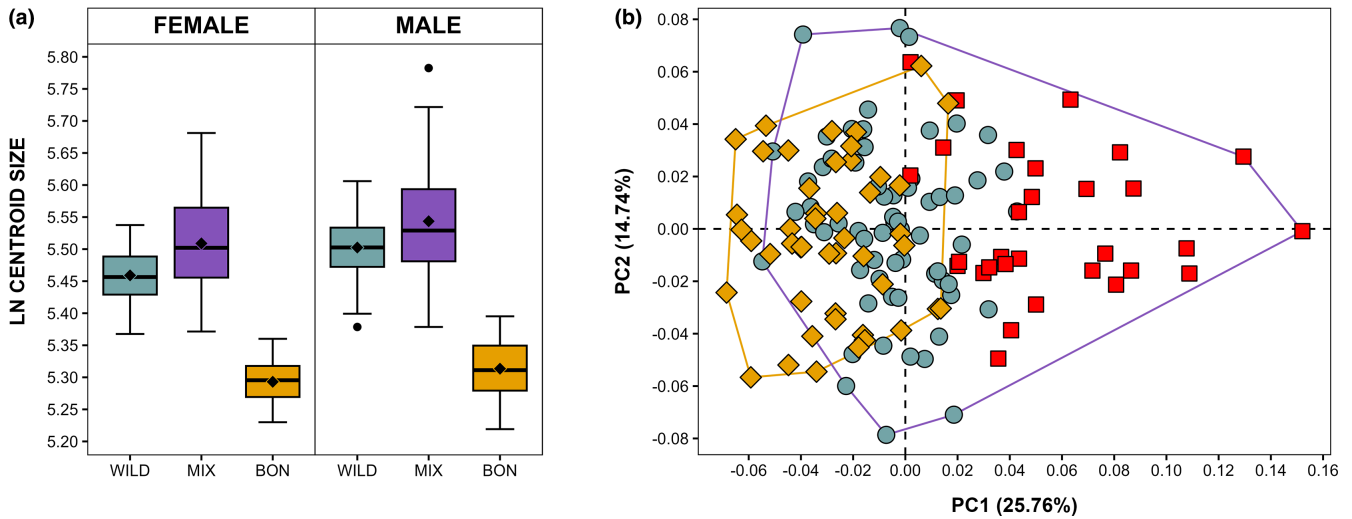


FIGURE 8 Boxplots of the natural logarithms of centroid sizes (a) showing the maxillary size differences between wild chimpanzees (WILD), a random mixed sample of wild and captive chimpanzees (MIX), and bonobos (BON) per sex, and plot of PC1 and PC2 (b) showing the maxillary shapes of a random mixed sample of wild (blue circles) and captive (red squares) chimpanzees and bonobos (yellow diamonds).

in chimpanzees to assess whether the observed shape differences between the wild and captive groups can simply be attributed to individuals growing larger in captivity. When examining developmental trajectories in chimpanzees, research has shown that their face becomes more prognathic, wider, and longer (Bastir & Rosas, 2004; Cobb & O'Higgins, 2004; Lieberman et al., 2007; Mitteroecker et al., 2004; Penin et al., 2002). Captive specimens do indeed show a strong projection of the anterior dental arcade and have more prognathic faces, yet their maxillae are narrower compared to wild individuals. Moreover, that captive and wild specimens differ significantly from each other even after allometric size adjustment of the shape data suggests other factors independent of size also contribute to the shape differences. In other words, even if wild specimens would reach sizes comparable to captive individuals, they still would not exhibit the exact same morphology.

Skull morphology is influenced by a range of external factors, including the mechanical properties of food, feeding behaviour, and in some cases prey capture behaviour as well (see Curtis et al., 2018; Dumont et al., 2012; Hartstone-Rose et al., 2014; Herring, 1993; O'Regan & Kitchener, 2005; Ravosa et al., 2008; Samuels, 2009; Santana et al., 2012; van Valkenburgh, 1999). It can be expected that the maxillary morphology of captive chimpanzees reflects that of animals fed on different, perhaps softer diets. The food provided to captive individuals has been formulated to provide the nutritional requirements for growth, but historically lacked texture and interest (Kapoor et al., 2016; Lindburg, 1998), which could have a distinct effect on cranial morphology and dental health (Aronsen & Kirkham, 2017; O'Regan & Kitchener, 2005). In experimental studies, individuals fed softened diets have narrower maxillae than groups raised on hard food in rats (Beecher & Corruccini, 1981a; Moore, 1965; Watt & Williams, 1951), Yucatan minipigs (Ciochon et al., 1997), squirrel monkeys (Beecher et al., 1983; Corruccini & Beecher, 1982), rhesus macaques (Beecher & Corruccini, 1981b), and baboons (Corruccini & Beecher, 1984), which is consistent with

our results for captive chimpanzees. In contrast, the maxillary arch length of squirrel monkeys and rhesus macaques was observed to be rather unaffected by dietary texture (Beecher & Corruccini, 1981b; Corruccini & Beecher, 1982), while we found dental arcades projecting relatively more anteriorly in captive chimpanzees. Our results do corroborate the research on Yucatan minipigs where the soft diet group displays longer palates and marked differences in facial prognathism and midfacial width compared to individuals fed on hard foods (Ciochon et al., 1997). The relatively deeper anterior palate of captive chimpanzees has also been observed for squirrel monkeys raised on artificially softened foods (Beecher et al., 1983). Moreover, soft diets reduce the amount of muscular effort needed, and thus, less mechanical stress is applied to the cranial bones involved in mastication. This could potentially result in greater morphological variation (Siciliano-Martina et al., 2021a), as was indeed observed here for the maxillae of captive chimpanzees.

Although often overlooked in the literature, a skewed social environment in captivity can also impact skull growth and development (Singleton, 2012). Androgenic hormones, such as testosterone, have a direct and indirect influence on craniofacial development, especially during adolescence (Abu et al., 1997; Barrett & Harris, 1993; Byron et al., 2004; Cray, 2009; Fujita et al., 2004; Lin et al., 2004; Noda et al., 1994; Verdonck et al., 1999). Testosterone levels are associated with social ranking and dominance (Eisenegger et al., 2011; Muller & Wrangham, 2004; Setchell & Dixson, 2002), and such social dynamics certainly differ in captive settings (Honeiss & Marin, 2006; Hosey, 2005; Marriner & Drickamer, 1994; Morgan & Tromborg, 2007; Price & Stoinski, 2007). For example, captive males typically lack or have a limited number of male peers to avoid the aggression that occurs in naturalistic multimale-multifemale primate groups (Bassett, 2000). Males may thus experience unchallenged dominance and consequently prolonged exposure to high testosterone levels, allowing them to grow faster and longer. Indeed,

Singleton (2012) demonstrated through developmental simulations that the cranial morphology of captive *Mandrillus* can mostly be explained by an extended ontogenetic trajectory in males. Moreover, mandibular shape differences between wild and captive Japanese macaques resemble sexual dimorphism trends, with captive individuals exhibiting to some extent exaggerated male features (Kamaluddin et al., 2019). Likewise, the direction of maxillary shape differences between wild and captive chimpanzees in this research is similar to those between females and males in each group. Additionally, we found that wild and captive males differ more from each other than do wild and captive females, even after allometric adjustment of the shape data, suggesting that captivity has a greater effect on the maxillary size and shape of males. It should however be kept in mind that sexes overlap extensively in shape space, and thus, the effect of changed social factors on the maxillary morphology is small. Moreover, that maxillary shapes of captive males and females are not significantly different from each other, while sexes in the wild are, corroborates previous research showing reduced sexual dimorphism in ranch American minks (Lynch & Hayden, 1995), domesticated foxes (Trut, 1999), and captive black-footed ferrets (Wisely et al., 2002).

Another factor to consider is that some captive specimens are first-generation individuals while others were born in captivity as part of established breeding programmes spanning multiple generations. As would be expected, the latter are more distinct from wild chimpanzees, being even larger and further removed in shape space from wild populations than are the first-generation captive specimens. Unfortunately, sample sizes for each group are too small to allow meaningful statistical testing of the size and shape differences between the different generations of captive chimpanzees. Increased morphological disparity with number of generations in captivity has previously been documented for old-field mice (McPhee, 2004) and Japanese macaques (Geiger, 2021), although morphological changes were not uniform among populations and not always cumulative between generations. This pattern was interpreted as the result of relaxed selective pressures in captivity coupled with founder effects (Geiger, 2021; MCPhee, 2004). Additionally, captive specimens in present-day sanctuaries and modern zoos live in much better conditions than decades ago when animals were held in small enclosures, sometimes permanently living in cages. Food provided to captive animals nowadays certainly resembles their natural diet more closely. Specimens collected in the past may therefore be more different from wild chimpanzees than those of a same generation living more recently in better provisioned captive environments, yet this trend could not be investigated as such information is not always provided in museum records.

The larger morphological space occupied by captive chimpanzees, at least in terms of shape, may be indicative of relaxed selective constraints. That is to say, there are few to no fitness consequences to captive individuals displaying a variety of phenotypes without the selective pressures of living in the wild (Bryant & Reed, 1999; Lynch & O'Hely, 2001; MCPhee, 2004; MCPhee &

McPhee, 2012). Similarly, the degree of shape variation was observed to be larger in captive Mexican wolves (Siciliano-Martina et al., 2022), farm foxes (Zatoń-Dobrowolska et al., 2018), and captive-bred chinchillas (Crossley & del Mar Miguélez, 2001), but not for captive coyotes (Curtis et al., 2018) compared with their wild counterparts.

Captive chimpanzees are also more asymmetric than wild specimens and show higher levels of both directional asymmetry and fluctuating asymmetry. Although the potential adaptive and functional significance of directional asymmetry remains unclear (Klingenberg et al., 1998; Pélabon et al., 2006; Pélabon & Hansen, 2008), fluctuating asymmetry is widely used as a measure of developmental instability due to its association with environmental stressors such as climate, diet, and toxins, as well as with adverse genetic conditions such as aneuploidy, heterozygosity, hybridisation, and inbreeding (Graham & Özener, 2016; Klingenberg, 2003, 2015; Møller & Swaddle, 1997; Palmer, 1994; Palmer & Strobeck, 1986, 2003; Schaefer et al., 2006; Van Dongen et al., 2003). The lateral nasal margin, labial canine alveolar margin, and especially the take-off of the zygomatic process and the inferior orbital margin are most affected by asymmetry. Although these landmarks are prone to measurement error as they are placed on shallow curves, this factor does not negate the susceptibility of these areas to asymmetry.

Multiple subspecies were analysed together in this study, and although it would be interesting to investigate wild–captive trends at the subspecies level, low sample sizes and skewed sample compositions can confound results. For example, the five captive *P. t. schweinfurthii* specimens are all females and no captive specimens of *P. t. troglodytes* were available (Table S1). Sample sizes are larger for *P. t. verus*, and when only considering this subspecies, similar trends are observed between the wild and captive samples as at the species level.

As an important practical consideration, we assessed how impactful the observed size and shape differences of captive chimpanzees are when including these specimens in morphometric analyses alongside wild individuals. Mitchell et al. (2021), for example, showed that bolstering small sample sizes with damaged or pathological specimens provides an adequate assessment of the major shape components in the cranium and mandible of crab-eating macaques, although finer scale differences were also identified. Captive individuals could similarly increase the pool of potential specimens available for analyses, but at least in the case of maxillary morphology in chimpanzees, statistical outputs are significantly altered when bolstering a sample with captive specimens. Mixed samples are not only larger and distinct in their shape from wild maxillae but also show higher levels of size and shape variation. Moreover, size and shape differences with bonobos are exaggerated and these shape differences are expressed prominently on the most dominant shape component.

In conclusion, significant differences were detected in the maxillae of captive and wild chimpanzees, and these were discussed in the context of growth patterns, changes in dietary texture, an altered social environment, and captive generations. Even though wild and captive chimpanzees overlap in shape space, especially after allometric adjustment of the

shape data, the changes in maxillary morphology induced by captivity nevertheless significantly affect morphometric analyses. Hence, captive individuals are atypical specimens, unrepresentative of the wild morphology, and the findings of this study validate the notion that including captive specimens in craniometric analyses of *Pan troglodytes* should be avoided when the aim is to characterise this species.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ORCID

Hester Hanegraef  <https://orcid.org/0000-0002-2205-5702>

Fred Spoor  <https://orcid.org/0000-0002-8829-7421>

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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