



Morphological variation of the maxilla in modern humans and African apes

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ABSTRACT

Differences in morphology among modern humans and African apes are frequently used when assessing whether hominin fossils should be attributed to a single species or represent evidence for taxic diversity. A good understanding of the degree and structure of the intergeneric, interspecific, and intraspecific variation, including aspects such as sexual dimorphism and age, are key in this context. Here we explore the variation and differences shown by the maxilla of extant hominines, as maxillary morphology is central in the diagnosis of several hominin taxa. Our sample includes adults of all currently recognized hominine species and subspecies, with a balanced species sex ratio. In addition, we compared the adults with a small sample of late juveniles. The morphology of the maxillae was captured using three-dimensional landmarks, and the size and shape were analyzed using geometric morphometric methods. Key observations are that 1) the maxillae of all extant hominine species and subspecies show statistically significant differences, but complete separation in shape is only seen at the genus level; 2) the degree of variation is not consistent between genera, with subspecies of *Gorilla* being more different from each other than are species of *Pan*; 3) the pattern of sexual shape dimorphism is different in *Pan*, *Gorilla*, and *Homo*, often showing opposite trends; and 4) differentiation between maxillary shapes is increased after adjustment for static intraspecific allometry. These results provide a taxonomically up-to-date comparative morphological framework to help interpret the hominin fossil record, and we discuss the practical implications in that context.

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1. Introduction

The maxillae are the most centrally located bones in the face, structurally linking the orbits, nasal cavity, and zygomatic arches, as well as the mandible via the dental arcades. Maxillary morphology thus reflects a multitude of requirements and constraints associated with vision, respiration, smell, and mastication, frequently expressing functional adaptations that may underlie speciation. Indeed, morphological features of the maxilla take a central role in differential diagnoses of several hominin taxa, including *Homo neanderthalensis* (Stringer et al., 1984; Rak, 1986; Trinkaus, 1987), *Homo antecessor* (Bermúdez de Castro et al., 1997; Freidline et al., 2013), *Paranthropus* (Rak, 1983; Grine, 1988; Constantino and Wood, 2004), species of early *Homo* (Stringer, 1986; Lieberman

et al., 1988; Wood, 1992; Rightmire, 1993; Blumenschine et al., 2003; Leakey et al., 2012; Spoor et al., 2015), *Kenyanthropus platyops* (Leakey et al., 2001; Spoor et al., 2010), and *Australopithecus deyiremeda* (Haile-Selassie et al., 2015; Spoor et al., 2016).

Assigning fossil specimens to separate species is typically informed by the question of whether or not morphological differences exceed the degree and pattern of intraspecific variation shown by related taxa, most commonly the extant hominines or hominids, when assessing the hominin fossil record (e.g., Wood, 1991a; Lockwood et al., 2000; Spoor et al., 2010, 2015, 2016). This approach requires a good understanding of the variation and differences among extant taxa at the genus, species, and subspecies level. A complicating factor here is that the consensus view of hominid taxonomy has changed over the last decades, with several more species and subspecies recognized (e.g., Shea et al., 1993; Ruvolo et al., 1994; Garner and Ryder, 1996; Xu and Arnason, 1996; Zhi et al., 1996; Gonder et al., 1997; Gagneux et al., 1999; Sarmiento and Oates, 2000; Groves, 2001, 2003, 2018; Stumpf et al., 2003;

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Fischer et al., 2006; Scally et al., 2012; Prado-Martinez et al., 2013; Nater et al., 2017). Consequently, what is interpreted as intraspecific variation and interspecific differences has changed as well. A good example is the reclassification of *Gorilla* and *Pongo* from being monospecific to including two species each, perhaps three in the case of *Pongo* (Nater et al., 2017). Hence, previous studies using the monospecific interpretation in their comparisons with hominin samples (e.g., Richmond and Jungers, 1995; Lockwood et al., 2000; Terhune et al., 2007) quantified intraspecific variation in *Gorilla* or *Pongo* that is now considered intrageneric variation, including interspecific differences. This reinterpretation is therefore directly relevant when the context is species recognition in the hominin fossil record.

Recognizing the important role of the maxilla in hominin taxonomy and phylogeny, as well as the need for an up-to-date and comprehensive extant comparative framework, this study sets out to evaluate maxillary morphology among modern humans and African apes. Included in our analyses are substantial, sex-balanced samples of all genera, species, and subspecies recognized in the current consensus view of hominine taxonomy (Table 1), noting that alternative interpretations have been proposed. For instance, genetic studies have suggested that *Pan troglodytes verus* should be elevated to full species rank (Morin et al., 1994) and that a fourth chimpanzee subspecies, *Pan troglodytes ellioti*, should be recognized (Gonder et al., 1997, 2011; Oates et al., 2009).

We quantitatively assess key morphological features of the hominine maxilla using three-dimensional (3D) landmark-based geometric morphometric analyses, with reference to both size and shape. The specific aims of this research are 1) to investigate the amount of variation within hominine taxa, 2) to examine differences between genera (2a), species (2b), and subspecies (2c), 3) to explore sexual dimorphism in each species, 4) to assess the effects of aging in adults of each species, 5) to evaluate differences between late juveniles and adults of each species, and 6) to assess the impact of allometry on maxillary shape differences. These aims are descriptive in nature, documenting the various aspects of extant hominine maxillary morphology that can aid interpretation of the fossil record. However, in the following paragraphs we also formulate specific predictions in relation to each aim as a way to focus the exploration of each topic.

Morphological variation of a taxon will likely be related to multiple factors, such as its time span and taxic diversity, the degree of sexual dimorphism, as well as geographical area inhabited. In this context, extant *Homo* stands out as the only monospecific genus, but with a particularly large geographic distribution. In contrast, *Gorilla* includes several species and subspecies, is overall highly sexually dimorphic, but inhabits more restricted parts of Africa. How such factors jointly impact a taxon's variation in maxillary size and shape (aim 1) is difficult to predict. Differences in maxillary size and shape between taxa (aim 2) can be affected by similar factors. Deeper divergence times between sister taxa are

expected to be associated with greater morphological differences following genetic drift or adaptive change. Hence, we predict that both variation and differences will be largest at the genus level and smallest at the subspecies level. This pattern will likely apply within each genus, but given that the degree of subspecific and interspecific differentiation varies even between closely related taxa (Groves, 1967, 1970b; Shea and Coolidge, 1988; Albrecht and Miller, 1993; Guy et al., 2003; Taylor and Groves, 2003; Pilbrow, 2007; White et al., 2020), it is unclear if this will be the case when taxa of different genera are compared.

Among hominine species, males are generally larger than females and their cranial morphology differs to a variable degree, with *Gorilla* being most and *Pan* or extant *Homo sapiens* least sexually dimorphic (e.g., Ashton and Zuckerman, 1950, 1956; Ashton, 1957; Schultz, 1962; Deblock and Fenart, 1973; Mahler, 1973; Almquist, 1974; Fenart and Deblock, 1974; Wood, 1976; Cramer and Zihlman, 1978; O'Higgins et al., 1990a, b; Wood et al., 1991; Uchida, 1992, 1996; O'Higgins and Dryden, 1993; Kelley, 1995; Lockwood, 1999; Guy et al., 2003; Schaefer et al., 2004; Cobb and O'Higgins, 2007). To explore in detail how these broader differences are reflected in the maxilla specifically, we compare male and female morphology in each species (aim 3).

Schaefer et al. (2004) found that craniofacial morphology is sexually dimorphic in all hominine species, with the highest levels in size and shape shown by *Gorilla* and the lowest levels in size shown by *Pan paniscus* and in shape by both *P. paniscus* and *H. sapiens*. Cobb and O'Higgins (2007) subsequently found no statistically significant evidence for *P. paniscus* being sexually dimorphic in either craniofacial size or shape. Informed by the results of these two studies, we predict a similar pattern for the maxilla, with the highest levels of sexual dimorphism in *Gorilla* and the lowest levels in *P. paniscus*. The most striking sex-related difference in the maxillae of African apes is the larger size of the male canines (Oxnard et al., 1985; Plavcan, 2001). We thus predict that sexual dimorphism in African apes will be most clearly expressed by morphological features that are linked with canine development, such as the length and the shape of the snout (Wood et al., 1991; Scott and Lockwood, 2004), whereas such differences will not be seen in extant *Homo*. The cranial, dental, and mandibular patterns of sexual dimorphism differ between hominines, although more closely related species show more similar patterns (e.g., Wood, 1976; Oxnard et al., 1985; Oxnard, 1987; O'Higgins et al., 1990a, b; Wood et al., 1991; O'Higgins and Dryden, 1993; Lockwood, 1999; Plavcan, 2002; Taylor, 2006; Cobb and O'Higgins, 2007). Hence, we expect the pattern of sexual dimorphism to be genus-specific.

To assess the impact of aging shown by the adult maxilla (aim 4), we compare younger and older adult individuals of each species. Age-related changes in maxillary morphology have been reported as a consequence of dental wear, including interproximal wear reducing the length of the tooth rows due to mesial drift (Wolpoff, 1971; Fishman, 1976; Hylander, 1977; Yilmaz et al., 1980; Kaifu

Table 1
Currently accepted hominine taxonomy.

Genus	Species	Subspecies	Common name	Original reference
<i>Pan</i>	<i>P. troglodytes</i>	<i>P. t. troglodytes</i>	Central chimpanzee	Blumenbach (1775)
		<i>P. t. schweinfurthii</i>	Eastern chimpanzee	Giglioli (1872)
		<i>P. t. verus</i>	Western chimpanzee	Schwarz (1934)
<i>Gorilla</i>	<i>P. paniscus</i>	—	Bonobo	Schwarz (1929)
		<i>G. gorilla</i>	Western lowland gorilla	Savage and Wyman (1847)
	<i>G. beringei</i>	<i>G. g. diehli</i>	Cross River gorilla	Matschie (1904a)
		<i>G. b. beringei</i>	Mountain gorilla	Matschie (1903)
		<i>G. b. graueri</i>	Eastern lowland gorilla	Matschie (1914)
<i>Homo</i>	<i>H. sapiens</i>	<i>H. s. sapiens</i>	Modern human	Linnaeus (1758)

et al., 2003), and severe wear of the anterior dentition resulting in lingual tipping of the incisors and alveolar process, which can affect the subnasal morphology substantially (Lundström and Lysell, 1953; Lysell and Filipsson, 1958; Hasund, 1965; Hylander, 1977; Seddon, 1984; Varrela, 1990; Dean et al., 1992; Kaifu, 2000; Kaifu et al., 2003; d’Incau et al., 2012; Villmoare et al., 2013). Moreover, there is some evidence of ongoing cranial growth after dental maturation in African apes and modern humans (Krogman, 1931a, b; Randall, 1943a; Ruff, 1980; Balolia et al., 2013). Hence, we predict that older adults will have a somewhat different dental arcade shape, marked by shorter postcanine segments and a less-projecting anterior segment, whereas other parts of the maxilla are slightly larger.

The current study is not concerned with ontogenetic development as such, but we nevertheless compare late juveniles with adults for each species (aim 5). The practical reason is to explore whether the maxillary morphology of late juvenile specimens can be used when describing adult characteristics of a species, noting that the holotypes of *Paranthropus boisei* (Leakey, 1959), *Homo habilis* (Leakey et al., 1964), and *Australopithecus sediba* (Berger et al., 2010) all fall in this age category. Typically, the third molars of late juveniles have not (fully) erupted, affecting the postcanine tooth rows, but whether other aspects of maxillary size and shape have fully matured at that developmental stage is not clear. Since certain features of craniofacial morphology are not ontogenetically stable at the late juvenile stage in African apes and modern humans (e.g., Kimbel and Rak, 2017), we predict some morphological differences with adults. Nonetheless, we expect that late juveniles will be encompassed within the adult variation, as was previously found for the maxillary dental arcade shape (Spoor et al., 2015).

Finally, we investigate whether any differences in maxillary shape between hominine species are related to differences in size (aim 6). Allometric scaling adds to biological shape variation. Hence, we predict that adjusting for intrageneric or intraspecific static allometry will reduce shape variation of individual taxa (Mitteroecker et al., 2013), resulting in less overlap between these taxa. When comparing two taxa that differ in size, it seems plausible that size-related shape variation will generally add to their overall shape differences. Adjusting for this allometric component is thus predicted to reduce the shape differences, as has been observed interspecifically for *Pan* (Shea et al., 1993; Taylor and Groves, 2003). However, in comparisons of *Gorilla* taxa, the effect of size adjustment was found to be more ambiguous, either increasing or reducing differences (Taylor and Groves, 2003) or having no impact (Stumpf et al., 2003; Pilbrow, 2010).

2. Materials and methods

2.1. Sample

Our sample comprises 479 specimens of *H. sapiens*, *Pan troglodytes*, *P. paniscus*, *Gorilla gorilla*, and *Gorilla beringei* (Supplementary Online Material [SOM] Table S1) housed in the Anatomisches Institut, Universität Leipzig, Leipzig, Germany (ULAC); Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany; Royal Museum of Central Africa, Tervuren, Belgium (RMCA); National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM); American Museum of Natural History, New York, USA (AMNH); Naturmuseum Senckenberg, Frankfurt am Main, Germany (SMF); Museo de La Plata, La Plata, Buenos Aires, Argentina (MLP); Peabody Museum of Archaeology and Ethnology, Harvard University, Cambridge, USA; Museum of Comparative Zoology, Harvard University, Cambridge, USA; Department of Anatomical Sciences, Stony Brook University, Stony Brook, USA; National Museums of Kenya, Nairobi, Kenya

(KNM); and Natural History Museum, London, UK. The modern human specimens are from geographically diverse preindustrial populations. Sex attributions were taken from museum records when available. For the 55 *Pan* and *Gorilla* specimens without this information, sex was determined based on canine size (Kelley, 1995) and the stronger development of crests and muscle markings in males. For the *H. sapiens* specimens, the recorded sex will likely have been based on conventional criteria used in physical anthropology as there is no evidence that autopsy or burial records were available. For 18 specimens, the sex was not recorded and difficult to establish with any certainty without a wider population context. These specimens were therefore excluded from the sexual dimorphism analyses.

We assigned all specimens to three age categories based on dental development and wear (Smith, 1984; Dean et al., 1992): 1) late juveniles with the second molars and canines in occlusion, but the third molars not in occlusion; 2) younger adults with all teeth in occlusion, and second molars with dentine islands over fewer than three cusps; and 3) older adults with all teeth in occlusion, and one or both of the second molars with dentine islands over at least three cusps. Fifteen specimens with heavy wear over the lingual cusps, but nearly no wear over the buccal cusps, as the result of unusual occlusion, were also classified as older adults. One modern human specimen (MLP 379), with a fully formed third molar that has closed roots but is not in occlusion, was classified as adult. In cases where the third molars never developed or it was difficult to establish whether they were in occlusion, the late juvenile or adult status was determined based on root closure of the second molars, tooth wear, and the fusion of the spheno-occipital synchondrosis. For nine specimens classified as adults, but with missing or broken second molars, the younger or older age category was estimated based on wear of the other teeth. One *H. sapiens* adult (USNM 276080) and one *P. paniscus* adult (RMCA RG 29039) are missing all teeth and could therefore not be classified as younger or older. A summary of the study sample is given in Table 2.

All specimens were analyzed using 3D digital surface visualizations extracted from computed tomography (CT) scans (SOM Table S1) using Avizo v. 7.1 (FEI Visualization Sciences Group, Berlin). MicroCT scans (isotropic voxel size: 0.06–0.27 mm) were obtained from the Department of Human Evolution at the Max Planck Institute for Evolutionary Anthropology (Leipzig, Germany) and downloaded from MorphoSource (<https://www.morphosource.org/>). Medical CT scans (pixel size: 0.15–0.71 mm, slice interval: 0.2–1.0 mm, slice thickness: 0.4–1.5 mm) were acquired from the Royal Museum of Central Africa (Tervuren, Belgium), Copes (2012), and the last author (F.S.). When creating the digital surfaces, the μ CT data were downsampled to approximately the pixel sizes of the medical CT scans.

Table 2
Sample size and composition.

	Total	Sex									
		Age				Late juveniles			Adults		
		LJ	YA	OA	AD	M	F	U	M	F	U
<i>P. troglodytes</i> ^a	101	11	61	29	—	6	5	—	46	44	—
<i>P. paniscus</i>	61	14	31	15	1	5	9	—	21	26	—
<i>G. gorilla</i> ^b	105	7	36	62	—	2	5	—	55	43	—
<i>G. beringei</i> ^c	106	5	46	55	—	1	4	—	56	45	—
<i>H. sapiens</i>	106	16	56	33	1	3	5	8	51	29	10

Abbreviations: LJ = late juvenile, YA = younger adult, OA = older adult, AD = unclassified adult; M = male, F = female, U = unknown sex.

^a Including *P. t. troglodytes* (n = 33), *P. t. schweinfurthii* (n = 33) and *P. t. verus* (n = 33).

^b Including *G. g. gorilla* (n = 80) and *G. g. diehli* (n = 24).

^c Including *G. b. beringei* (n = 26) and *G. b. graueri* (n = 80).

2.2. Analyses

The shape of the maxillae was captured by 68 3D landmarks (Table 3; Fig. 1) that were placed on the surfaces and recorded using Avizo v. 7.1. These landmarks describe the orientation as well as relative position and size of the upper dental arcade (excluding the third molar alveolus), the midline palate and subnasal area, the takeoff of the zygomatic process, and the inferior parts of the nasal aperture and orbits. This core landmark configuration quantifies the main maxillary architecture, and by not relying on sliding semilandmarks, it is particularly easy to adapt in future studies when combining the extant sample explored here with the variably preserved hominin fossil record. We did not record zygomaxillare because the zygomaxillary suture was not visible externally and internally in part of the African ape sample, and we found that the scar representing the anteriormost origin of the masseter muscle was not a reliable indicator.

Missing landmarks were estimated using standard procedures based on bilateral symmetry or thin-plate spline interpolation (Gunz et al., 2009). All landmark data were symmetrized using reflected relabeling (Bookstein, 1991; Klingenberg and McIntyre, 1998; Mardia et al., 2000; Gunz et al., 2009) and then converted into shape variables using a generalized Procrustes analysis, removing size, position, and orientation from the landmark dataset (Gower, 1975; Rohlf and Slice, 1990; Bookstein, 1991; Rohlf and Marcus, 1993; Adams et al., 2004; Mitteroecker and Gunz, 2009).

To explore variation within hominine genera, species, and subspecies (aim 1), size was assessed in the adult sample based on the standard deviations of the natural logarithm of centroid size, and two-tailed F-tests to compare two variances were performed to determine statistical significance. Shape variation within each taxon was examined for the adults through Procrustes distances between all possible specimen pairs from that taxon, and statistical significance of differences in variation was determined through two-tailed Student's *t*-tests.

To examine differences between hominine taxa, sexes, and age groups (aims 2–5), size was compared based on the natural logarithm of centroid sizes and statistical significance was determined using two-tailed Student's *t*-tests. The amount of shape difference between genera, species, and subspecies (aim 2) was assessed by calculating Procrustes distances between all possible specimen pairs from different taxa. We performed principal component analyses (PCAs) to assess the nature of shape differences between taxa, sexes, and age groups (aims 2–5). Only adults were included in these analyses, except when assessing the age differences between late juveniles and adults. The statistical significance of group differences in shape was tested through one-way Procrustes analyses of variance with permutation procedures (shape ~ group). When significant, the effect size was quantified using Cohen's *d*, to explore how strong the shape differences are between groups (Lipsey and Wilson, 2001; Wilson, 2001; Cohen, 2013).

Mean shapes were calculated for the relevant principal component (PC) axes to explore the relative shape differences between groups. Groups were compared by superimposing their mean shapes, minimizing the distance between the postcanine alveolar landmarks as the most effective way to describe distinct morphology. Relative facial differences described as wider or narrower pertain to bilateral proportions, lower or higher pertain to inferosuperior proportions, and shorter or longer pertain to anteroposterior proportions. Prognathism relates to the orientation of the subnasal segment and inferior face relative to the postcanine alveolar margin, and the infraorbital area refers to the segment between the lateral nasal margin, inferior orbital margin, and anteroinferior takeoff of the zygomatic process (Fig. 1). Any reference to genus names concerns extant taxa only.

Intraspecific static allometry was explored in the adult sample of each species through Procrustes analyses of variance with permutation procedures (aim 6). To assess if sex should be considered when adjusting for allometry, we tested three regression models for each species separately: one including only size (shape ~ size), a

Table 3
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 takeoff 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 median palatine suture and a line connecting left and right distal M ¹ intersect.
68	Midline point of the posterior border of the palate. ^e

^a When 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.

^b Based on Spoor et al. (2010).

^c Sometimes located on the zygomatic, rather than the maxilla.

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

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

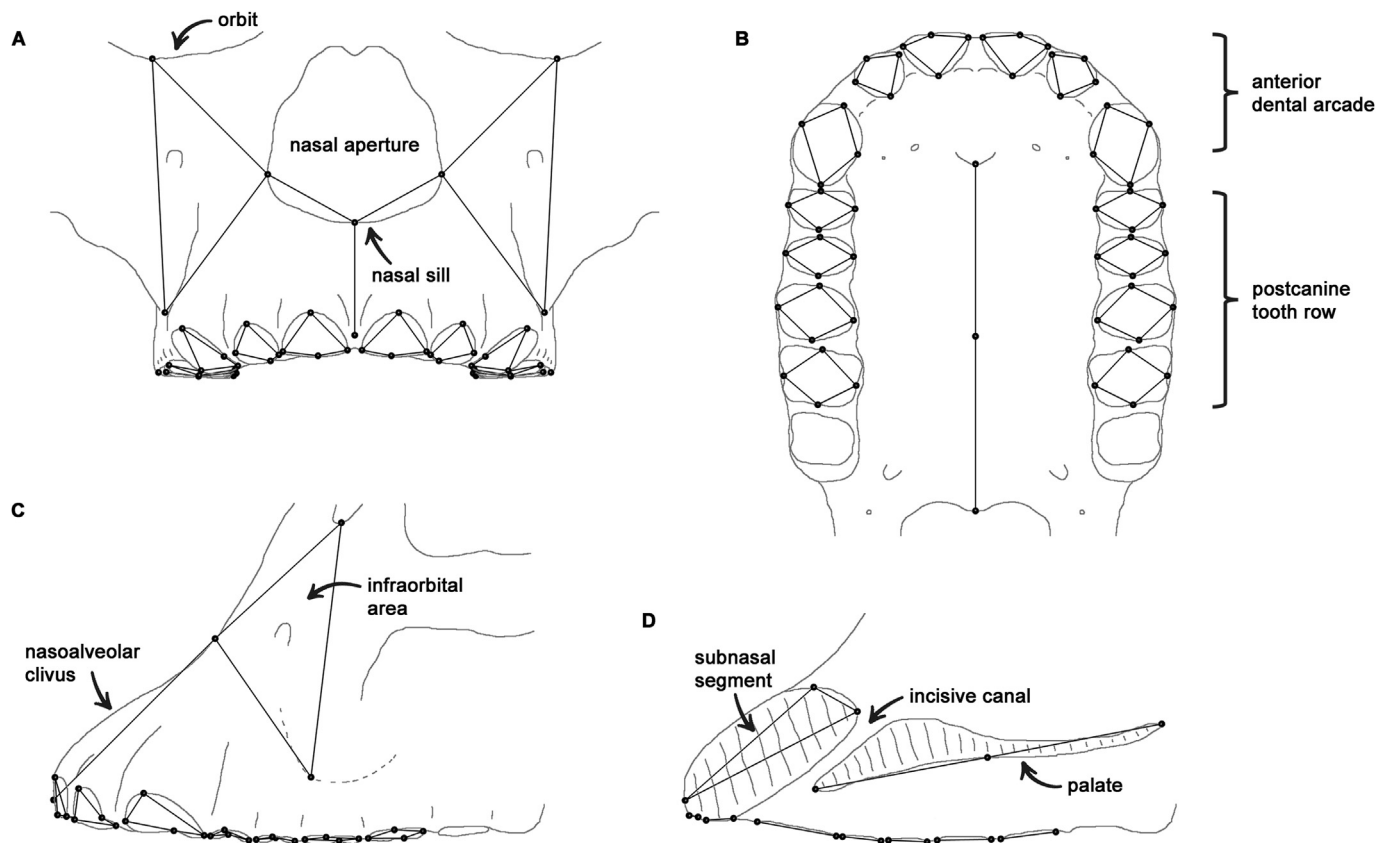


Figure 1. Position of the landmarks and wireframes used to capture the shape of the maxillae, shown for a chimpanzee skull in frontal (A), occlusal (B), lateral (C), and midplane (D) view. Key morphological features are highlighted in the figure. Line drawings are based on USNM 176228.

second including size and sex (shape \sim size + sex), and a third including size, sex, and the interaction between size and sex (shape \sim size * sex). Based on the lowest Akaike information criterion values, showing which model fits the data best, the first regression model including only size was chosen for all species. Further analyses were performed for those species with a significant size-shape regression. Allometric effects were explored by predicting and then comparing the maxillary shape of the smallest and largest centroid size for each species using the size-shape regressions. To investigate how static intraspecific allometry impacts shape comparisons between two taxa, we obtained the allometrically adjusted shapes by scaling all specimens to the same mean natural logarithm of centroid size using the species-specific size-shape regressions. When comparing two species, this mean natural logarithm of centroid size was calculated by taking the mean of the two species mean sizes. When comparing two genera, the mean size of each genus was first calculated from their respective species, followed by calculating the overall generic mean. A PCA was performed on the allometrically adjusted shapes and the results were compared with the PCA of isometrically adjusted Procrustes shapes.

For both the allometrically and isometrically adjusted shapes, we calculated the shape variation within each taxon as the distances between all possible specimen pairs from that taxon and then examined statistical significance using two-tailed Student's *t*-tests. The shape differences between two compared taxa were also determined for the allometrically and isometrically adjusted sets. To assess if the two sets differ significantly from each other in the degree of shape difference between taxa, we used the following procedure. First, we calculated the mean shape coordinates for each taxon. We then computed the components of the vector pointing

from the mean shape of one taxon to the mean shape of the other taxon (mean shape vector), and from each specimen in one taxon to each specimen in the other taxon (specimen-pairs vectors), by subtracting the coordinates of one from the other. The dot products between each specimen-pair vector and the mean shape vector were then obtained by multiplying the corresponding components of each vector and taking their sum. Each dot product was subsequently divided by the magnitude of the mean shape vector, which is computed as the square root of the sum of squares of each component of that vector. This geometrical manipulation projects the specimen distances onto the mean shape axis, and statistical significance of mean shape distances after isometric and allometric adjustment can be assessed using pairwise *t*-tests. Mean shapes were then visualized to examine the effect of size on maxillary shape.

All data were measured by the first author (H.H.). Intraobserver error was assessed through three repeated measurements of one random specimen per species (*H. sapiens*: ULAC 769, *P. troglodytes*: SMF 361, *P. paniscus*: RMCA RG 29065, *G. gorilla*: AMNH A-99/9687, *G. beringei*: RMCA RG 10051), with a measurement interval ranging from three months to more than one year. Procrustes distances between repeated measurements were considerably smaller than the smallest Procrustes distance between all possible specimen pairs of the same species (SOM Table S2). Based on these results, we concluded that intraobserver error does not meaningfully affect our results.

All statistical analyses and visualizations were performed in R v. 4.1.2 (R Core Team, 2021), using the geomorph (Baken et al., 2021) and Morpho (Schlager, 2017) packages. All *p*-values were adjusted for multiplicity, controlling the false discovery rate (Benjamini and

Hochberg, 1995). Adjustments were applied separately by genus, species, and subspecies for each variable, and the significance level was set at $p < 0.05$.

3. Results

3.1. Variation within taxa (aim 1)

The standard deviations of the natural logarithm of centroid size obtained for the hominine taxa indicate that maxillary size is significantly more variable in *Gorilla* and *Pan* than in *Homo* (SOM Tables S3 and S4). At the species level, *G. gorilla* and *G. beringei* are more variable in size than *H. sapiens*, *P. troglodytes*, and *P. paniscus*. Size variation does not differ significantly between the species and subspecies of *Pan* or *Gorilla*.

Procrustes distances within hominine taxa indicate that the maxillary shape of *Homo* and *Gorilla* is more variable than that of *Pan*, and at the species level, there is a statistically significant reduction in shape variation from *H. sapiens* to *G. gorilla* to *G. beringei* to *P. troglodytes* to *P. paniscus* (Fig. 2A; SOM Tables S5 and S6). At the subspecies level, *Gorilla gorilla diehli* is less variable in shape than *Gorilla gorilla gorilla*, *Gorilla beringei graueri* is less variable than *Gorilla beringei beringei*, and *P. t. verus* is less variable than *Pan troglodytes troglodytes* and *Pan troglodytes schweinfurthii*. Notably, *G. b. beringei* is more variable in shape than the species *G. beringei* overall, a pattern not seen for the other taxa.

3.2. Differences between taxa (aim 2)

Size differences between taxa, based on their respective natural logarithm of centroid size, are largest at the genus level and smallest between subspecies (SOM Tables S3 and S7) and will be discussed in more detail in sections 3.3–3.5.

The amount of difference in maxillary shape between hominine genera, species, and subspecies is compared in Figure 2B by plotting the distribution of Procrustes distances between all possible specimen pairs of different taxa. The maxilla is most distinct among the three genera, with the largest differences found between *Homo* and *Gorilla* and the smallest between *Pan* and *Gorilla*. At the species level, maxillae of *G. gorilla* and *G. beringei* differ more from each

other than those of *P. troglodytes* and *P. paniscus*. In fact, even the subspecies of *G. gorilla* and *G. beringei* differ, on average, more from each other than the species of *Pan*. Moreover, *G. b. beringei* and *G. b. graueri* differ almost as much from each other as do *G. gorilla* and *G. beringei*. Maxillary shape differences between the subspecies of *P. troglodytes* are the smallest among the groups considered.

The results of the PCAs are provided in SOM Table S8, listing those PCs that account for at least 5% of the total variance. The distribution of how much each PC contributes shows two distinct patterns. When comparing genera, the first principal component (PC1) accounts for almost two-thirds of all variance (63%), and only PC2 and PC3 contribute 5% or more. In contrast, for interspecific and intraspecific comparisons, PC1 contributes less than a third, and a further three or four PCs contribute 5% or more. For each comparison, we will only discuss those PCs where groups are visibly separated.

3.3. Differences between genera (aim 2a)

The mean centroid size is smallest for *Homo* and largest for *Gorilla* (SOM Table S3), and all differences are statistically significant (SOM Table S7). It is worth noting that even though *Homo* maxillae are on average smaller than those of *Pan*, this is only true for *P. troglodytes*. The mean maxillary centroid size for *H. sapiens* is significantly larger than that of *P. paniscus* ($t = 2.644, p = 0.009$). The shape differences between the three genera are statistically significant, and the effect sizes indicate that *Gorilla* is most different from *Homo* and least different from *Pan* (Table 4), as also shown by the Procrustes distances (Fig. 2B). A plot of PC1 and PC2 of the shape comparison shows this pattern, and without any overlap between *Homo*, *Pan*, and *Gorilla* (Fig. 3A). All three genera are differentiated on PC1, and *Homo* most strongly, whereas PC2 separates *Pan* from *Gorilla* and *Homo*. Mean shapes show that the maxilla of *Homo* is relatively wider, shorter, and substantially less prognathic than those of African apes (Fig. 3B–E). The subnasal segment is shorter, projects less anteriorly, and is considerably less prognathic in the midplane (Fig. 3E). The parabolic, rather than U-shaped, dental arcade typically shows smaller canine alveoli (Fig. 3C), and the palate is shorter and arched in the midplane, in contrast to the upward sloping palate of *Pan* and *Gorilla* (Fig. 3E). The incisive canal

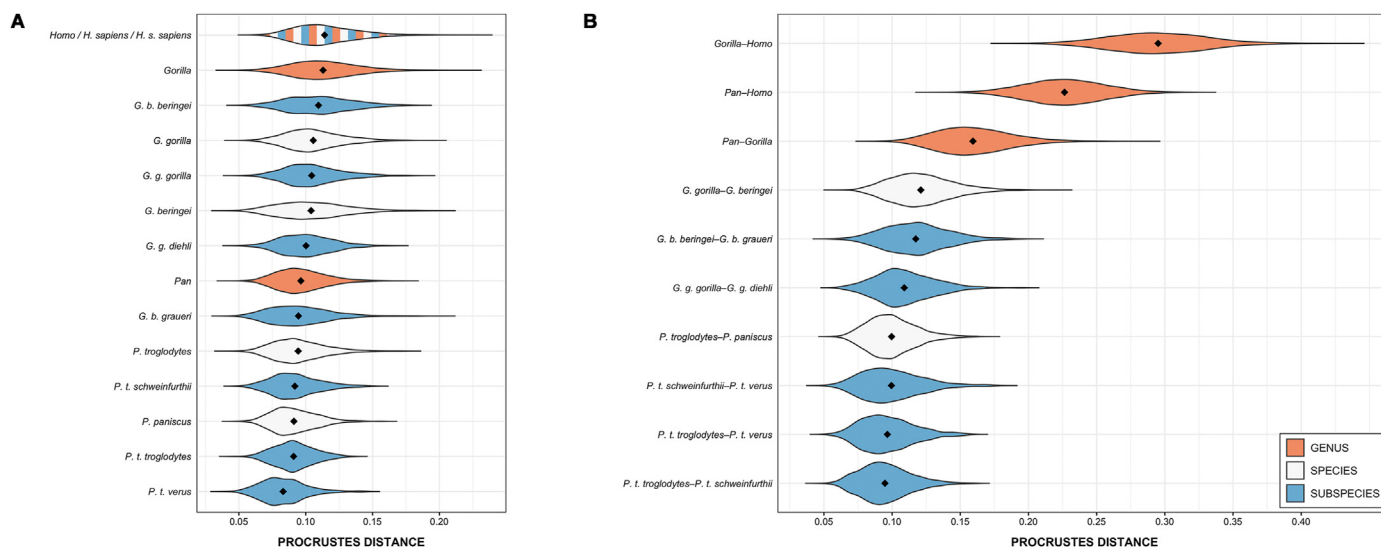


Figure 2. Variation within (A) and between (B) hominine genera (orange), species (white), and subspecies (blue). Comparisons are ordered from smallest to largest average Procrustes distance (black diamonds), highlighting that the degree of shape variation varies between taxa. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article).

Table 4

Results of one-way Procrustes analyses of variance comparing shape differences between groups and the mean (95% confidence intervals in parentheses) and variance (v) of the effect sizes (Cohen's d).

	SS	F-value	p-value ^a	Cohen's d	v
Genus					
<i>Pan</i> vs. <i>Gorilla</i>	1.19013	201.107	< 0.001	1.5743 (1.3263–1.8224)	0.0160
<i>Pan</i> vs. <i>Homo</i>	2.20569	394.439	< 0.001	2.6948 (2.3312–3.0583)	0.0344
<i>Gorilla</i> vs. <i>Homo</i>	4.64708	692.711	< 0.001	3.3433 (2.9742–3.7125)	0.0355
Species					
<i>P. troglodytes</i> vs. <i>P. paniscus</i>	0.04472	9.89739	< 0.001	0.5662 (0.2071–0.9252)	0.0336
<i>G. gorilla</i> vs. <i>G. beringei</i>	0.18717	32.4958	< 0.001	0.8083 (0.5193–1.0973)	0.0217
Subspecies					
<i>P. t. troglodytes</i> vs. <i>P. t. schweinfurthii</i>	0.01489	3.45234	< 0.001	0.4722 (-0.0328)–(0.9772)	0.0664
<i>P. t. troglodytes</i> vs. <i>P. t. verus</i>	0.03030	7.70369	< 0.001	0.7363 (0.1991–1.2735)	0.0751
<i>P. t. schweinfurthii</i> vs. <i>P. t. verus</i>	0.03940	9.80335	< 0.001	0.8182 (0.2852–1.3512)	0.0740
<i>G. g. gorilla</i> vs. <i>G. g. diehli</i>	0.02972	5.33906	< 0.001	0.5602 (0.0785–1.0420)	0.0604
<i>G. b. beringei</i> vs. <i>G. b. graueri</i>	0.06844	13.4464	< 0.001	0.8454 (0.3788–1.3121)	0.0567
Sexual dimorphism					
<i>P. troglodytes</i>	0.01936	4.33049	< 0.001	0.4388 (0.0206–0.8571)	0.0455
<i>P. paniscus</i>	0.01653	4.11465	< 0.001	0.5951 (0.0076–1.1826)	0.0898
<i>G. gorilla</i>	0.07248	14.2034	< 0.001	0.7672 (0.3540–1.1804)	0.0444
<i>G. beringei</i>	0.10368	21.9026	< 0.001	0.9369 (0.5238–1.3500)	0.0444
<i>H. sapiens</i>	0.01533	2.29098	0.016	0.3520 (-0.1071)–(0.8111)	0.0549
Younger vs. older adult					
<i>P. troglodytes</i>	0.00873	1.90244	0.040	0.3111 (-0.1333)–(0.7555)	0.0514
<i>P. paniscus</i>	0.00773	1.85713	0.040	0.4286 (-0.1940)–(1.0513)	0.1009
<i>G. gorilla</i>	0.01184	2.06408	0.040	0.3010 (-0.1118)–(0.7139)	0.0444
<i>G. beringei</i>	0.02243	4.03892	0.009	0.4015 (0.0060–0.7970)	0.0407
<i>H. sapiens</i>	0.01786	2.68565	0.014	0.3596 (-0.0737)–(0.7930)	0.0489
Late juvenile vs. adult					
<i>P. troglodytes</i>	0.02209	4.72510	< 0.001	0.6943 (0.0610–1.3276)	0.1044
<i>P. paniscus</i>	0.03929	9.60753	< 0.001	0.9438 (0.3239–1.5636)	0.1000
<i>G. gorilla</i>	0.03547	6.21578	< 0.001	0.9754 (0.1973–1.7535)	0.1576
<i>G. beringei</i>	0.01377	2.43802	0.017	0.7154 (-0.1877)–(1.6185)	0.2123
<i>H. sapiens</i>	0.03440	5.27004	< 0.001	0.6228 (0.0845–1.1612)	0.0754

^a Significant p-values are highlighted in bold ($p < 0.05$).

is longer in *Homo*. Among the African apes, *Gorilla* has relatively narrower, higher, and longer maxillae than *Pan* (Fig. 3B–E). Diastemata, canine alveoli, and postcanine alveoli are larger in *Gorilla*, while *Pan* has larger incisive alveoli (Fig. 3C). The palate is longer and slightly deeper in *Gorilla* (Fig. 3E).

3.4. Differences between species (aim 2b)

Pan troglodytes* and *Pan paniscus *Pan paniscus* mean centroid size is significantly smaller than that of *P. troglodytes* (SOM Tables S3 and S7). Plots of the first three PCs describing maxillary shape show substantial overlap between *P. troglodytes* and *P. paniscus* specimens (Fig. 4A), but their shape is nevertheless significantly different (Table 4). On average, *P. paniscus* has lower scores on PC2 and higher scores on PC3 (Fig. 4A). There is no separation on PC1 between the two species. Maxillae of *P. paniscus* are relatively wider and shorter than those of *P. troglodytes* (Fig. 4B–E). The anterior dental arcade projects less anteriorly and is superiorly rotated, with smaller canine alveoli and diastemata (Fig. 4C–E). In contrast, the postcanine tooth row is longer than in *P. troglodytes*. The subnasal segment of *P. paniscus* projects less anteriorly and is less prognathic in the midplane, and there is less overlap with the palate, which is shorter, shallower, and slopes less superiorly than in *P. troglodytes* (Fig. 4E). The infraorbital area is located more posteriorly on the face of *P. paniscus* and is bilaterally and inferosuperiorly expanded (Fig. 4B, D).

Gorilla gorilla* and *Gorilla beringei The maxilla of *G. beringei* is significantly larger than that of *G. gorilla* (SOM Tables S3 and S7). Their shapes also differ significantly, more so than the shape difference between *Pan* species, as indicated by the effect sizes (Table 4) and the Procrustes distances (Fig. 2B). Plots of the first three maxillary shape PCs indeed show less species overlap for

Gorilla (Fig. 5A) than for *Pan* (Fig. 4A). *Gorilla beringei* has on average lower scores on PC1 and higher scores on PC2 and PC3 (Fig. 5A). Maxillae of *G. beringei* are relatively narrower, lower, longer, and substantially more prognathic than those of *G. gorilla* (Fig. 5B–E). The infraorbital area is located more posteriorly on the face, especially the inferior orbital margin, which is also located more medioinferiorly in *G. beringei* (Fig. 5B, D). The subnasal segment is longer, more prognathic, and projects more anteriorly in the midplane (Fig. 5E), resulting in the nasal sill being located more superiorly on the face (Fig. 5B). The incisive canal is longer in *G. beringei*, with more overlap between the midsagittal alveolar process and palate (Fig. 5E). The latter is substantially longer and slopes less superiorly in *G. beringei*, with the anterior part deeper, but the posterior end shallower than in *G. gorilla*. The dental arcade is longer and narrower in *G. beringei*, but the canine alveoli and diastemata are nevertheless slightly smaller (Fig. 5C).

3.5. Differences between subspecies (aim 2c)

Pan troglodytes troglodytes*, *Pan troglodytes schweinfurthii*, and *Pan troglodytes verus The observed mean centroid size is largest in *P. t. schweinfurthii* and smallest in *P. t. verus* (SOM Table S3), but none of these differences are statistically significant (SOM Table S7). On the other hand, shape differences between all three subspecies are significant (Table 4), although plots of the first three PCs show substantial overlap (Fig. 6A). On average, *P. t. troglodytes* has higher scores on PC1 and lower scores on PC2 and PC3, *P. t. schweinfurthii* has higher scores on PC1, PC2, and PC3, and *P. t. verus* has lower scores on PC1 and higher scores on PC3 (Fig. 6A). The effect sizes (Table 4) and Procrustes distances (Fig. 2B) suggest that *P. t. verus* has the most distinct morphology of the three subspecies, but the

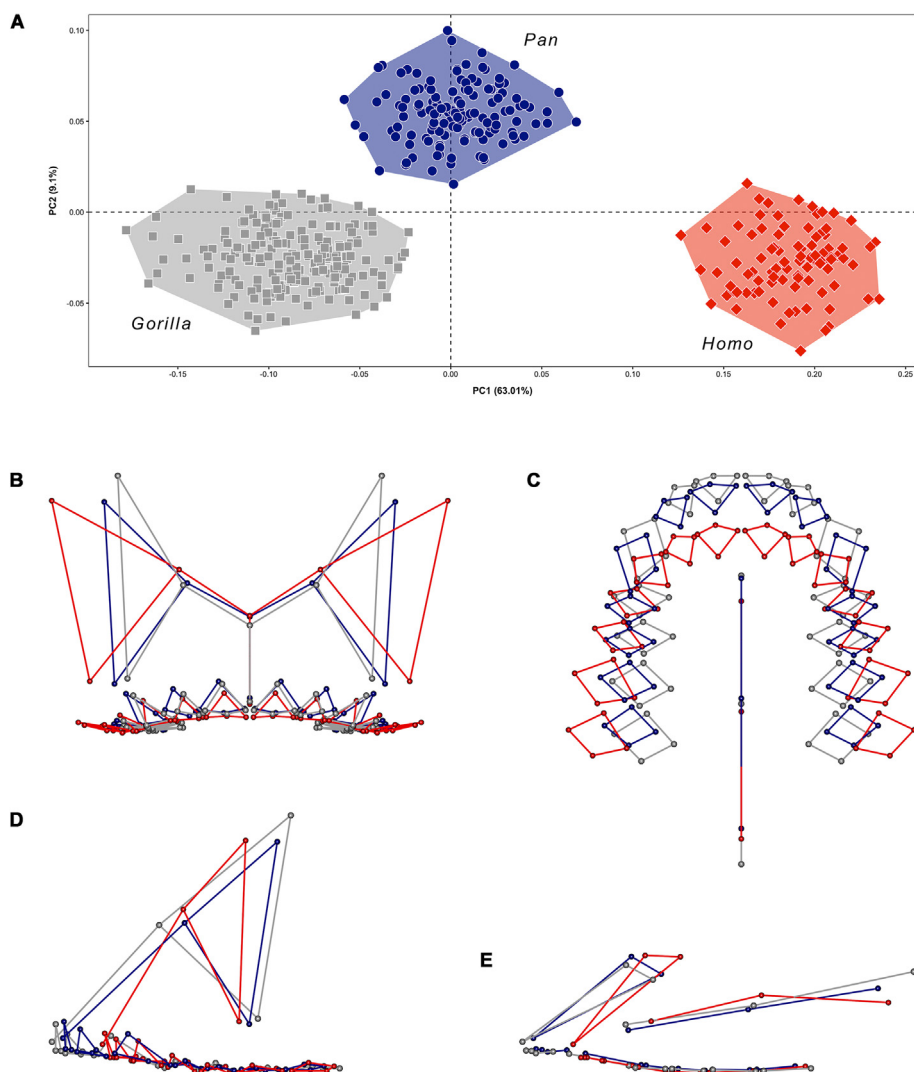


Figure 3. Plot of PC1 and PC2 (A) showing no overlap in maxillary shape among adult *Pan* (navy circles), *Gorilla* (gray squares), and *Homo* (red diamonds) and relative shape differences between their mean morphology on the first two PCs in frontal (B), occlusal (C), lateral (D), and midplane (E) view. Shapes are rotated to minimize the distance between postcanine alveolar landmarks. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article).

confidence intervals and variance of the effect sizes are large, indicating that this conclusion is tentative (Table 4). Mean shape comparisons of the three subspecies do show *P. t. verus* as most distinct (Fig. 6B–E), with a relatively shorter and less prognathic maxilla, overall and subnasally, associated with a more antero-inferior position of the nasal aperture and infraorbital area (Fig. 6B, D, E). The incisive canal is shorter, and there is considerably less overlap between the midsagittal alveolar process and palate (Fig. 6E). The latter is shorter and anteriorly shallower, with the midline palatal surface inferiorly convex in *P. t. verus* and slightly concave in *P. t. schweinfurthii* and *P. t. troglodytes*. The anterior dental arcade is rotated superiorly in *P. t. verus* (Fig. 6D, E), and the posterior tooth row is somewhat longer (Fig. 6C). Although more similar, *P. t. troglodytes* and *P. t. schweinfurthii* still differ in certain aspects of their shape, with the maxillae of the latter being relatively higher, longer, inferiorly narrower, and less prognathic (Fig. 6B–E). The subnasal segment of *P. t. schweinfurthii* projects more anteriorly and is less prognathic in the midplane (Fig. 6E), in association with a more anteriorly projecting dental arcade with larger canine alveoli, but smaller diastemata than in *P. t. troglodytes* (Fig. 6C). The infraorbital area is located more superiorly on the

face of *P. t. schweinfurthii* and is anteroposteriorly expanded (Fig. 6B, D). The palate is longer and somewhat deeper than that of *P. t. troglodytes* (Fig. 6E).

Gorilla gorilla gorilla* and *Gorilla gorilla diehli *Gorilla g. diehli* mean centroid size is significantly smaller than that of *G. g. gorilla* (SOM Tables S3 and S7), and their maxillary shape differs significantly (Table 4), but with substantial overlap on the first two PCs (Fig. 7A). On average, *G. g. diehli* has lower scores on PC1 and PC2. Maxillae of *G. g. diehli* are relatively lower, superiorly narrower, and anteriorly longer than those of *G. g. gorilla* (Fig. 7B–E). The anterior dental arcade projects more anteriorly with somewhat larger diastemata (Fig. 7C, D, E), combined with a substantially shorter and anteriorly projecting subnasal segment in the midplane (Fig. 7E). As a result, the nasal aperture and infraorbital area are located more antero-inferiorly on the face of *G. g. diehli* (Fig. 7B, D, E). The incisive canal is substantially shorter, with a smaller overlap between the midsagittal alveolar process and palate, which is positioned somewhat more anteriorly relative to the postcanine tooth row (Fig. 7E). The midline palatal surface is inferiorly slightly convex in *G. g. diehli*, and flat in *G. g. gorilla*.

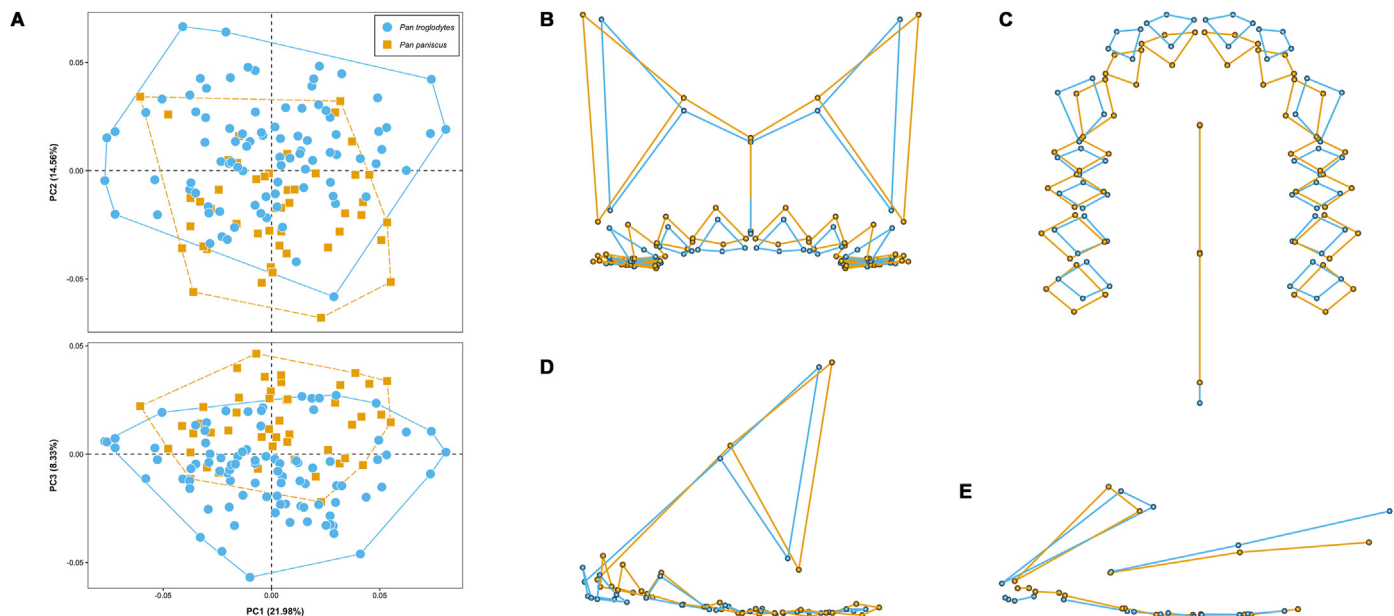


Figure 4. Plots of PC1, PC2, and PC3 (A) showing substantial overlap in maxillary shape of adult *P. troglodytes* (blue circles) and *P. paniscus* (yellow squares) and relative shape differences between their mean morphology (± 1 sd) on the second and third PCs in frontal (B), occlusal (C), lateral (D), and midplane (E) view. Shapes are rotated to minimize the distance between postcanine alveolar landmarks. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article).

Gorilla beringei beringei and *Gorilla beringei graueri* The observed mean centroid size is smaller in *G. b. graueri* than in *G. b. beringei* (SOM Table S3), but the size difference is not statistically significant (SOM Table S7). In contrast, their maxillary shape differs significantly (Table 4), even though there is overlap on the first two PCs (Fig. 8A). *Gorilla b. graueri* has on average higher scores on PC1 and lower scores on PC2. Maxillae of *G. b. graueri* are relatively wider and particularly shorter anteriorly than those of

G. b. beringei (Fig. 8B–E). The subnasal segment and anterior dental arcade project substantially less anteriorly, with smaller canine alveoli and diastemata (Fig. 8C, E), associated with a posterior position of the nasal aperture and infraorbital area on the face of *G. b. graueri* (Fig. 8D, E). The palate is positioned somewhat more posteriorly relative to the postcanine tooth row, and the midline palatal surface is inferiorly concave in *G. b. graueri* but convex in *G. b. beringei* (Fig. 8E).

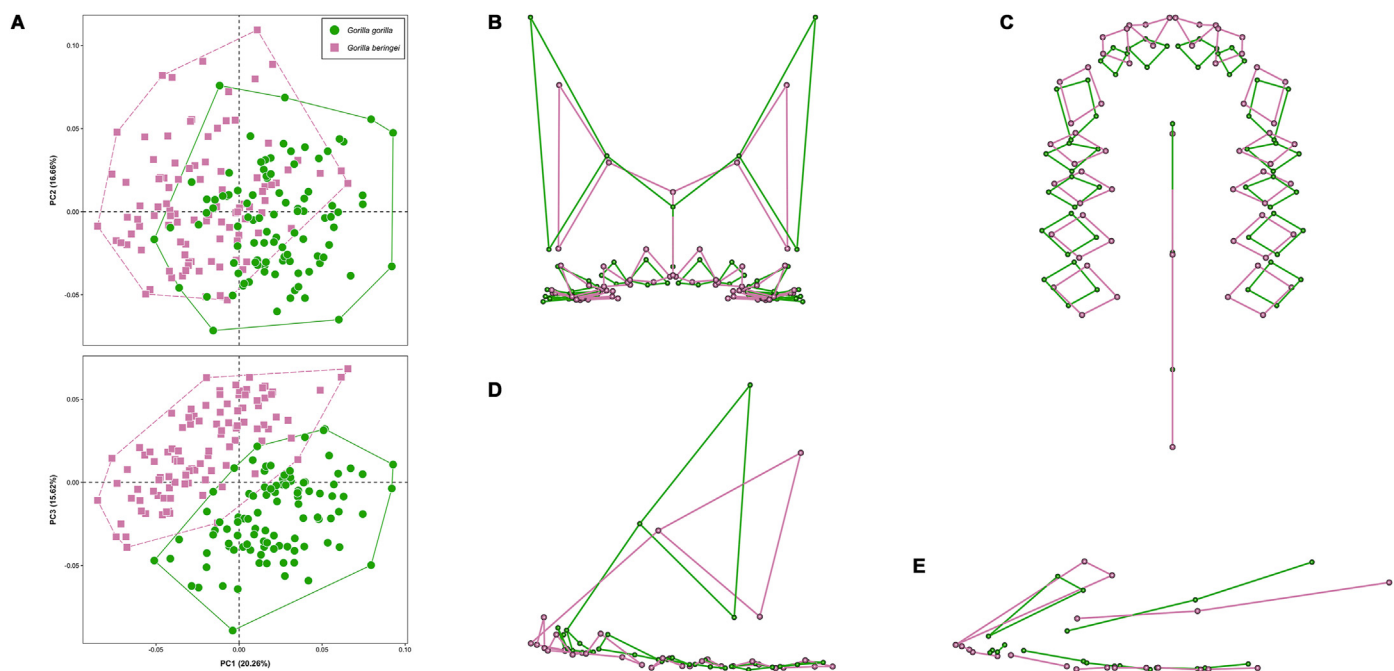


Figure 5. Plots of PC1, PC2, and PC3 (A) showing overlap in maxillary shape of adult *G. gorilla* (green circles) and *G. beringei* (pink squares) and relative shape differences between their mean morphology (± 1 sd) on the first three PCs in frontal (B), occlusal (C), lateral (D), and midplane (E) view. Shapes are rotated to minimize the distance between postcanine alveolar landmarks. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article).

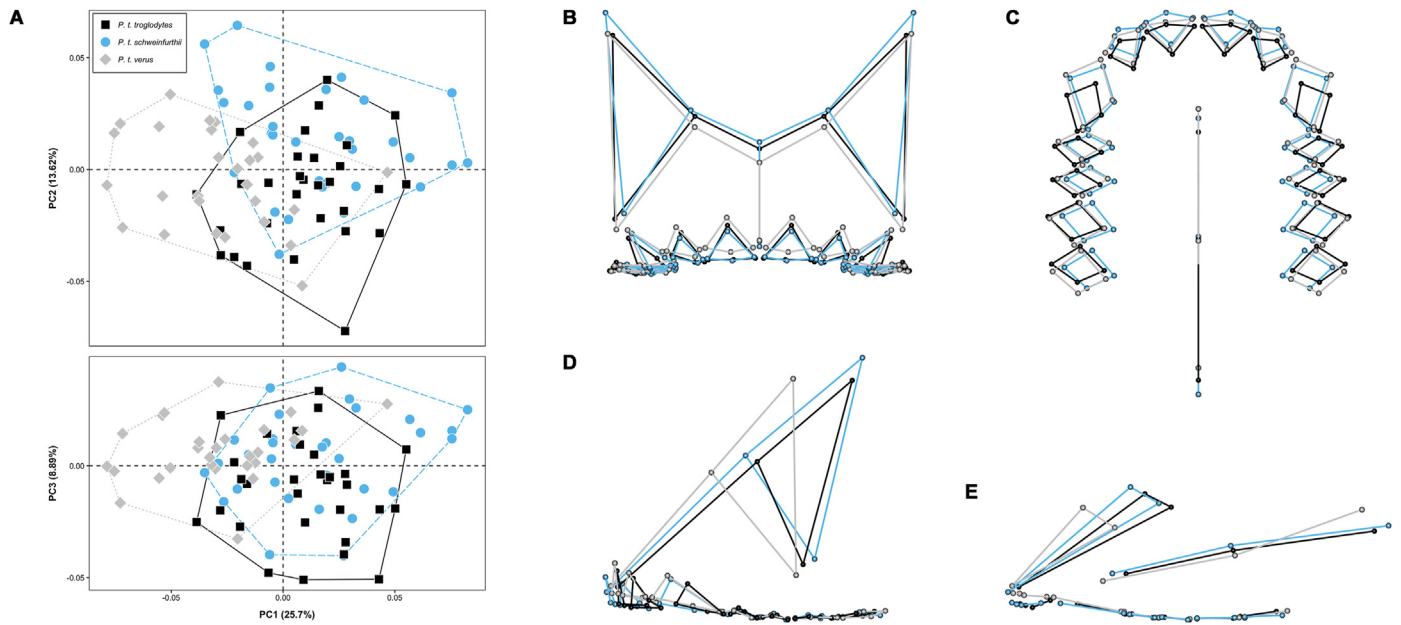


Figure 6. Plots of PC1, PC2, and PC3 (A) showing substantial overlap in maxillary shape of adult *P. t. troglodytes* (black squares), *P. t. schweinfurthii* (blue circles), and *P. t. verus* (gray diamonds) and relative shape differences between their mean morphology (± 1 sd) on the first three PCs in frontal (B), occlusal (C), lateral (D), and midplane (E) view. Shapes are rotated to minimize the distance between postcanine alveolar landmarks. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article).

3.6. Sexual dimorphism (aim 3)

Size differences between sexes of each hominine species are shown in SOM Table S9. Mean centroid size is always larger in males than in females, with the differences being most pronounced in *Gorilla* species, and not statistically significant for *P. paniscus*. Maxillary shape differs significantly between the sexes of all hominine species, most strongly in *Gorilla* species and the least in *H. sapiens* (Table 4). However, the latter may not differ from the *Pan* species in shape dimorphism, given the large variance and

confidence intervals of the effect sizes (Table 4). In shape space, the sexes overlap on the first two PCs to a variable degree, most clearly for *P. troglodytes*, *P. paniscus*, and *H. sapiens* (Fig. 9A, B, E) and the least for *G. gorilla* and *G. beringei* (Fig. 9C, D).

In *Pan*, male maxillae are relatively lower, longer, and inferiorly narrower than those of females (Fig. 10A–H). The male maxilla is slightly more prognathic in *P. troglodytes* (Fig. 10C), but not in *P. paniscus* (Fig. 10G). In both species, the anterior dental arcade projects more anteriorly in males, with larger canine alveoli (Fig. 10B, C, F, G), in association with an anteriorly projecting

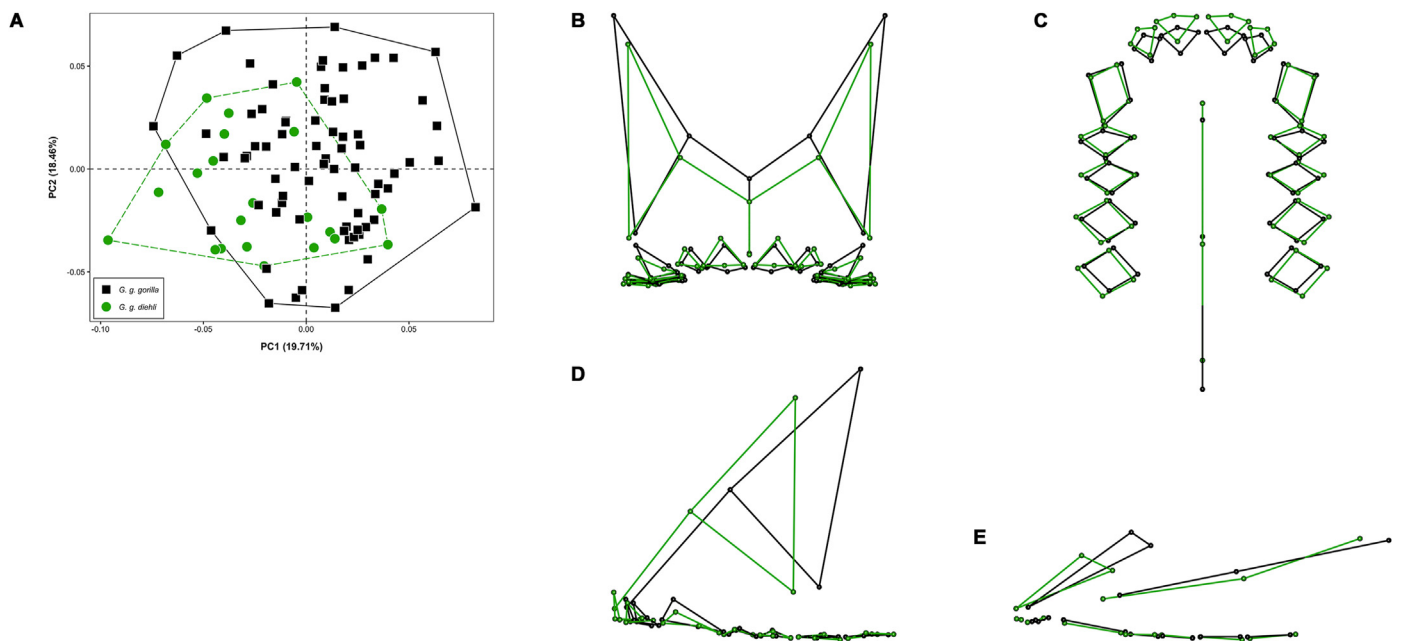


Figure 7. Plot of PC1 and PC2 (A) showing substantial overlap in maxillary shape of adult *G. g. gorilla* (black squares) and *G. g. diehli* (green circles), and relative shape differences between their mean morphology (± 1 sd) on the first two PCs in frontal (B), occlusal (C), lateral (D), and midplane (E) view. Shapes are rotated to minimize the distance between postcanine alveolar landmarks. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article).

subnasal segment in the midplane (Fig. 10D, H). As a result, the nasal aperture and infraorbital area are located more anteriorly on the face of males (Fig. 10C, D, G, H). The subnasal segment of *P. troglodytes* males is also shorter, leading to the nasal aperture and infraorbital area being located more inferiorly on the face (Fig. 10A, C, D). The incisive canal of males in both species is shorter than in females, and the palate is positioned slightly more anteriorly relative to the postcanine tooth row (Fig. 10D, H). The palate is somewhat shallower in *P. troglodytes* males (Fig. 10D) but slightly deeper in *P. paniscus* males (Fig. 10H).

In *Gorilla*, male maxillae are relatively higher, narrower, and longer than those of females (Fig. 10I–P). The subnasal segment is more prognathic in *G. gorilla* males (Fig. 10K, L), while there is no difference in prognathism between *G. beringei* males and females (Fig. 10O, P). In both species, males have a longer and anteriorly projecting subnasal segment in the midplane (Fig. 10L, P), associated with a more posterosuperior position of the nasal aperture and infraorbital area (Fig. 10I, K, L, M, O, P). The incisive canal is longer in males, with a larger overlap between the midsagittal alveolar process and palate. The latter is notably longer and posteriorly projecting in males (Fig. 10L, P). Relative canine alveolar dimensions and diastemata are considerably larger in males, whereas the relative postcanine alveolar dimensions are substantially smaller than in females (Fig. 10J, N).

Compared with females, male *H. sapiens* have a maxilla that is relatively higher so that the nasal aperture and inferior orbital margin are located more superiorly, with the latter also positioned more laterally (Fig. 10Q, S, T). In males, the subnasal segment is longer and substantially less prognathic, the incisive canal longer, and the palate considerably deeper in the midplane (Fig. 10T). Minimal differences are observed in dental arcade shape between the sexes (Fig. 10R).

3.7. Younger and older adults (aim 4)

Younger and older adults do not differ significantly in average centroid size (SOM Table S10). Shape differences do show statistically significant differences (Table 4), but in shape space, the two

groups of all species largely overlap (Fig. 11). Mean shapes are very similar, without evidence for dental wear-related shape changes of the dental arcade (SOM Fig. S1).

3.8. Late juveniles and adults (aim 5)

With the sexes combined, adult mean centroid size is significantly larger than that of late juveniles in all species except *H. sapiens*, with the greatest differences seen in *G. gorilla* and *G. beringei* (SOM Table S11). This trend is upheld when comparing the two age groups separately for males and females, but only the differences observed for male *Gorilla* species are statistically significant.

Maxillary shape differs significantly between late juveniles and adults of all species when sexes are combined (Table 4). However, when males and females are compared separately, this difference is not significant for both sexes of *G. beringei* and male *H. sapiens* (SOM Table S12). Effect sizes are inconclusive, as small sample sizes result in large confidence intervals and variance (Table 4; SOM Table S12). Late juveniles tend to cluster along one side of PC1 but still fall within the range of adults on this axis, except those of *P. paniscus* which partially fall outside the adult variation (Fig. 11). Late juveniles and adults are not separated along PC2 (not shown). On PC3, late juveniles of African apes tend to have lower scores than adults, although still showing substantial overlap, while *H. sapiens* late juveniles and adults cannot be visibly separated along this axis. The PC1 and PC3 jointly provide the best separation of the two age groups, both with the sexes combined (Fig. 11A–C) and for males and females separately (SOM Fig. S2).

With late juveniles represented by small samples, we only consider the main trends suggested by the mean shape comparisons (Fig. 12). In all species, the adult postcanine tooth row is relatively shorter than in late juveniles, particularly among the African apes (Fig. 12B, F, J, N). Moreover, in all species, the adult maxilla is relatively larger superior to the dental arcade (Fig. 12). Adults show less anterior projection of the snout in *G. gorilla* (Fig. 12J, K, L) and *G. beringei* (Fig. 12N, O, P), and to a lesser extent in

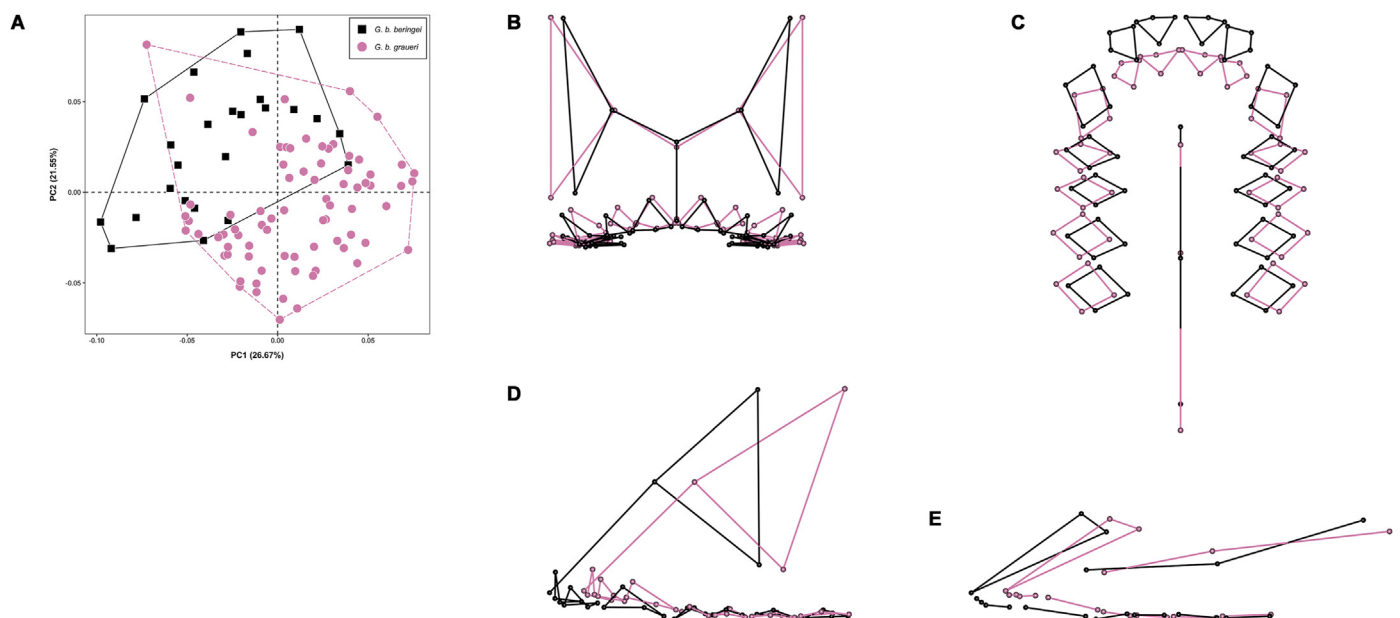


Figure 8. Plot of PC1 and PC2 (A) showing overlap in maxillary shape of adult *G. b. beringei* (black squares) and *G. b. graueri* (pink circles) and relative shape differences between their mean morphology (± 1 sd) on the first two PCs in frontal (B), occlusal (C), lateral (D), and midplane (E) view. Shapes are rotated to minimize the distance between postcanine alveolar landmarks. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article).

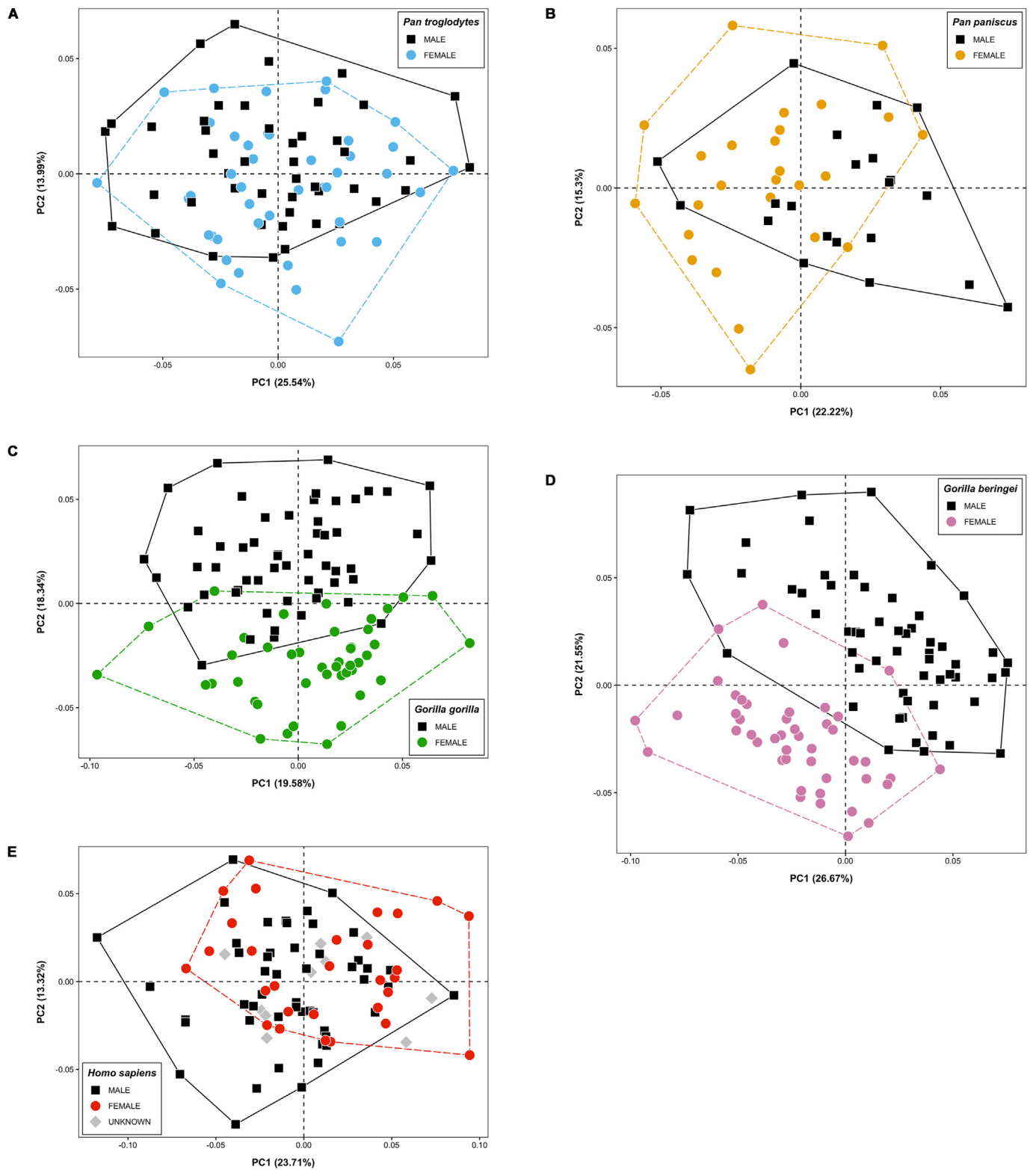


Figure 9. Plots of PC1 and PC2 describing sexual dimorphism in the maxillary shape of adult males (black squares) and females (colored circles) for *P. troglodytes* (blue; A), *P. paniscus* (yellow; B), *G. gorilla* (green; C), *G. beringei* (pink; D), and *H. sapiens* (red; E). The separation between males and females is most distinct for the *Gorilla* species. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article).

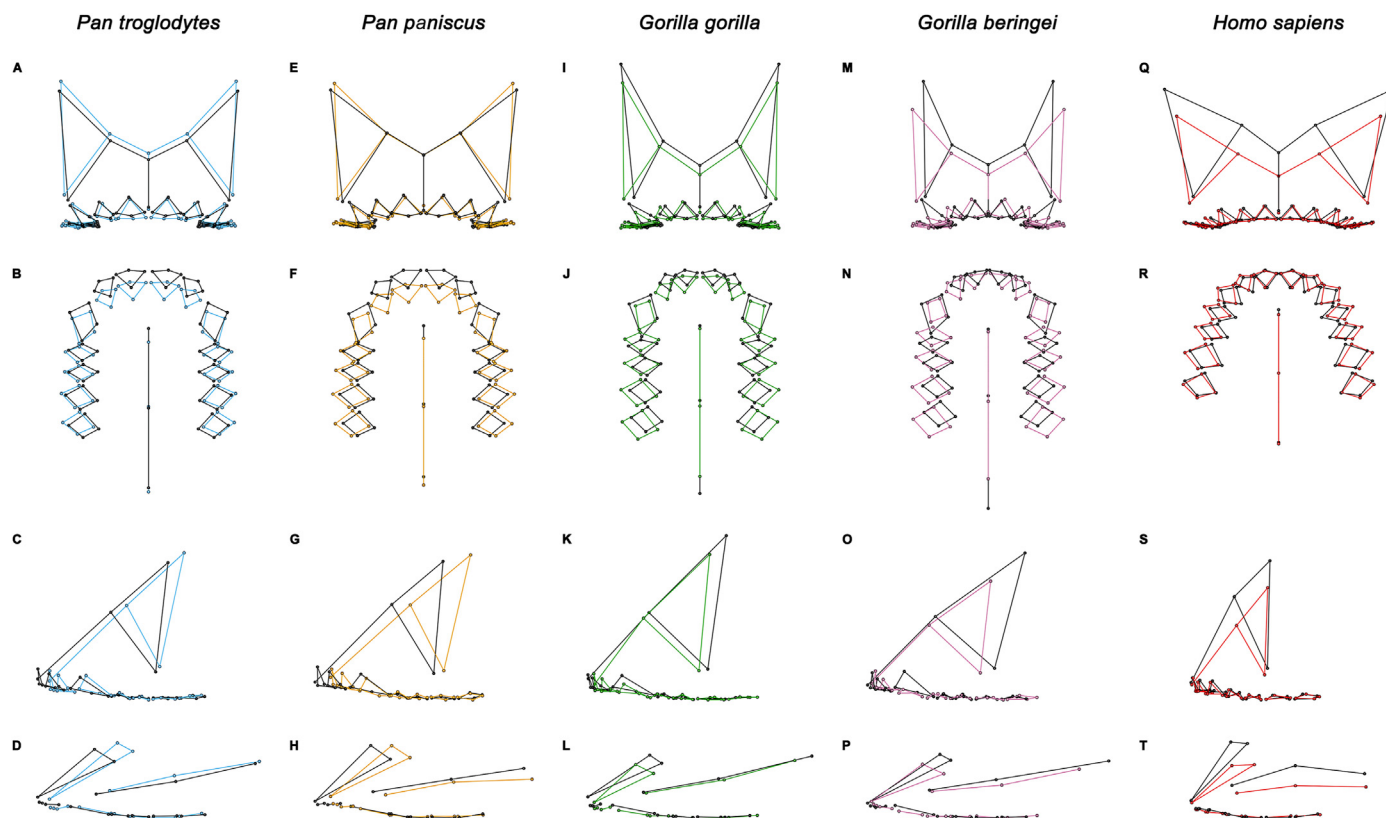


Figure 10. Relative shape differences on PC1 and PC2 between mean adult male (black) and female (color) maxillary morphology (± 1 sd) of *P. troglodytes* (blue; A–D), *P. paniscus* (yellow; E–H), *G. beringei* (pink; M–P), and *H. sapiens* (red; Q–T). For *G. gorilla* (green; I–L), mean shape differences (± 1 sd) on PC2 are shown. From top to bottom: frontal, occlusal, lateral, and midplane view. Shapes are rotated to minimize the distance between postcanine alveolar landmarks. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article).

H. sapiens (Fig. 12R, S, T) and *P. paniscus* (Fig. 12F, G, H). In *P. paniscus*, the anterior dental arcade and midline alveolar process are rotated inferiorly (Fig. 12G, H).

3.9. Allometry (aim 6)

Among the African apes, maxillary size is significantly correlated with shape, but it explains only 5–17% of the total shape variation (SOM Table S13). The differences between the predicted maxillary shapes for the smallest and largest centroid size found in each species of African ape (SOM Fig. S3) are similar to those observed between males and females (Fig. 10A–P). The size-shape regression is not significant for *H. sapiens* (SOM Table S13).

Comparisons of the PCAs of the isometrically and allometrically adjusted shapes reveal that taxa are more distinct after allometric adjustment (Fig. 13). The increased shape differentiation is the consequence of both reduced shape variation shown by all taxa (except intragenerically in *Pan*; SOM Table S14) and increased shape differences between all three pairs of taxa that are compared (SOM Table S15).

Mean shape differences between adult *Pan* and *Gorilla* for the isometrically and allometrically adjusted shapes are shown in SOM Figure S4. After allometric adjustment, *Pan* and *Gorilla* maxillae are more similar in relative width at the takeoff of the zygomatic roots (SOM Fig. S4A, E), in the projection of the anterior dental arcade (SOM Fig. S4B, F), in the midplane length of the palate (SOM Fig. S4D, H), and in the width of the incisor chord (SOM Fig. S4B, F). However, the canine and postcanine alveoli are more distinctive, with the former being relatively smaller and the latter mesiodistally longer in *Gorilla* (SOM Fig. S4B, F).

Mean shape differences between *P. troglodytes* and *P. paniscus* show that allometric adjustment has little impact, except for slightly more projection of the anterior dental arcade and subnasal segment in *P. paniscus*, and canine alveoli that are somewhat narrower buccolingually in *P. troglodytes* (SOM Fig. S5). Equivalent comparisons between *G. gorilla* and *G. beringei* show no differences after allometric adjustment (SOM Fig. S6).

4. Discussion

In this study, we examined the size and shape of the maxilla among extant hominines, exploring differences and the degree of variation at the genus, species, and subspecies level, as well as sexual dimorphism and age-related trends from late juvenile to full adulthood. The key observations are that 1) the maxillae of all extant hominine species and subspecies show statistically significant differences, but complete separation in shape is only seen at the genus level; 2) the degree of variation is not consistent between genera, with subspecies of *Gorilla* being more different from each other than are species of *Pan*; 3) the pattern of sexual shape dimorphism is different in *Pan*, *Gorilla*, and *Homo*, often showing opposite trends; and 4) differentiation between maxillary shapes is increased after adjustment for static intraspecific allometry.

4.1. Differences and variation

An extensive body of literature has considered morphological differences between modern humans and African apes as the latter became gradually known to Western science, predominantly from the 19th century onward (e.g., Owen, 1835; Savage and Wyman,

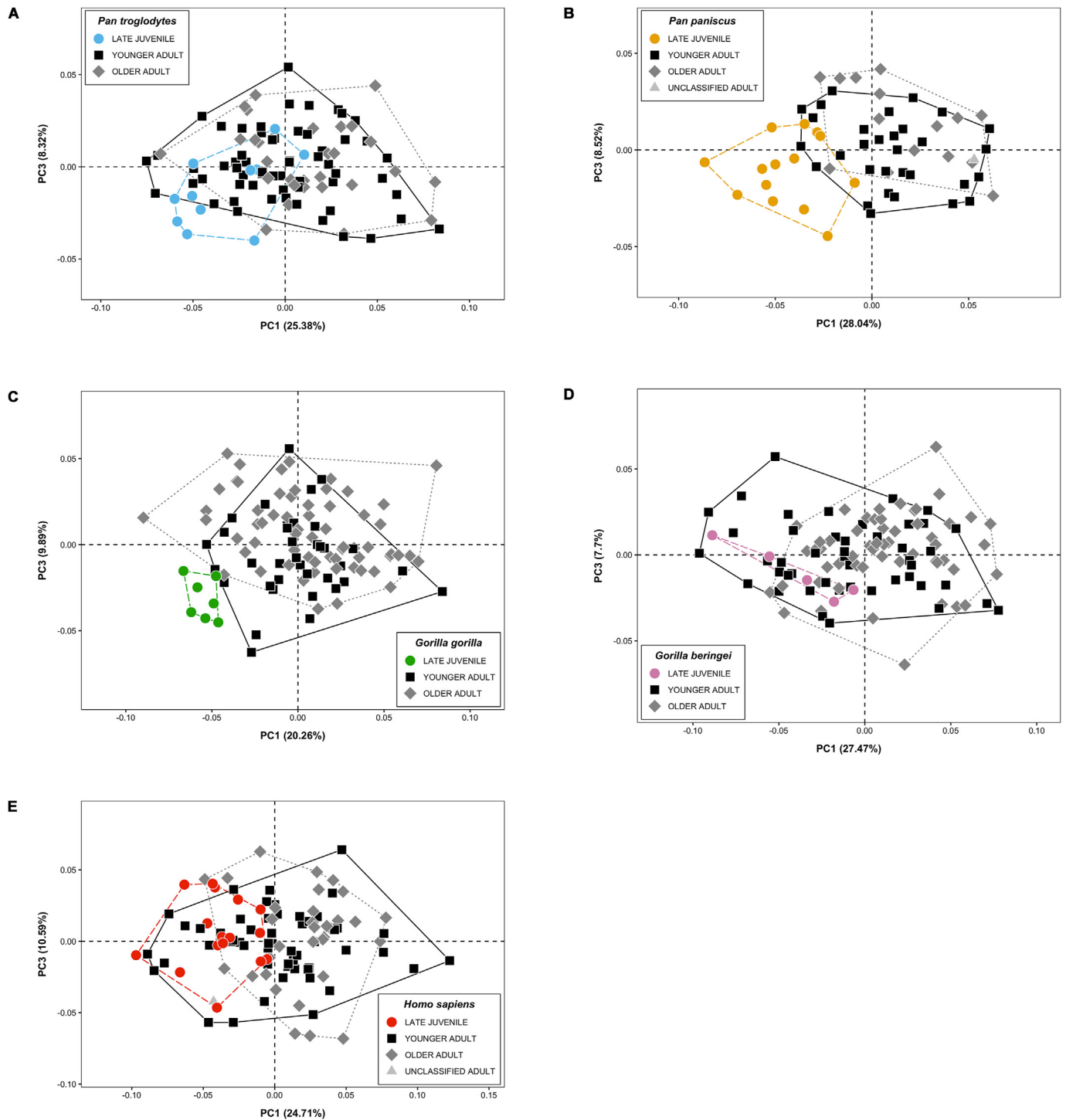


Figure 11. Plots of PC1 and PC3 describing age differences in the maxillary shape of late juveniles (colored circles), younger adults (black squares), and older adults (gray diamonds) for *P. troglodytes* (blue; A), *P. paniscus* (yellow; B), *G. gorilla* (green; C), *G. beringei* (pink; D), and *H. sapiens* (red; E). Late juveniles tend to cluster at the extreme end of the adult variation. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article).

1847; Matschie, 1903; Schwarz, 1929). The main craniofacial characteristics of *Homo*, *Pan*, and *Gorilla* are well established and typically reviewed in textbooks (e.g., Aiello and Dean, 1990; Ankel-Simons, 2007; Fleagle, 2013; Zihlman and Underwood, 2019). Prominent features that relate to maxillary size and shape are shown by our results, including differences in facial prognathism, dental arcade shape, and the absolute and relative size of incisor, canine, and postcanine alveoli. Our analyses also confirm

previously reported differences between sister species, including the absolutely smaller facial dimensions of *P. paniscus* than those of *P. troglodytes* (Schwarz, 1929; Coolidge, 1933; Heintz, 1966; Hill, 1969; Schultz, 1969; Cramer, 1977; McHenry and Corruccini, 1981; Jungers and Susman, 1984; Shea, 1984; Groves, 1986, 2001; Shea et al., 1993; Guy et al., 2003; Groves et al., 1992; Williams et al., 2003), and the longer and narrower palate of *G. beringei* than that of *G. gorilla* (Matschie, 1903, 1904a; Elliot, 1912; Lönnberg, 1917;

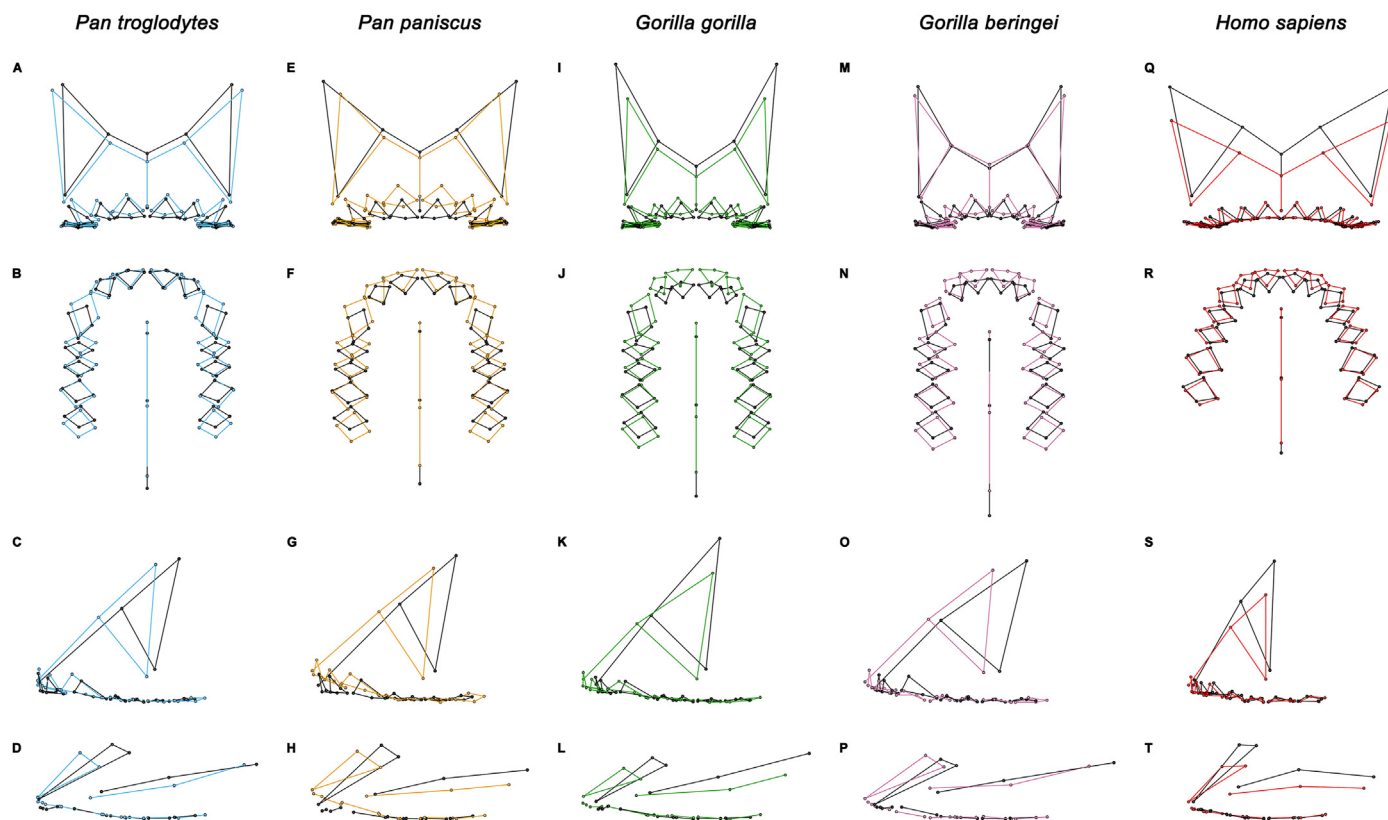


Figure 12. Relative shape differences on PC1 and PC3 between mean late juvenile (color) and adult (black) maxillary morphology (± 1 sd) of *P. troglodytes* (blue; A–D), *P. paniscus* (yellow; E–H), *G. gorilla* (green; I–L), and *G. beringei* (pink; M–P). For *H. sapiens* (red; Q–T), mean shape differences (± 1 sd) on PC1 are shown. From top to bottom: frontal, occlusal, lateral, and midplane view. Shapes are rotated to minimize the distance between postcanine alveolar landmarks. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article).

Coolidge, 1929; Haddow and Ross, 1951; Groves, 1970a, b, 2003; Uchida, 1992, 1996; Stumpf et al., 2003; Taylor, 2003).

With respect to differences at the subspecies level, our finding that the maxillary morphology of *P. t. verus* is most distinct among the three chimpanzee subspecies confirms the pattern found previously for the skull more broadly (Shea et al., 1993; Braga, 1995a, b, 1998; Uchida, 1996; Taylor and Groves, 2003; Guy et al., 2003; Lockwood et al., 2004; Pilbrow, 2006a, b, 2007; Lawrence and Robinson, 2020). *Gorilla g. diehli* has been described as most distinct from *G. g. gorilla* in the nuchal region, but notably less so in the face (Stumpf et al., 2003). The latter is consistent with our results that the maxillary morphology of the two subspecies largely overlap, although with differences that are nevertheless statistically significant. For the mandible, Taylor and Groves (2003) found no differences between *G. g. diehli* and *G. g. gorilla*, and a similar result might have been expected for the maxilla, given their close functional integration and morphological covariation (Stelzer et al., 2017). However, of the maxillary differences found by us (Fig. 7), the anterior dental arcade shape was not assessed for the mandible by Taylor and Groves (2003), and the relative position of the infraorbital area is less likely to covary with mandibular morphology.

Overall, it proved difficult to make more detailed comparisons with observations reported in many past studies because methods or sample composition are not compatible. Older analyses often consider differences in absolute dimensions rather than shape (e.g., Matschie, 1903, 1904a, b; Rotschild, 1904; Elliot, 1912; Duckworth, 1915; Lönnberg, 1917; Sonntag 1924; Coolidge, 1929, 1933; Schwarz, 1929, 1934; Schultz, 1934) and score qualitative characteristics (e.g., McCollum et al., 1993; McCollum, 1995; McCollum

and Ward, 1997). Moreover, key maxillary features have been defined in multiple ways, with prognathism as a prominent example. Both the facial or subnasal landmarks tend to vary, as does the cranial line segment used as reference to obtain the angle of prognathism (e.g., Coolidge, 1933; Schultz, 1969; Bilsborough, 1971; Cramer, 1977; Spoor et al., 2005). Dental size is mostly examined based on crown measurements (e.g., Ashton and Zuckerman, 1950; Shuman and Brace, 1954; Booth, 1971; Mahler, 1973; Johanson, 1974a, b; Shea, 1983c; Kinzey, 1984; Uchida, 1992, 1996, 1998; Pilbrow, 2003, 2006b, 2007, 2010; Skinner et al., 2009), while a few studies, including this one, analyze alveolar dimensions, reflecting spatial demands and constraints of both crown and root sizes (Spoor et al., 2015; Stelzer et al., 2017). Lastly, changes in hominine taxonomy over the last decades complicate comparisons, as many studies examining *Gorilla* used the prevalent nonspecific interpretation at that time (e.g., Groves, 1967, 1970a, b, 1986; Groves and Stott, 1979; Uchida, 1992, 1996, 1998; Guy et al., 2003; Stumpf et al., 2003; Taylor and Groves, 2003; Pilbrow, 2007), while this study recognizes two species (Table 1).

We predicted that both variation and differences would be largest at the genus level and smallest at the subspecies level, and the results do indeed mostly show this pattern. However, two clear exceptions are apparent. The subspecies *G. b. beringei* was found to be more variable than the species *G. beringei* (Fig. 2A). This perhaps unexpected pattern follows from the contrasting characteristics of the two *G. beringei* subspecies. *Gorilla b. beringei* is on average the most variable of the *Gorilla* subspecies but has a small range of variation, whereas *G. b. graueri* is on average the least variable but has the largest range. Whether this unexpected pattern is a

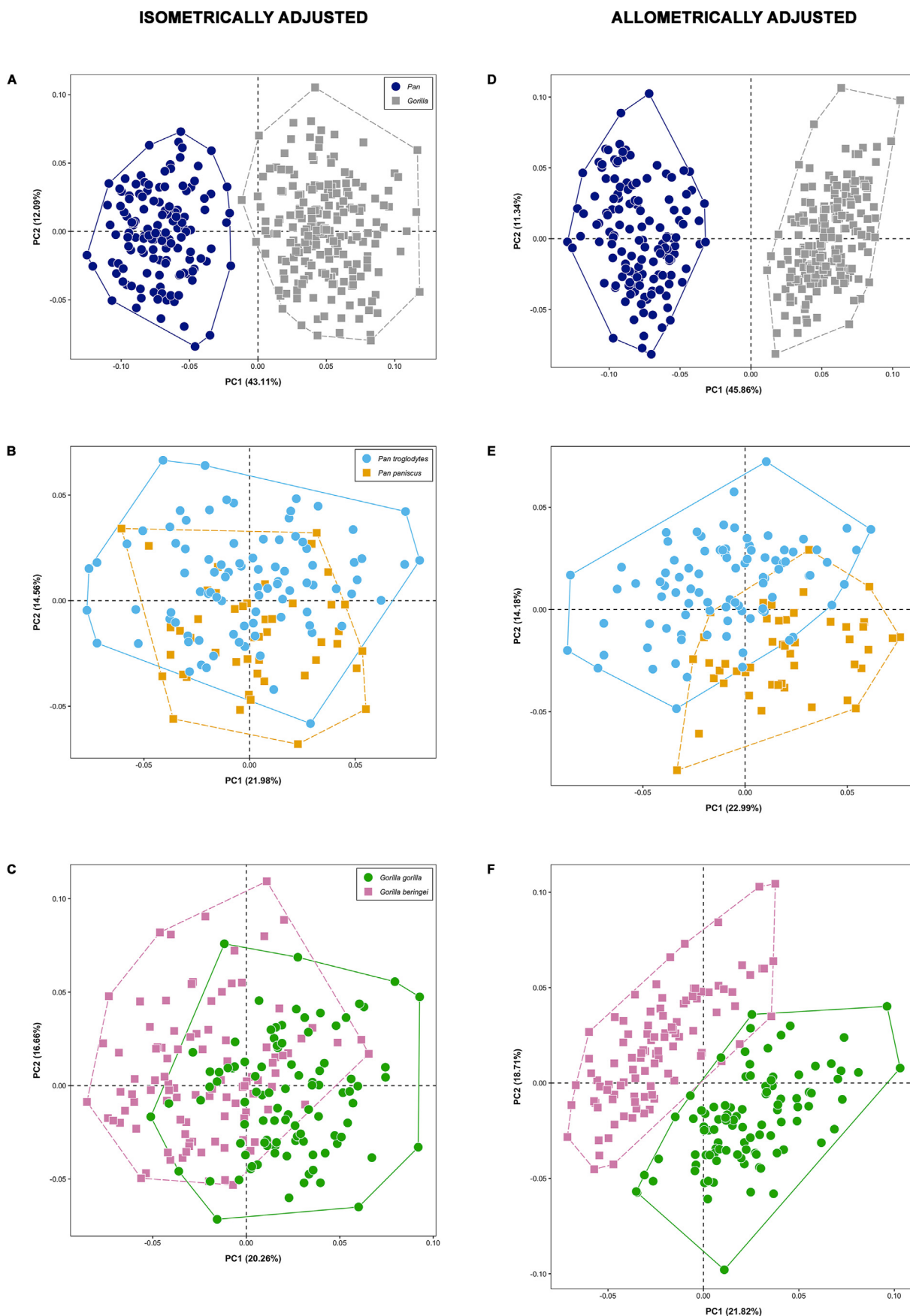


Figure 13. Plots of PC1 and PC2 showing isometrically (A–C) and allometrically (D–F) adjusted shapes of the maxilla when comparing *Pan* with *Gorilla* (A, D), *P. troglodytes* with *P. paniscus* (B, E), and *G. gorilla* with *G. beringei* (C, F). Allometrically adjusted specimens are scaled to the mean size of the genera (D) or the species (E, F). Shape differentiation increases after allometric adjustment.

sampling artifact or rooted in the actual population structures would require further investigation of other cranial morphology and for an expanded sample, of *G. b. beringei* in particular.

The second exception to the aforementioned prediction is that maxillary shape is more distinct between *Gorilla* subspecies than between *Pan* species (Fig. 2B), illustrating that the degree of subspecific and interspecific differentiation varies even between closely related taxa (Albrecht and Miller, 1993). This result matches the pattern shown by the supraorbital morphology (White et al., 2020), but other craniodental research found *Gorilla* subspecies to be more similar than *Pan* species (Groves, 1967, 1970b; Shea and Coolidge, 1988; Guy et al., 2003; Taylor and Groves, 2003; Pilbrow, 2007). Such contrasting results may reflect differences in morphology assessed and methods used. For example, here and in the study by White et al. (2020), variation was quantified on the basis of Procrustes distances, but Mahalanobis distances were used elsewhere.

Of particular interest is whether any morphological features of the extant hominine maxilla stand out as being taxonomically diagnostic more broadly, both at the genus and species level. *Homo*, *Pan*, and *Gorilla* differ in overall maxillary size, prognathism, dental arcade shape, and alveolar dimensions. In contrast, these features do not consistently characterize sister species, with *G. gorilla* and *G. beringei* differing in palate length and prognathism, whereas *P. troglodytes* and *P. paniscus* mainly differ in overall size. Hence, maxillary morphology that is taxonomically diagnostic among extant hominines, as far as captured by our methods, varies from taxon to taxon, and cannot necessarily be used to identify related taxa, whether extant or extinct.

4.2. Sexual dimorphism

Following the pattern described for the skull more generally (e.g., O'Higgins et al., 1990a; Wood et al., 1991; Lockwood, 1999; Guy et al., 2003; Schaefer et al., 2004; Cobb and O'Higgins, 2007) and our prediction for the maxilla specifically, the two *Gorilla* species show the highest levels of sexual dimorphism, both in size and shape, and *P. paniscus* males and females are not different in size. The lowest levels of sexual dimorphism in maxillary shape are seen in *H. sapiens* and the two *Pan* species, and the results are best interpreted as inconclusive with respect to the question whether one of these is less dimorphic than the others. Unlike Cobb and O'Higgins (2007), we did find statistically significant shape differences for *P. paniscus*, and our results for levels of sexual dimorphism are most consistent with those of Schaefer et al. (2004) based on a broader assessment of craniofacial morphology.

Finding similar levels of sexual dimorphism for the maxillae of *H. sapiens* and *Pan* does obviously not mean that the pattern of dimorphism is the same. The minimal canine sexual dimorphism in *H. sapiens* (Wood, 1976; Oxnard et al., 1985; Wood et al., 1991; Scott and Lockwood, 2004) is typically expressed in our results by less difference in associated alveolar morphology than shown by *Pan*. On the other hand, the latter lacks the clear differences in facial height and palatal depth seen in *H. sapiens*.

Consistent with our prediction, sexual dimorphism in shape among *Gorilla* and *Pan* is most strongly associated with canine alveolar size, thus reflecting the well-documented dimorphism of this tooth (Schultz, 1969; Mahler, 1973; Almquist, 1974; Wood, 1976; Oxnard et al., 1985; Dierbach, 1986; Uchida, 1992; Kelley, 1995; Plavcan, 2001). A sexually dimorphic feature that is partially linked with canine alveolar size is dental arcade shape in *Pan* and *Gorilla*. It is wider anteriorly than posteriorly in males, and the reverse in females, resulting in more horseshoe-shaped and more U-shaped dental arcades, respectively (Fig. 10; Bischoff, 1867; Hartmann, 1875a, b; Coolidge, 1933; Randall, 1943a; Ashton, 1957;

Schultz, 1962, 1969; Krogman, 1969; Fenart and Deblock, 1974; Casimir, 1975; McCown, 1982; O'Higgins et al., 1990a, b). In *Pan*, with its lower degree of canine dimorphism, the shape difference is less distinct and reported to be absent in *P. t. verus* (Dierbach, 1986; Anemone and Swindler, 1999), an observation we did not replicate here. With regard to the incisors and postcanine teeth, it has previously been found that the crowns in hominine species show greater sex differences in buccolingual width than in mesiodistal length (Ashton and Zuckerman, 1950; Schuman and Brace, 1954; Garn et al., 1966; Booth, 1971; Mahler, 1973). Here, this pattern is not obviously reflected in the alveolar shapes, underscoring the limitations of using the latter to infer crown size and shape, for example in the fossil record.

Previous studies found different patterns of craniodental sexual dimorphism among hominine species (Wood, 1976; Oxnard, 1987; O'Higgins et al., 1990a, b; Wood et al., 1991; O'Higgins and Dryden, 1993; Lockwood, 1999; Plavcan, 2002; Taylor, 2006; Cobb and O'Higgins, 2007), and this lack of uniformity is confirmed here. The maxillary height, posterior palate length, and subnasal segment length are relatively smaller in *Pan* males, yet larger in *Gorilla* males. The postcanine tooth row is relatively longer in *P. troglodytes* males but significantly shorter in *Gorilla* males. *H. sapiens* males are mostly differentiated from females by relatively greater maxillary height. In contrast, an overall longer and narrower palate in males is shared by all species, including, to some extent, *H. sapiens* (Fig. 10; Schwarz, 1934; Randall, 1943b; Ashton, 1957; Schultz, 1962, 1969; Krogman, 1969; Fenart and Deblock, 1974; Casimir, 1975; Cramer, 1977; McCown, 1982; Dierbach, 1986; Johnson et al., 1989; O'Higgins et al., 1990a, b; Uchida, 1992; Anemone and Swindler, 1999; Cobb and O'Higgins, 2007; Zihlman et al., 2008).

The striking difference in relative maxillary height between males and females, found here for *H. sapiens* (Fig. 10Q–T), is not normally listed in the context of established criteria to assign sex to human crania (Brothwell, 1981; Bass, 1987; Buikstra and Ubelaker, 1994; Mays and Cox, 2000; White et al., 2011). Whether this morphology is genuinely diagnostic for sex in all or some human populations will have to be explored in more detail. For now, our results should be considered with caution given that the *H. sapiens* sample was compiled to maximize individual geographic diversity, rather than to provide a good representation of specific populations with a balanced sex ratio. Moreover, collection records do not appear to report sex from autopsy or burial records, and historical sex attribution based on cranial morphology will include elements of size and perceived robusticity that can potentially bias the findings here.

4.3. Age

In contrast to our predictions, we found no differences in maxillary size between younger and older adults and no noticeable differences in shape, despite statistical significance of the comparisons. Hence, dental wear and its associated processes, such as the lingual tipping of worn upper incisors, do not appear to have a substantial impact on the shape of the maxillary dental arcade or the overall subnasal length and orientation. The latter does not exclude differences not captured by our landmarks, such as curving of the subnasal surface associated with cementum deposition on incisor roots in older adults (Dean et al., 1992; Kaifu, 2000), because no landmarks were placed between nasospinale and prosthion. Our results are consistent with the conclusion of Albrecht et al. (2003) that age-related changes in the adult gorilla skull are only a small component of the morphological variation in comparison to the differences between individuals. However, they do not reflect the evidence of ongoing adult growth reported for the cranium (Krogman, 1931a, b; Randall, 1943a; Ruff, 1980; Balolia et al., 2013).

When comparing late juveniles with adults in the current study, it is most appropriate to consider males and females separately because the late juvenile samples have dissimilar sex ratios (Table 2), and all species are sexually dimorphic to a variable degree (SOM Table S9). The average maxillary size in adults is consistently larger than in late juveniles, but the differences are only statistically significant for the males of *Gorilla* species. Shape differences are statistically significant, except for both sexes of *G. beringei* and for male *H. sapiens*. These results, limited by small samples of late juveniles but broadly consistent with our predictions, indicate that at least in male *Gorilla* there is some ongoing maxillary growth at this developmental stage. Moreover, the consistent pattern of size differences for all groups suggests that this phenomenon may be more widespread. The evidence from mean shape comparisons locates any such growth in the infraorbital, nasal, and subnasal areas (Fig. 12), rather than the dental arcade. In fact, to a variable degree, all species show a shortening of the postcanine tooth row, not including any changes related to third molar eruption, as this was not captured by our landmarks. This shortening has been observed previously (Johanson, 1974a; Spoor et al., 2015) and is thought to be the consequence of gradual interstitial dental wear and mesiodistal compacting of the tooth row in adults (Wolpoff, 1971; Fishman, 1976; Hylander, 1977; Yilmaz et al., 1980; Kaifu et al., 2003). Our evidence for late juvenile growth among great apes and humans is also consistent with previous reports looking at the cranium more widely (Balolia et al., 2013; Kimbel and Rak, 2017).

Some mean shape differences suggest more taxon-specific changes, such as the reduction in anterior projection of the snout in *G. gorilla* and *G. beringei* and the inferior rotation of the subnasal area in *P. paniscus*. These contrast with the pattern of increased facial prognathism and upward rotation of the anterior maxilla reported for hominine postnatal development overall (Schultz, 1950, 1962, 1969; Krogman, 1969; McCollum and Ward, 1997; Cobb and O'Higgins, 2004), suggesting that our findings may represent localized ontogenetic changes in late juveniles, specific to particular taxa only.

Although our results point to changes in maxillary size and shape from late juvenile to adult, the morphology of many of the late juveniles falls within the range of adult variation, as was previously found for dental arcade shape (Spoor et al., 2015), and in line with our predictions. An exception is *P. paniscus*, which shows substantially less overlap between late juveniles and adults than the other species (Fig. 11B). Hence, as an overall pattern, the main adult morphology of hominine maxillae appears to be established before full third molar eruption, but *P. paniscus* could perhaps show a more extended period of facial development.

4.4. Allometry

In our analyses of static allometry, we found that size explains a relatively small amount of the total shape variation. Adjusting for allometry nevertheless results in statistically significant increased differentiation in maxillary shape between *Pan* and *Gorilla*, between *P. troglodytes* and *P. paniscus*, and between *G. gorilla* and *G. beringei* (Fig. 13; SOM Tables S14 and S15), as has been observed before for cranial morphology among gorilla taxa after size adjustment (Taylor and Groves, 2003). Our prediction that less overlap between taxa would follow from reduced intrataxon variation is indeed confirmed here. The one exception is that the variation shown by the genus *Pan* shows an overall increase, but for the individual *Pan* species, this variation is reduced (SOM Table S14). Hence, this pattern appears to reflect how *P. paniscus* and *P. troglodytes* each contribute to the joint variation structure at the genus level. Our second prediction that allometric adjustment would reduce shape differences is clearly not supported since all

three pairs that are compared show an increase, thus contributing to the increased intertaxon differentiation jointly with the reduction in shape variation.

Among the African apes, mean shape differences representing static allometry (SOM Fig. S3) are very similar to those between males and females (Fig. 10), indicating that the observed allometric effects in these species are generally linked with sexual dimorphism, as was previously found for the dental arcade (Spoor et al., 2015). Even the fractions of variation explained by size correspond with the amount of sexual dimorphism, being smallest in *H. sapiens* and largest in *Gorilla*.

Allometric scaling has been an important part of studies considering the underlying factors that contribute to morphological differences between great ape taxa. In particular, there has been a focus on whether the skull of *P. paniscus* is pedomorphic compared with that of *P. troglodytes* and whether the skulls of *Gorilla* and *Pan* are, to some extent, scaled versions of each other (e.g., Giles, 1956; McHenry and Corruccini, 1981). Most studies have approached these questions exploring ontogenetic allometry in growth studies (Shea, 1983a, b, 1984; Godfrey and Sutherland, 1996; Ackermann and Krovitz, 2002; Williams et al., 2003; Berge and Penin, 2004; Cobb and O'Higgins, 2004; Mitteroecker et al., 2004, 2005; McNulty et al., 2006; Ponce de León and Zollikofer, 2006; Lieberman et al., 2007; Simons and Frost, 2021), and our results dealing with static allometry are less informative in this context. Nevertheless, the increased differentiation in maxillary shape between taxa after allometric adjustment is not consistent with the notion that some of these taxa are scaled versions of each other. In other words, a particularly large *Pan* maxilla is less rather than more similar in shape to a small *Gorilla* maxilla, and the same applies when comparing the species.

4.5. Implications for human evolution research

It is worth considering the practical implication of our study in the context of our stated aim of obtaining a taxonomically up-to-date comparative morphological framework to help interpret the hominin fossil record. The results imply that for the maxillary morphology assessed here, there are no singular extant hominine criteria that can be applied when exploring whether a hominin sample is too variable to be attributed to a single species or whether a particular maxilla is female or male. Instead, the extant taxic diversity mapped out here is best used as reference series, providing a quantitative backdrop when discussing possible taxon- or sex-specific morphological differences present in fossil samples. In this context, caution is warranted when considering shape differences of a magnitude similar to those seen between extant species of *Pan* or *Gorilla*, given the substantial overlap in shape space observed for each. However, when maxilla samples show consistent shape differences on a par with those between extant hominine genera, it seems justified to argue that this is indicative of at least species-level differentiation. Each genus pools the variation of two species, which can be used as a proxy for the impact of time depth of a fossil assemblage (Richmond and Jungers, 1995; Lockwood et al., 2000; Terhune et al., 2007).

Our findings suggest that when maxillary shape is compared between two hominine species that differ in size, it is worth exploring the impact of static intraspecific allometry, especially when the hypodigm of either shows substantial size variation. Adjustment for allometry may increase shape differences between the two taxa, but evidently, a prerequisite is that the sample of at least one of the two is large enough to obtain a statistically meaningful allometric regression. Examples in the hominin fossil record where these conditions apply include comparisons involving *Australopithecus afarensis* or *P. boisei*. Both show notable

size variation, assumed to represent sexual dimorphism, and their hypodigms are relatively large (Wood, 1991b; Lockwood et al., 1996, 2000).

Among key specimens in the hominin fossil record are a substantial number of late juveniles where gnathic morphology provides prominent diagnostic information. The *Homo erectus* specimens KNM-WT 15000 (Walker and Leakey, 1993) and D2700 (Rightmire et al., 2006), the *Homo rudolfensis* face KNM-ER 62000 (Leakey et al., 2012), and the *P. boisei* cranium KNM-WT 17400 (Leakey and Walker, 1988) are examples in addition to the holotypes of *P. boisei*, *H. habilis*, and *A. sediba* mentioned previously. Our analyses suggest small changes in size or shape of the maxilla going from late juvenile to adult, but the majority of late juveniles nevertheless fall within the adult shape variation, although not in *P. paniscus* (Fig. 11). This pattern would suggest that for broad comparisons, the late juveniles can be included cautiously to describe adult morphology of a species. However, when specific features are singled out, it is important to explore the possibility of late growth and development of the relevant morphological area in more detail. For example, it is reasonable to infer that the overall architecture of the late juvenile KNM-ER 62000 maxilla is similar to that of KNM-ER 1470, the holotype of *H. rudolfensis* (Leakey et al., 2012). However, when specifically considering the takeoff position of the zygomatic process along the postcanine dental row, we find a small but consistent shift in posterior direction in all five extant hominine species (Fig. 12C, G, K, O, S), making it plausible that a similar shift would have happened, had KNM-ER 62000 grown up. It is less likely that its distinctly orthognathic subnasal orientation would have changed notably, given that all extant species other than *P. paniscus* show developmental stasis of this particular feature (Fig. 12D, H, L, P, T). Importantly, these preliminary observations require confirmation by larger scale studies in the future.

Lastly, we find very little change between younger and older adults in our samples, suggesting that, as an overall pattern, dental wear does not strongly affect dental arcade shape and subnasal orientation, despite the well-documented impact on the shape of the nasoalveolar surface itself (Dean et al., 1992; Villmoare et al., 2013). Hence, heavy tooth wear of older hominin specimens, such as the paratype maxilla KNM-KP 29283 of *Australopithecus anamensis* (Ward et al., 2001) or the Sts 5 *Australopithecus africanus* cranium (Villmoare et al., 2013), should not preclude their inclusion in analytical samples per se, as long as the morphology that is assessed is selected carefully.

5. Conclusions

In this study, we analyzed the size and shape of the extant hominine maxilla, with the aim of obtaining a taxonomically up-to-date comparative framework to help interpret the hominin fossil record. We explored differences and the degree of variation at the genus, species, and subspecies levels, as well as sexual dimorphism and age-related trends from late juvenile to full adulthood. We found statistically significant differences at all taxonomic levels, between adult males and females, and between late juveniles and adults. However, there is substantial overlap in shape space at the interspecific and intraspecific level, and the magnitude and pattern of shape variation varies between taxa. The level of sexual dimorphism in both maxillary size and shape is higher in *Gorilla* than in *Pan* and *Homo*, and the pattern of shape differences between the sexes is unique to each genus, often showing opposite trends. These findings imply that for maxillary morphology, the extant comparative evidence does not provide consistent characteristics or criteria to assign hominin fossils to a single or multiple species or to identify their sex. However, our inventory of extant diversity does

provide a morphological reference frame when describing variation and differences seen in fossil assemblages.

Maxillary shape is correlated with size among the African ape species, but not in modern humans. This allometric correlation explains only small parts of the total shape variation and seems largely linked with differences between males and females. Adjustment for static intraspecific allometry does result in better shape discrimination between extant taxa and should be considered when analyzing larger fossils samples that show substantial size variation, allowing allometry to be identified statistically. We found no noticeable change in maxillary morphology between younger and older adults among the extant hominines. In contrast, our analyses did pinpoint small differences in size or shape between late juveniles and adults, although the majority of late juveniles fall within the adult shape variation. This age-related pattern suggests that for broad comparisons among hominin fossils, the late juveniles can be included cautiously to describe adult morphology of a species. However, when focusing on specific features, it is important to explore the possibility of late growth and development of the relevant morphology, and the changes highlighted in our study can provide a starting point in this respect.

Conflicts of interest

The authors declare no conflict of interest.

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Supplementary Online Material

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