Hominoid arcade shape: pattern and magnitude of covariation

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Abstract

The shape of the dental arcade and canine size distinguish extant humans from all apes. Humans are characterized by a parabolic arcade with short postcanine tooth rows and small canines, whereas apes have long, U-shaped arcades with large canines. The evolutionary and biomechanical mechanisms underlying arcade shape differences between and within groups are not well understood. It is unclear, for example, whether evolutionary changes in the covariation among modules comprising the upper and lower jaws are the cause and/or consequence of different arcade shapes. Here we use 3D geometric morphometric methods to explore to what extent the morphological differences in arcade shape between living hominoids are related to differences in covariation of upper and lower jaws, and the premaxilla and the maxilla. We show that all extant hominoids follow a very similar covariation pattern between upper and lower dental arcades, as well as between the premaxilla and the maxilla. We find comparably high magnitudes of covariation between the premaxilla and the maxilla in all groups. Between the upper and lower jaws, levels of covariation are similar in apes (*Pan*, *Gorilla*, *Pongo*, and *Hylobates*), but overall lower in extant humans. Our results demonstrate an independence of the pattern of arcade shape covariation from dental spatial arrangements. Importantly, we show that a shared hominoid pattern of covariation between premaxilla and maxilla together with the covariation of upper and lower jaw is consistent with major evolutionary arcade shape changes in hominoids. We suggest that with the reduction of canine and diastema size in hominins, the incisors move posteriorly and the tooth row becomes more parabolic. Our study provides a framework for addressing questions about fossil hominin dentognathic diversity, including inter- and intraspecific variation and associations of upper and lower jaw morphology.

Introduction

Dentognathic morphology of extant humans and apes differs notably in canine size and arcade shape. In apes, the arcades are U-shaped with narrow and near-parallel postcanine tooth rows. Furthermore, dental arcade shape varies within and between ape species: posteriorly diverging or converging postcanine tooth rows result in a range of arcade contours (Hellman, 1919). In some individuals the arcade tapers in the premolar region to diverge again more posteriorly, giving it a saddle shape (Hellman, 1919; Remane, 1921). The large lower canines are accommodated in a diastema between the upper lateral incisor and the enlarged upper canine; in the mandible, the upper canine is accommodated between the lower canine and the lower premolars (Angle, 1899; Hellman, 1942), where canine size can vary strongly inter- and intraspecifically (Almquist, 1974; Leutenegger and Kelly, 1977; Oxnard et al., 1985; Leutenegger and Shell, 1987; Plavcan and van Schaik, 1992; Plavcan, 1993; Kelley, 1995).

Modern human dental arcades are usually referred to as being parabolic (Angle, 1899; Broomell, 1902; Le Gros Clark, 1950; Genet-Varcin, 1969), elliptic (Black, 1902; Garn, 1968; Currier, 1969; Brader, 1972) or catenary (MacConaill and Scher, 1949; Scott, 1957; Engel, 1979), with upper and lower arcades having slightly different shapes (Hellman, 1919; Engel, 1979). Incisors and canines are of almost equal size (Schwartz, 1995) and their occlusal surfaces are on the same level as the postcanine dentition.

Intra- and interspecific differences in cranial and mandibular architecture among primates have been related to differences in masticatory behavior, including varying mechanical stress (Hrdlicka, 1940; Hylander, 1972; Carlson and Vangerven, 1977; Hylander, 1979; Weijs and Hillen, 1984; Bouvier, 1986; Weijs and Hillen, 1986; Armelagos et al., 1989; Ravosa, 1990; Corruccini, 1991; Herring, 1993; Anapol and Lee, 1994; Larsen, 1995; Cassidy et al., 1998; Sardi et al., 2004; Lieberman, 2008; von Cramon-Taubadel, 2011; Prasad et al., 2013). These biomechanical arguments emphasize that relative position and length of the dental arcade influence the stress distribution (Witzel and Preuschoft, 2002). In this view, phenotypic variation of the upper and lower jaw is seen as a consequence rather than a precondition for different force distributions. In apes relatively long tooth rows and prognathic dental arcades seem to be biomechanically advantageous, whereas in humans the parabolic arcade is seen as a side effect of reduction in bite- and chewing forces and the reorganization of the face (Preuschoft, 1989; Witzel and Preuschoft, 1999) with little biomechanical significance (Preuschoft and Witzel, 2004). Recent studies in capuchin monkeys (Makedonska et al., 2012) and modern humans (Noback and Harvati, 2015) showed that, at least within groups, dental arcade shape (in contrast to size and position) is largely independent from masticatory forces. These authors found correlations between diet and shape of the temporalis muscle and the cranium, but none between subsistence and maxillary arch shape.

The evolutionary and biomechanical mechanisms underlying the differences in arcade shape between extant humans and apes, as well as those underlying the within-group variability, are not well understood. The evolutionary trajectory of our lineage is interesting in this regard, as arcade shape varies considerably among fossil hominins (e.g., Weidenreich, 1936; Tobias, 1967; Johanson et al., 1978; Johanson and White, 1979; Greenfield, 1992). Besides a general reduction in absolute canine size, early hominins like *Australopithecus anamensis* and *A. afarensis* possess primitive features such as a small diastema between the upper incisor and the canine, as well as parallel to slightly diverging tooth rows (Schwartz, 1995; White et al., 2000; Ward et al., 2001; Kimbel and Delezene, 2009). Some early *Homo* specimens retain long and almost parallel tooth rows, whereas others have shorter postcanine rows and non-projecting frontal tooth rows (Tobias, 1991; Wood, 1991; Rightmire, 1993; Kimbel et al., 1997; Clarke, 2012; Leakey et al., 2012; Spoor et al., 2015). Large-scale differences in jaw shapes have been used to support arguments about species diversity in early *Homo* (Spoor et al., 2015). Moreover, it has been argued that high variation in the anterior maxillary region, the premaxilla, indicates that it might have been subject to selection in hominin evolution (Villmoare et al., 2014). Understanding the mechanisms contributing to the variation and covariation of jaw shapes in extant hominoids is thus informative for interpreting the hominin fossil record.

Morphological covariation is the statistical interrelationship of morphometric variables (Mitteroecker and Bookstein, 2007). It is the consequence of developmental, evolutionary, genetic, and functional processes (Cheverud, 1996a) that in combination lead to integration of structures. Integrated traits must covary, however, traits that covary are not necessarily integrated (Villmoare et al., 2014). Although not equivalent (compare Porto et al., 2009; Young et al., 2010; Grabowski et al., 2011), integration and covariation are mutually dependent in that covarying structures influence the way an organism can react to evolutionary forces. On the other hand, evolution can also act on the covariation of structures. Using 3D geometric morphometric methods we explore the pattern and magnitude of the covariation between and within upper and lower arcades in extant hominoids. We seek to understand if and how the morphological differences in arcade shape between living hominoids are related to differences in covariation of upper and lower jaws.

Previous studies of cranial integration and covariation have consistently demonstrated conserved patterns among primates and even mammals (Cheverud, 1996b; Ackermann and Cheverud, 2000; Lieberman et al., 2000; Marroig and Cheverud, 2001; Ackermann, 2002; Gonzalez-Jose et al., 2004; Marroig et al., 2004; Ackermann, 2005; Goswami, 2006; Gunz and Harvati, 2007; Mitteroecker and Bookstein, 2008; Porto et al., 2009; Makedonska et al., 2012; Villmoare et al., 2014). In this study we assess (1) whether the same applies to hominoid upper and lower dental arcades, or (2) whether the variation in extant arcade shapes is associated with a variation of the underlying patterns of covariation.

The magnitude of covariation has been related to material properties of food, in that taxa relying on a mechanically challenging diet have stronger integrated upper and lower jaws (Marroig and Cheverud, 2001; Makedonska et al., 2012). *Pan*, *Pongo*, *Gorilla*, and *Hylobates* consume different proportions of leaves, fruit, other plant parts, or insects, and their dietary preferences are dependent on season, food availability, habitat and sex. In general, however, *Pan*, *Pongo,* and *Hylobates* are more frugivorous, whereas *Gorilla* is more reliant on leaves (MacKinnon, 1974; Rijksen, 1978; Gittins and Raemaekers, 1980; Watts, 1984; Galdikas, 1988; Tutin and Fernandez, 1993; Knott, 1998; McConkey et al., 2003; Rogers et al., 2004; Boesch et al., 2006; Doran-Sheehy et al., 2009). Morphologically, this difference is reflected in relative dental sizes. Frugivores have relatively larger incisors, while foliovores have relatively larger molars (Hylander, 1975; Kay and Hylander, 1978). In comparison to apes, modern humans have a more generalist diet, where extra-oral food processing via tool use or cooking is thought to have reduced the masticatory effort since the emergence of our species or even earlier (e.g. Brace et al., 1987; Wrangham et al., 1999; Richards et al., 2001; Teaford et al., 2002; Henry, 2010). While a correlation with diet seems likely, some authors have suggested that the lower covariation magnitudes in the human cranium (Marroig et al., 2009; Porto et al., 2009) and pelvis (Grabowski et al., 2011) may indicate a general relaxation of integration in the hominin lineage. These authors argued that the change in magnitude of integration might have paved the way for the development of the morphological changes characterizing our lineage. In addition to the two aforementioned aims, we therefore also assess (3) whether there are differences in the magnitude of covariation between the groups, and (4) whether there are differences between females and males within groups.

It has been argued that within the maxilla, the premaxilla represents its own module that has been a target of selection in the hominin lineage leading to higher variation in the anterior region in hominins compared to other anthropoids (Villmoare et al., 2014). The reduction of canine and thereby diastema size is associated with an earlier closure of the premaxillary sutures (McCollum and Ward, 1997; Braga, 1998). We explore whether those differences are associated with a change in the pattern or the magnitudes of covariation. We therefore also assess (5) the pattern and magnitudes of covariation between the premaxilla and the maxilla.

Materials and methods

Samples

Our samples are summarized in Table 1 and in the Supplementary Online Material (SOM) Table S1. The modern human sample (*n*=53) comprises geographically diverse pre-industrial populations, and was obtained from the Institute of Anatomy at Leipzig University (ULAC), Germany; the Natural History Museum London, UK; the National Historical Museum, Buenos Aires, Argentina; the American Museum of Natural History, New York; and the Smithsonian Institution, Washington, D.C., USA. The *Pan troglodytes* sample (*n*=44) is comprised of specimens from Côte d'Ivoire, Liberia, Gabon, Cameroon and Equatorial Guinea, housed at the Senckenberg Museum, Frankfurt, Germany; at the Max Planck Institute for Evolutionary Anthropology in Leipzig (MPI-EVA), Germany; the Phyletisches Museum, Jena, Germany; and the Smithsonian Institution; plus one zoo specimen housed in the Phyletisches Museum Jena. The *Gorilla* sample (*n*=53) includes *Gorilla gorilla* specimens from Cameroon, Gabon, and the Congo, and *Gorilla beringei* from Rwanda, housed at the Museum für Naturkunde Berlin, Germany; the Phyletisches Museum, Jena and the Smithsonian Institution. The *Pongo* sample (*n*=52) comprises *P. pygmaeus* and *P. abelii* specimens from Borneo and Sumatra, respectively, and one specimen with unknown provenance. The *Pongo* specimens are housed at the Museum für Naturkunde Berlin and the Smithsonian Institution. The *Hylobates* specimens (*n*=63) include the species *H. agilis* (Sumatra), *H. albibarbis* (Borneo), *H. klossii* (Sumatra), *H. lar* (Thailand, Myanmar), and *H. muelleri* (Borneo). The specimens are housed at the Museum für Naturkunde Berlin and the Smithsonian Institution. Sex attributions were taken from museum records when available. Sex of the remaining specimens of *Pan*, *Gorilla* and *Pongo* was determined by several observers based on the formation of cranial superstructures and canine size.

We used computed tomography (CT) of all specimens, including both industrial CT (BIR ACTIS 225/300 at the Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany; isotropic voxel sizes 0.03 – 0.093 mm) and medical CT (Vivantes Klinikum Berlin, Germany; CIMED, La Plata, Argentina; the Senckenberg Museum, and the Smithsonian Institution, Washington, U.S.A. (modern human CT scans obtained as part of Copes (2012)); pixel sizes 0.13 –0.47 mm, slice intervals 0.33 - 0.50 mm). Our sample comprises scans of adult individuals (defined as third molars in occlusion) that preserved both cranium and mandible and did not display malocclusions or other severe pathologies. So as to achieve comparably large sample sizes for all groups that meet these strict criteria, we pooled the respective species of *Gorilla*, *Pongo*, and *Hylobates* in our analyses. Species specific morphologies within genera are known (e.g. Groves, 1970, 1972; Rörer-Ertl, 1984; Uchida, 1998; Guy et al., 2003; Schmittbuhl et al., 2007, but see Groves et al. 1992; Courtenay et al. 1998 for a different view on Pongo), however, the differences in dental arcade shape seem to be negligible, when compared to the shape differences between genera, as can be seen in SOM Figures S1-S3, in which the species of each individual are color coded to illustrate that they are randomly scattered within the convex hulls of their respective genera.

Data

The occlusal surfaces of teeth are modified by wear, which makes placing homologous landmarks problematic. Hence, we took landmarks on the alveolar margin of every tooth and on the cervix of the postcanine dentition in order to capture arcade shape, spatial arrangement of the teeth, and dental size proportions. We recorded 224 homologous 3D landmarks on the mandibular and the maxillary dental arcades (112 landmarks each) (Fig. 1). All measurements were taken in Avizo 7.1 (Visualization Sciences Group).

To capture overall length and breadth patterns, landmarks were placed on the distal, buccal, mesial and lingual surfaces of the incisor, canine and premolar alveolus. On the molars, besides a distal and a mesial landmark, we set two landmarks buccally and two lingually at the position of each root. On the third molar we took one landmark buccally and lingually at the position of the mesial root. The cervical landmarks were positioned distally, buccally, mesially, and lingually.

- Table 1 -

- Figure 1 -

Analysis

Landmarks on the upper and the lower jaw were superimposed separately applying Generalized Procrustes Analysis (GPA) to extract shape information independent from rotation, translation and scaling (Rohlf and Slice, 1990; Bookstein, 1991). We performed a principal component analysis (PCA) on the Procrustes shape coordinates for mandibles and maxillae separately to assess taxonomic shape differences.

Landmarks on the premaxilla (incisors) and the maxilla (canines, premolars, and molars) were superimposed together to retain information on the exact position of the premaxilla relative to the maxilla. In the analysis of the covariation between premaxilla and maxilla, only the alveolar, not the cervical, landmarks were used to capture the morphology of the postcanine dentition.

Pattern of covariation A two-block partial least squares (PLS) analysis was used to quantify the covariation of the mandibular and the maxillary arcade shape, or the premaxilla and the maxilla, respectively (Rohlf and Corti, 2000; Bookstein et al., 2003). We used the mean of the original data and the reflected relabeled landmark configuration in order to symmetrize the data and therewith remove asymmetric shape variation that also arises from asymmetric measurement error (Klingenberg and McIntyre, 1998; Mardia et al., 2000; Mitteroecker and Gunz, 2009). The PLS analysis computes correlated pairs of vectors, so-called singular warps (SW), for the maxilla and for the mandible, or the premaxilla and the maxilla, respectively, that account for the maximum covariance between the two sets of landmarks (Wold, 1966; Rohlf and Corti, 2000; Bookstein et al., 2003).

We performed two PLS analyses per data set: one includes all groups with the data mean centered for each group. This explores the overall pattern of covariation while accounting for large-scale differences between the groups. The second PLS analysis was performed for every group separately, mean centered by sex. If all groups follow a similar pattern of covariation, shape variation associated with PLS axes of the pooled sample and within groups should be similar.

Magnitude of covariation We used two metrics to quantify the magnitude of covariation; the covariance ratio (CR, Adams, 2016) and the correlation coefficient between the singular warp scores (Bookstein et al., 2003). The CR has been proposed recently by Adams (2016) as an alternative to the RV coefficient that overcomes some of the fundamental methodological issues associated with the RV coefficient (Smilde et al., 2009; Fruciano et al., 2013; Bookstein, 2016). The CR quantifies the overall pattern of covariation between the blocks. Therefore one does not know which aspect of covariation the CR is quantifying. In contrast, the correlations of the singular warp scores pertain to the pattern visualized in the respective singular warp plots, and are easier to interpret. As our sample sizes are not equal across all groups, we used a resampling approach for computing the values for the CR. To get a representative distribution, the CR was calculated for 30 randomly selected individuals in 1000 iterations per group.

A permutation test (Good, 2000) was used to determine the significance of the mean differences between the permutated CR values (Bonferroni-corrected for multiple testing, considered significant at $\alpha < 0.05$).

Sexual dimorphism A permutation test (Good, 2000) was used to determine the significance of the mean shape differences between male and female mandibles and maxillae. To do so, we randomly selected individuals and assigned them to male or female and computed a mean shape and shape difference between the permuted sexes 10 000 times (considered significant at $\alpha < 0.05$).

Allometry To assess the amount of the total shape variance that can be explained by jaw size we separately computed multivariate regressions of upper and lower arcade shapes on the natural logarithms of their centroid sizes. We evaluated the statistical significance of these regressions using a permutation test based on the explained variance (Mitteroecker et al., 2013).

Intra-observer error All data were measured by one of the authors (S.S). Intra-observer error was assessed by an analysis of repeated measurements: one specimen (*Gorilla gorilla*, ZMB 14645, medical CT scan, voxel size 0.227x0.227x0.335 mm) was measured fifteen times. The largest Procrustes distance between repeated measurements of this individual was considerably smaller than the smallest Procrustes distance between different specimens of the same species. Specimen affinity is therefore not affected by intra-observer error.

All analyses and visualizations were performed in Mathematica 8.0 (Wolfram Research Inc., 2010).

Results

1. PCA

Table 2 shows the results of the principal components (PC) analysis. The first PC (PC1, 66.9% of total shape variance in maxillae, 70.8% in mandibles) separates humans from the other groups. Both, maxillae (Fig. 2a) and mandibles (Fig. 2c), have short parabolic arcades and small canines on the positive end (humans) compared to a U-shaped arch, long parallel tooth rows with large canines on the negative side (apes).

For the maxillae, PC2 (11.0% of the total shape variance) describes the relation between a relatively large postcanine dentition with relatively small incisors in the positive direction (*Gorilla*); and relatively large incisors with a relatively small postcanine dentition in the negative direction (*Pan*) (Fig. 2a). For the mandibles (10.9% of the total shape variance), PC2 combines a long postcanine tooth row with small incisors on the positive end (*Gorilla*), whereas the negative extreme of PC2 combines a short postcanine tooth row with a large anterior dentition (*Pan*) (Fig. 2c).

PC3 (5.8% of total shape variance in maxillae, 6.3% for mandibles) separates *Hylobates* from the other hominoids. For the maxilla in the negative direction, relatively small postcanine teeth are accompanied by relatively large canines and small incisors; the arcade is slightly V-shaped (*Hylobates*) (Fig. 2b). For the mandibles, moderately sized canines are associated with relatively large postcanine teeth and incisors in the positive direction of PC3 (other groups). The lower scores of PC3 describe relatively small postcanine dentition associated with relatively small incisors and slightly enlarged canines (*Hylobates*).

- Figure 2 –

- Table 2 –

2. Pattern and magnitudes of covariation between the upper and the lower arcades

Pattern of covariation (all groups, group-mean centered) Table 3 shows the percentages of the explained covariance for the first five PLS components. On the positive side of PLS1 (61.4% of the total covariance, r = 0.73), parabolic mandibles are associated with parabolic maxillae. On the negative side, maxillary and mandibular arcades are U-shaped (Fig. 3a). Humans have positive PLS1 scores and are separated from the apes that have decreasing scores along a diagonal line, starting at chimpanzees, to gibbons, orang-utans and then gorillas.

At the negative extreme of PLS2 (21.6% of the total covariance, $r = 0.81$) large maxillary canines are associated with large mandibular canines. The postcanine dentition is relatively small, short and parallel. At the positive extreme, small mandibular canines and V-shaped arcades are associated with small maxillary canines and arcades that are more rounded than the mandibles (Fig. 3b). Humans have positive PLS2 scores and are separated from the apes along a diagonal line.

At the negative end of PLS3 (7.9% of the total covariance, $r = 0.73$), both arcades are broad and converge distally (more pronounced in the maxilla). In the maxillary arcade, the front teeth lie on the bicanine line. At the positive end of PLS3, both upper and lower arcades are V-shaped. The anterior region is narrow and projecting anteriorly (more pronounced in the maxilla) (Fig. 3c). Separation among groups along the PLS3 axis is less clear.

In all PLS dimensions the specimens of all five groups scatter around a diagonal line, indicating that the patterns of covariation of all groups are similar along these PLS axes. In PLS2 *Hylobates* specimens are shifted away from the hominid trajectory, but their trajectory has the same slope.

- Figure 3 -

- Table 3 -

Pattern of covariation (groups separate, sex-mean centered) Table 3 shows the percentages of the explained covariance for the first five PLS components for each group. At the positive end of PLS1, in all groups, rounded maxillae are associated with broad and rounded mandibles (Fig. 4 a-e). In the apes, the maxillary arcade is anteriorly wider than the mandibular arcade. At the negative end of PLS1, long and straight postcanine maxillary arcades are associated with straight mandibular postcanine arcades that taper slightly in the premolar region. In *Hylobates*, PLS1 and PLS2 are interchanged, so that the aforementioned shape changes are described by PLS2 (SOM Fig. S4). In addition, the maxillary arcade in *Hylobates* also tapers in the premolar region. The anterior regions in both upper and lower arcades are rounded and extend anteriorly. PLS scores of PLS2 and PLS3 and wireframes of the first three PLS components are shown in SOM Figs. S4 and S5.

At the positive end of PLS2 in all groups, straight diverging posterior maxillary arcades are associated with likewise diverging mandibular arcades. At the negative end of PLS2, straight converging posterior maxillary tooth rows are associated with mandibular tooth rows that behave similarly. These shape changes are described by PLS1 in *Hylobates*. In addition, on the positive side of this PLS component, *Hylobates* is more straight than converging. In *Homo*, PLS2 and PLS3 are interchanged. The incisal part of the upper and lower arcades in all groups are flat, with the exception of *Homo* and *Hylobates*, where the mandibular arcades are more rounded anteriorly (SOM Figs. S4 and S5).

At the negative end of PLS3 in all groups, straight posterior tooth rows and flat anterior teeth in the maxilla are associated with likewise shaped mandibular arcades. In *Pan*, *Gorilla* and *Pongo*, the postcanine tooth rows are parallel, in *Homo* and *Hylobates* the arcades diverge in both upper and lower jaws. At the positive end of PLS3, anteriorly extending incisors and large diastemata in the maxilla are associated with long straight mandibular arcades, where the incisors extend anteriorly as well. In *Homo* both arcades are more rounded in the postcanine row and less pointed in the anterior region (SOM Figs. S4 and S5).

Overall, all groups show similar covariation patterns.

Morphological comparison between the variation within blocks and the covariation between blocks

The associated shape (co)variation between the maxillary arcades and the mandibular arcades along PLS1 and PLS2 is comparable to the shape variation within the maxillae and within the mandibles along PC1 (i.e., parabolic arcades with small canines versus long U-shaped arcades with large canines).

Also the shape changes along PLS3 are partly represented by the variation described by PC3 (broad versus V-shaped arcades).

Magnitude of covariation (all groups combined) Results for the covariance ratio (CR) are given in Table 4. The distribution of values for the permutated CRs from varied sample composition is shown in Fig. 5. The apes overlap completely with CRs varying from 0.71 to 0.89. *Homo* shows values between 0.64 and 0.89. Median values are 0.81 (*Pongo*), 0.81 (*Pan*), 0.80 (*Gorilla*), 0.81 (*Hylobates*), and 0.76 (*Homo*). *Homo* is significantly different from every other group (*p*<0.02, Bonferroni corrected). *Pan, Gorilla, Pongo,* and *Hylobates* are not significantly different from each other (*p*>0.12 at least) (Table 4).

The correlation coefficient of PLS1 is lowest in *Gorilla*, followed by *Homo*, *Pongo*, and *Pan*. *Hylobates* show the highest value (Table 5). The correlation coefficient of PLS2 is lowest in *Hylobates*, followed by *Homo*. *Pan*, *Pongo*, and *Gorilla* show higher values. In PLS3, the correlation coefficient is lowest in *Hylobates* and *Homo*. *Gorilla* falls between the latter two and *Pongo* and *Pan*.

- Figure 5 -

- Table 4 -

- Table 5 -

Magnitude of covariation (groups separate) We used a subsample of 15, i.e., the smallest number of subsamples (female *Homo*) minus one, and considered the bootstrapping distribution resulting from 1000 iterations for the calculation of the CR (Table 6). Correlation coefficients are given in Table 7.

Overall, female *Pan*, *Gorilla*, *Pongo* and *Homo* show higher mean values in the covariance ratio than their male conspecifics (SOM Fig. S6) in the CR. In *Hylobates*, however, the males show higher values.

In PLS1 female *Gorilla*, *Pongo*, and *Homo* show higher correlation coefficients than in their male counterparts. *Hylobates* show the opposite pattern, so do male *Pan* even though the difference from the females is small. In PLS2 male *Pan*, *Gorilla*, and *Homo* show higher values than the females. *Pongo*, *Homo*, and *Hylobates* show the opposite pattern. In PLS3 males show higher values than females in all groups.

- Table 6 –

- Table 7 -

3. Allometry

For the maxillary arcades, size explains 14.3% of the total variance in *Gorilla*, 12.6% in *Pongo*, 6.8% in *Pan*, 2.5% in *Homo*, and 2.4% in *Hylobates* ($p<0.01$). For the mandibular arcades size explains 8.5% of the total variance in *Gorilla*, 9.7% in *Pongo*, 4.8% in *Pan*, 2.4% in *Homo*, and 3.6% in *Hylobates* ($p<0.01$) (Table 8).

4. Sexual dimorphism

Mean arcade shapes of female and males differ significantly (all *p*-values smaller than 0.05) in *Gorilla*, *Pan* and *Pongo*. While the mandible shapes of female and male *Homo sapiens* are not statistically different, the maxillae fall just below the significance level ($p=0.047$). There is no significant shape difference between female and male *Hylobates* (Fig. 6).

The main difference between male and female great apes is basal crown area of the canine. In *Pongo* and *Gorilla*, this is associated with small differences in the anterior region. In females, the incisors are shifted slightly posteriorly. In the postcanine dentition, the premolars are shifted anteriorly, whereas the molar region remains unaffected. In humans, the subtle difference is also canine crown area.

- Figure 6 -

5. Pattern and magnitudes of covariation between the premaxilla and the maxilla

Pattern of covariation (all groups, group-mean centered) Table 9 shows the percentages of explained covariance for the first five PLS dimensions. In PLS1 (84.1% of the total covariance, *r* = 0.96), all groups scatter along a diagonal (Fig. 7a). At the negative end of PLS1 (gorillas followed by the other non-human apes) large incisors are placed far anteriorly, creating a diastema between the maxilla and the premaxilla. The posterior dentition is parallel, and canines are large. At the positive end (humans), incisors and canines are small and incorporated in the dental arcade, and the posterior arcade is parabolic (Fig. 7a).

In PLS2 (10.2% of the total covariance, *r* = 0.59), the groups still cluster along the diagonal, but are shifted parallel from each other with large overlap among groups (Fig.7b). At the negative end of PLS2, large spaciously arranged incisors are associated with rounded posterior arcades and there is no diastema. At the positive end of PLS2, smaller incisors are positioned in closer proximity and are placed anteriorly followed by a diastema and the posterior dentition is straight and parallel (Fig. 7b).

- Figure 7 –

- Table 9 -

Pattern of covariation (groups separate, sex-mean centered) Table 9 shows the percentages of explained covariance for the first five PLS components for each group separately. SOM Figure S7 shows the PLS scores for every group in the first three PLS dimensions.

At the negative end of PLS1 for every group, anteriorly expanding incisors are associated with straight, parallel posterior tooth rows. In *Pan*, *Gorilla*, and *Pongo*, diastemata are present. At the positive end there are no diastemata between the premaxillae and the maxillae. The incisors are incorporated in the dental arcade. The posterior row is more rounded (SOM Fig. S8, top row).

In the negative direction of PLS2, rather flat anterior regions are associated with wide, more rounded posterior arcades. At the positive end, the incisal region extends anteriorly, creating a diastema between the premaxilla and the maxilla. The posterior arcade is straight. *Gorilla* differs in showing straight posterior arcades in both directions; *Homo* shows no diastema and the posterior arcades are parabolic in both directions (SOM Fig. S8, middle row).

PLS3 describes the spacing of the incisors. In the negative direction, incisors are narrowly positioned. In the positive direction, incisors are widely spaced (SOM Fig. S8, bottom row).

The associated shape changes along all three PLS dimensions in the separate PLS analysis correspond to the shape changes observed in the combined analysis.

Magnitudes of covariation (all groups) Magnitudes of covariation (covariance ratio) are slightly smaller between the premaxilla and the maxilla than between the upper arcade and the lower arcade in the apes (Fig. 8, Table 10). In *Homo*, the values are comparable.

Gorilla is significantly different from *Homo* and *Hylobates* ($p<0.015$, Bonferroni corrected), but not from *Pongo*. The difference between *Gorilla* and *Pan* is close to the significance level ($p\leq0.0559$). *Pan, Pongo, Homo,* and *Hylobates* are not significantly different from each other ($p>0.27$ at least) (Table 10).

The correlation coefficient in PLS1 is lowest in *Pan* and *Hylobates*, followed by *Pongo*, *Homo* and *Gorilla* (Table 11). In PLS2, the correlation coefficient is lowest in *Gorilla*, followed by *Pongo*. *Homo* and

Hylobates show similar values. *Pan* shows the highest correlation coefficient. In PLS3, *Gorilla* shows the highest value, followed by *Pongo*, *Pan*, and *Hylobates*. *Homo* shows the lowest correlation coefficient.

- Figure 8 –

- Table 10 –

- Table 11 -

Magnitudes of covariation (groups separate) We used a subsample of 15, i.e., the smallest number of subsamples (female *Homo*) minus one, and considered the bootstrapping distribution resulting from 1000 iterations for the calculation of the CR (SOM Table S2). Correlation coefficients are given in SOM Table S3.

Pan and *Gorilla* show a marked sexual dimorphism with females showing lower values than males in the covariance ratio (SOM Table S2). In *Pongo*, *Homo*, and *Hylobates*, male and female distributions overlap. In all groups, magnitudes of covariation are in general slightly smaller between the premaxilla and the maxilla than between the upper and the lower arcades. Only male *Gorilla* show higher magnitudes (SOM Fig. S9).

In PLS1 male *Pan*, *Gorilla*, *Hylobates* show higher correlation coefficients than their female counterparts. *Homo* shows the opposite pattern, in *Pongo* values are similar (SOM Table S3). In PLS2 male *Pan*, *Gorilla*, and *Pongo* show higher values than females. In *Homo* and *Hylobates* the opposite is true. In PLS3 correlation coefficients are low in all groups except for *Pan*, where males show higher values than females.

Discussion

In this study we sought to explore the pattern and magnitude of the covariation between the upper and the lower jaw, as well as between the premaxilla and the maxilla in extant hominoids. In the first three PLS components, that together explain more than 90% of the total covariance of the upper and the lower arcade, the data points scatter along the diagonal (Fig. 3). Such an arrangement is interpreted as the same pattern of covariation (e.g. Mitteroecker and Bookstein, 2008). While retaining the same slope, *Hylobates* are shifted from the hominid trajectory in PLS2 (Fig. 3b), probably owing to the presence of absolutely and relatively large canines in males and females in this group.

We also performed separate PLS analyses which showed that the related shape changes of the mandibular and the maxillary arcades are similar across species (Fig. 4 and SOM Figs. S4 and S5). In general, this result suggests a common hominoid pattern of covariation and that the evolutionary shape changes that led to hominoid arcade variation are not associated with modification of the underlying covariation of arcades. Importantly, our data demonstrate an independence of the pattern of covariation, which is similar in the analyzed species, from dental spatial arrangements, which are different in the analyzed species. This conclusion is in accordance with earlier studies that suggest conserved covariation patterns in primates and other mammals in cranial parts other than the jaws (Cheverud, 1996b; Ackermann and Cheverud, 2000; Lieberman et al., 2000; Marroig and Cheverud, 2001; Ackermann, 2002; Gonzalez-Jose et al., 2004; Marroig et al., 2004; Ackermann, 2005; Goswami, 2006; Gunz and Harvati, 2007; Mitteroecker and Bookstein, 2008; Porto et al., 2009; Makedonska et al., 2012; Villmoare et al., 2014).

To evaluate the magnitude of the covariation we used the covariance ratio (CR, Adams, 2016) and the correlations between upper and lower arcades, or the premaxilla and the maxilla, respectively. For the CR we considered the distributions from permutations. *Homo* stands out in showing lower overall CR values (Fig.5, Table 4). Covariation magnitudes of individual PLS axes are quantified by the correlation coefficient. When the first PLS is considered, which explains almost two thirds of the total covariance (i.e., arcade shapes from U-shaped to parabolic), *Gorilla* shows the weakest covariation, followed by *Homo*, *Pongo,* and *Pan* which show similar covariation magnitudes. *Hylobates* has slightly higher values (Table 5). Thus the magnitude of covariation does not reflect the shape gradient from U-shaped to parabolic, and might be more taxon specific than arcade shape specific. In PLS2, which explains almost 22% of the total covariance (i.e., canine size), *Homo* and *Hylobates* display lower correlations than the other groups. Interestingly, while it seems as if absolute canine size itself is of minor importance for the magnitude of covariation, this result might indicate that sexual dimorphism in canine size contributes to the magnitude of covariation, in a way that less dimorphic taxa show lower magnitudes of covariation. In PLS3, that explains about 8% of the total covariance (i.e., spatial arrangement of anterior dentition and postcanine divergence), *Homo* and *Hylobates* also show lower values, followed by *Gorilla* which falls in-between the latter and *Pan* and *Pongo* (Fig. 5d). These differences in covariation magnitudes might be related to different strategies of incorporating large canines into the dental arcade. While in *Pan*, *Pongo* and *Gorilla* intercanine distance is enlarged, which results in a flat anterior region, in *Hylobates* the incisal region is extended anteriorly, resulting in a V-shaped arcade. The lower magnitudes in *Homo* might be the consequence of the generally reduced canines. In combination with the results for the overall measure for the magnitude of covariation these findings imply that the lower magnitude in modern humans is not a reflection of the large-scale differences between humans and apes.

While hominoids do show variation in dental morphology and dental size proportions, the pattern of the interplay between upper and lower arcades remained generally unchanged. This suggests that selection acted on maintaining a proper fit between the upper and the lower arcade. The lower magnitudes of maxillo-mandibular covariation in modern humans which we report here may be related to a systemic change in the hominin lineage. It was shown previously that magnitudes of covariation in the cranium and the pelvis are relaxed in modern humans in general compared to other primates and mammals (Marroig et al., 2009; Porto et al., 2009; Grabowski et al., 2011). Following this argument, a relaxation initially allowed new body plans characteristic of hominins to emerge, potentially including the development of the parabolic arcade shape. If lower magnitudes can account for the development of hominin morphologies then they should be identifiable before new morphologies appear, i.e., at or shortly after the split from the chimpanzee lineage. While the resolution of the current fossil record might not be good enough to determine when this relaxation occurred in the hominin lineage, fossil evidence from about 2.1 to 1.5 million years ago suggests that bipedal adaptations, brain enlargement and short and rounded dental arcades are not necessarily associated with each other. While brain size of *H. habilis*, *H. rudolfensis* and *H. erectus* largely overlap in range, they show distinct facial morphologies including the primitive morphology of long and parallel post-canine tooth rows in *H. habilis*, the derived condition in *H. erectus*, and the distinct morphology of *H. rudolfensis* with short and parallel post-canine tooth rows plus a flat anterior region (Spoor et al., 2015). While these seemingly conflicting lines of evidence clearly need more data, another, mutually non-exclusive, explanation for a lower covariation in *Homo* compared to all apes could be diet. It has been found that those platyrrhine species consuming softer foods show lower magnitudes of covariation than species reliant on harder foods (Marroig and Cheverud, 2001; Makedonska et al., 2012). A similar relationship could contribute to the difference we found between apes and modern humans. This would be in accordance with the notion that at least in *H. sapiens* the masticatory effort was reduced due to extra-oral food processing via tool use and cooking (e.g. Brace et al., 1987; Wrangham et al., 1999; Richards et al., 2001; Teaford et al., 2002; Henry, 2010). This explanation, however, does not sufficiently explain the differences we observe between ape genera, which show similar magnitudes of covariation but at the same time different dietary habits.

We also analyzed the pattern and magnitudes of covariation between the premaxilla and the maxilla. Corroborating the results of Villmoare et al. (2014) the magnitudes of covariation between the premaxilla and the maxilla are in general slightly lower than between the upper and the lower jaw.

In the first PLS components, all groups follow a similar pattern of covariation between the premaxilla and the maxilla. When canines are large, incisors are placed anteriorly to create a diastema for the lower canine. The posterior dentition is long and parallel. With the reduction of canine and diastema size, incisors move posteriorly and the posterior arcades get more parabolic (PLS1). This finding of a shared pattern of covariation between the premaxilla and the maxilla as well as *Homo* falling within the apes' range of covariation magnitude is in accordance with Villmoare et al. (2014). Either result shows that the variation in hominin premaxilla is not associated with a change in the pattern of character covariation. Previous studies suggested that there is a relation between anterior tooth size and premaxilla size (Bromage, 1989; Mooney and Siegel, 1991; Lockwood, 1997; Braga, 1998). Our results show that canine and diastema size contributes substantially to maxillary arcade shape.

To assess differences related to sexual dimorphism, we evaluated magnitudes of covariation for females and males in each group between the upper and the lower jaw (SOM Fig. S6) and between the premaxilla and the maxilla (SOM Fig. S9). Magnitudes of the latter overlap almost completely in all groups except for *Pan* and *Gorilla*, where males show higher values. Mean magnitudes between the upper and the lower jaw are higher in females except for *Hylobates*, where males have higher values. Due to small sample sizes in the within-group comparisons these results should be treated with caution. Additionally, an uncertainty about modern human sex attribution must be considered, since their sexing is based on traditional morphological methods, rather than actual records (dissection, autopsy or graveyard). In general, it is probable that the mechanisms responsible for the results presented here might be multiple and different for each taxon as there are different patterns and magnitudes of dimorphism between species (Plavcan, 2002).

Our results suggest that variation in hominoid arcade shape is not the consequence of a change of the underlying covariation patterns. Our results provide a model for the evolutionary arcade shape change in the hominin lineage: with the loss of interlocking canines and the decreased need for space in the antagonistic arcade in the hominin lineage, the tooth rows become more rounded and eventually parabolic. Driven by the necessity of the upper and the lower jaw to form an effective masticatory apparatus, the morphological covariation between the mandibular and the maxillary arcade has been maintained.

The strong focus on dentognathic structures in palaeoanthropology is due to their good preservation and their taxonomic significance. Nonetheless, our limited understanding of the degree and pattern of intraspecific variation has resulted in different views regarding the number of species that can be recognized in the fossil record (e.g. Wood, 1992; Rightmire, 1993; Leakey et al., 2012). Another factor adding to differences in hypodigm composition is that there is a lack of consensus over which maxillae and mandibles can be accommodated within a single species (Spoor et al., 2015). The results of the current study will help address these issues, as they provide reference data which document the intraspecific and interspecific variation of the upper and lower dental arcades in extant taxa. Moreover, the degree and pattern of covariation between upper and lower jaws can help with identifying the probability that certain maxillae and mandibles in the fossil record are conspecific. Using a smaller landmark set, we have shown recently that this approach can indeed be used to recognize distinct morphs within early *Homo*, identifying those pairs of maxillae and mandibles which, based on extant hominid variation, can be excluded statistically from belonging to a single species (Spoor et al., 2015).

Conclusion

We found that *Pan*, *Gorilla*, *Pongo*, *Hylobates*, and *Homo* share a very similar covariation pattern between the upper and the lower arcade, as well as between the premaxilla and the maxilla, that is independent from dental spatial arrangements. We suggest that in the hominin lineage, with the reduction of canine and diastema size, the incisors move posteriorly and the whole arcade becomes parabolic. The upper and the lower arcades keep track of each other through high magnitudes of covariation. Modern humans show lower magnitudes of covariation between the upper and the lower jaw compared to apes, which might be related to a mechanically less challenging diet in living humans. Alternatively or additionally, lower magnitudes might follow from a general relaxation in covariation attributable to a systemic change in the hominin lineage that enabled the development of new shapes in the first place.

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Figure captions

Figure 1. Data acquisition. Landmarks are placed on the alveolar margin (blue) and on the cervix of the postcanine dentition (orange) of the maxilla (a) and the mandible (c); b) and d) show the wireframe of the symmetrized data.

Figure 2. Arcade shape space of maxillae (a, b) and mandibles (c). *Homo* is shown in yellow, *Pan* in blue, *Gorilla* in black, *Pongo* in red, and *Hylobates* in green. The wireframes show the shape variation along PC1, PC2 and PC3. In PC3, *Hylobates* mandibles plot similarly to the maxillae and are therefore not shown.

Figure 3. Two-block partial least squares (PLS) analysis between the maxillary and the mandibular arcade. Group colors as in Figure 2. The wireframes show the shape changes along SW1 (a), SW2 (b), and SW3 (c). All groups scatter along the diagonal. *Hylobates* shows a shift along SW2, parallel with the hominid trajectory.

Figure 4. Two-block partial least squares (PLS) analysis between the maxillary and the mandibular arcade for each group separately: *Pan* (a), *Gorilla* (b), *Pongo* (c), *Homo* (d), and *Hylobates* (e). Males are shown in dark, females in light colors. The wireframes show the shape changes along SW1.

Figure 5. Distribution of the covariance ratio (CR) (sample size 30, 1000 iterations). *Homo* shows lower overall values than the apes

Figure 6. Female (red) and male (blue) mean shapes for the maxilla (a-e) and the mandible (f-j). Mean shape differences statistically significant at $\alpha \leq 0.05$; *p*-values given below the wireframe. Female and male arcades are significantly different between *Pan*, *Gorilla*, *Pongo,* and *Homo* (maxillae). *Homo* mandibles and *Hylobates* are not significantly different. Smaller canines (females) are associated with a

more posteriorly placed anterior arcade. In the postcanine row, the premolars are placed more anteriorly, the molars remain unaffected.

Figure 7. PLS analysis between the premaxilla (anterior, black wireframe) and the maxilla (posterior, red wireframe). Group colors as in Figure 2.

Figure 8. Distributions of the CR (sample size 30, 1000 iterations) between the premaxilla and the maxilla.

SOM Figure S1. Species distribution within the genus *Gorilla* in arcade shape space of maxillae (a, b) and mandibles (c). *G. gorilla* is shown in black, *G. beringei* in gray. The wireframes show the shape variation along PC1, PC2 and PC3.

SOM Figure S2. Species distribution within the genus *Pongo* in arcade shape space of maxillae (a, b) and mandibles (c). *P. pygmaeus* is shown in light red, *P. abelii* in yellow, *Pongo* sp. in dark red. The wireframes show the shape variation along PC1, PC2 and PC3.

SOM Figure S3. Species distribution within the genus *Hylobates* in arcade shape space of maxillae (a, b) and mandibles (c). *H. muelleri* is shown in green, *H. lar* in pink, *H. klossii* in orange, *H. albibarbis* in blue, *H. agilis* in yellow. The wireframes show the shape variation along PC1, PC2 and PC3.

SOM Figure S4. Shape changes along SW1, SW2, SW3 between the maxillary arcade (black) and mandibular arcade (red) for each group separately. The left wireframe in each group is the negative extreme, the right wireframe is the positive extreme for each SW.

SOM Figure S5. PLS scores of the maxillary and the mandibular arcade for each group separately. Dark colors in each group are males, light colors females.

SOM Figure S6. Sexual dimorphism in the magnitude of covariation. For each taxon, distributions (sample size 15, 1000 iterations) and single values (horizontal lines) are given. Light group colors are females, dark group colors are males. Female hominids show higher magnitudes (distributions and single values) than their male counterparts. *Hylobates* show the opposite pattern. In *Pan*, the single values are almost the same.

SOM Figure S7. PLS scores of the premaxilla and the maxilla for each group separately. Dark colors in each group are males, light colors females.

SOM Figure S8. Shape changes along SW1 (a), SW2 (b), and SW3 (c) between the premaxilla (black) and the maxilla (red). The left column is the negative extreme, the right column is the positive extreme.

SOM Figure S9. Sexual dimorphism in the covariance ratio (CR) between the premaxilla and the maxilla. For each taxon distributions subsample size is 15 (1000 iterations); light group colors are females, dark group colors are males.

Table 1

Table 1. Sample composition

Taxon	♀	♂	**Unknown sex**
Pan	25	19	-
Homo	16	24	13
Gorilla	22	31	-
Pongo	25	27	-
Hylobates	29	30	4

Table 2

Table 2. Results of the PC analyses.

	Eigenvalues	**% variance**	**Cumulative %**
Maxillae			
PC1	0. 00789125	66.958	66.958
PC2	0. 00129874	11.02	77.978
PC3	0. 00067848	5.757	83.735
Mandibles			
PC1	0. 01059464	70.795	70.795
PC2	0. 00163547	10.928	81.723
PC3	0. 00093735	6.264	87.987

Table 3

Table 3. Percentage of the explained covariance between the upper and the lower arcade for the first five PLS components. Symmetrized data; combined PLS: group-mean centered; separate PLS: sex-mean centered.

	% covariance combined PLS	**% covariance separate PLS**				
		Pan	***Gorilla***	***Pongo***	***Homo***	***Hylobates***
PLS1	61.39	68.44	51.79	57.80	65.53	79.40
PLS 2	21.55	11.74	19.31	15.00	13.27	8.78
PLS 3	7.92	6.26	13.06	10.85	6.55	4.44
PLS 4	3.46	3.50	3.83	6.38	3.41	1.36
PLS 5	1.38	2.60	2.65	2.39	2.09	1.27

Table 4

Table 4. Results for the CR and the permutation tests for the upper and the lower jaw. Subsample size for the permutation is 30, 1000 resamples. Below, Bonferroni corrected *p*-values from permutation test of group mean differences (considered significant at α < 0.05).

	Pan	*Gorilla*	*Pongo*	*Homo*	*Hylobates*
CR	0.777	0.771	0.786	0.726	0.789
Min	0.712	0.715	0.739	0.635	0.721
Max	0.894	0.867	0.886	0.892	0.891
Median	0.805	0.804	0.812	0.755	0.814
Mean	0.805	0.802	0.813	0.757	0.814
SD	0.031	0.025	0.024	0.044	0.030
Pan	15	14.580	0.165	0.015	0.150
Gorilla	14.536	15	0.270	0.015	0.165
Pongo	0.120	0.240	15	0.015	11.613
Homo	0.015	0.015	0.015	15	0.015
Hylobates	0.210	0.150	10.984	0.015	15

Table 5

Table 5. Results for the correlation coefficient (*r*) between the upper and the lower arcade.

	PLS1	PLS2	PLS3
Pan	0.757	0.841	0.858
Gorilla	0.645	0.853	0.757
Pongo	0.728	0.851	0.828
Homo	0.695	0.664	0.668
Hylobates	0.831	0.569	0.625

Table 6

Table 6. Results for the CR and the permutation tests grouped by species and sex (subsample size 15, 1000 resamples) for the upper and the lower arcade. Below, Bonferroni corrected *p*-values from permutation test of sex mean differences (considered significant at α < 0.05).

	Pan M	*Pan* F	*Gorilla* M	*Gorilla* F	*Pongo* M	*Pongo* F	*Homo* M	*Homo* F	*Hylo* M	*Hylo* F
CR	0.837	0.831	0.720	0.809	0.771	0.834	0.756	0.859	0.836	0.795
Min	0.786	0.797	0.682	0.749	0.737	0.778	0.715	0.843	0.771	0.719
Max	0.926	0.921	0.912	0.910	0.893	0.933	0.904	0.872	0.940	0.935
Median	0.847	0.872	0.804	0.840	0.809	0.858	0.793	0.864	0.862	0.844
Mean	0.853	0.869	0.803	0.839	0.810	0.857	0.796	0.862	0.861	0.842
SD	0.030	0.023	0.038	0.029	0.023	0.031	0.033	0.007	0.032	0.040
p	0.950		0.002		0.002		0.002		0.214	

Table 7

Table 7. Correlation coefficients (r) grouped by species and sex for the upper and the lower arcade.

	PLS1	PLS2	PLS3
Pan M	0.924	0.810	0.879
Pan F	0.910	0.780	0.827
Gorilla M	0.660	0.906	0.876
Gorilla F	0.764	0.780	0.800
Pongo M	0.764	0.703	0.797
Pongo F	0.852	0.784	0.705
Homo M	0.745	0.858	0.860
Homo F	0.907	0.741	0.806
Hylobates M	0.865	0.779	0.802
Hylobates F	0.787	0.837	0.728

Table 8

Table 8. Percentage of the total variance explained by size.

	Maxillae		**Mandibles**	
Taxon	%	*p*	%	*p*
Pan	6.80	<0.001	4.84	<0.001
Gorilla	14.25	<0.001	8.53	<0.001
Pongo	12.58	<0.001	9.68	<0.001
Homo	2.49	<0.001	2.38	<0.004
Hylobates	2.36	<0.001	3.55	<0.001
Total	5.38	<0.001	8.39	<0.001

Table 9

Table 9. Percentage of the explained covariance between the premaxilla and the maxilla for the first five PLS components. Symmetrized data; combined PLS: group-mean centered; separate PLS: sex-mean centered.

	% covariance combined PLS	**% covariance separate PLS**				
		Pan	***Gorilla***	***Pongo***	***Homo***	***Hylobates***
PLS1	84.14	44.28	85.99	67.19	79.75	74.83
PLS2	10.18	39.06	7.37	17.07	7.72	13.70
PLS3	2.20	6.44	2.21	6.47	5.41	3.95
PLS4	1.16	3.55	1.42	3.87	2.50	3.11
PLS5	0.74	1.96	1.06	1.85	1.42	1.27

Table 10

Table 10. Results for the CR and the permutation tests between the premaxilla and the maxilla. Subsample size for the permutation is 30. 1000 resamples. Below, Bonferroni corrected *p*-values from permutation test of group mean differences (considered significant at α < 0.05).

	Pan	*Gorilla*	*Pongo*	*Homo*	*Hylobates*
CR	0.678	0.731	0.702	0.694	0.646
Min	0.611	0.621	0.620	0.596	0.576
Max	0.803	0.882	0.844	0.834	0.809
Median	0.707	0.751	0.727	0.719	0.688
Mean	0.707	0.749	0.726	0.719	0.687
SD	0.031	0.044	0.037	0.038	0.042
Pan	15	0.030	8.571	5.784	0.300
Gorilla	0.060	15	0.135	0.015	0.015
Pongo	8.796	0.120	15	3.267	0.270
Homo	5.619	0.015	3.282	15	2.742
Hylobates	0.554	0.015	0.360	2.892	15

Table 11

Table 11. Results of the correlation coefficient (*r*) between the premaxilla and the maxilla.

	PLS1	PLS2	PLS3
Pan	0.752	0.885	0.395
Gorilla	0.815	0.707	0.668
Pongo	0.798	0.752	0.492
Homo	0.814	0.794	0.060
Hylobates	0.758	0.796	0.207