



Using the covariation of extant hominoid upper and lower jaws to predict dental arcades of extinct hominins



Stefanie Stelzer^{a,*}, Philipp Gunz^a, Simon Neubauer^a, Fred Spoor^{a,b}

^a Department of Human Evolution, Max Planck Institute for Evolutionary Anthropology, Leipzig 04103, Germany

^b Department of Cell and Developmental Biology, University College London, London WC1E 6BT, UK

ARTICLE INFO

Article history:

Received 3 March 2017

Accepted 30 October 2017

Available online 21 November 2017

Keywords:

Estimation

Regression

Arcade shape

Reconstruction

Fossil hominins

ABSTRACT

Upper and lower jaws are well represented in the fossil record of mammals and are frequently used to diagnose species. Some hominin species are only known by either their maxillary or mandibular morphology, and in this study, we explore the possibility of predicting their complementary dental arcade shape to aid the recognition of conspecific specimens in the fossil record. To this end, we apply multiple multivariate regression to analyze 3D landmark coordinates collected on associated upper and lower dental arcades of extant *Homo*, *Pan*, *Gorilla*, *Pongo*, and *Hylobates*. We first study the extant patterns of variation in dental arcade shape and quantify how accurate predictions of complementary arcades are. Then we explore applications of this extant framework for interpreting the fossil record based on two fossil hominin specimens with associated upper and lower jaws, KNM-WT 15000 (*Homo erectus sensu lato*) and Sts 52 (*Australopithecus africanus*), as well as two non-associated specimens of *Paranthropus boisei*, the maxilla of OH 5 and the Peninj mandible. We find that the shape differences between the predictions and the original fossil specimens are in the range of variation within genera or species and therefore are consistent with their known affinity. Our approach can provide a reference against which intraspecific variation of extinct species can be assessed. We show that our method predicts arcade shapes reliably even if the target shape is not represented in the reference sample. We find that in extant hominoids, the amount of within-taxon variation in dental arcade shape often overlaps with the amount of between-taxon shape variation. This implies that whereas a large difference in dental arcade shape between two individuals typically suggests that they belong to different species or even genera, a small shape difference does not necessarily imply conspecificity.

© 2017 Elsevier Ltd. All rights reserved.

1. Introduction

The mammalian upper and lower jaw form a functional unit (e.g., Cheverud, 1982; Russell and Thomason, 1993; Dötsch, 1994). There must be a good match between their forms so that the occlusal surfaces of the upper and lower teeth come in appropriate contact to process food effectively (Enlow et al., 1969). When assessed quantitatively, the maxillary and mandibular dental arcades of extant hominoids were found to show high magnitudes of covariation (Spoor et al., 2015; Stelzer et al., 2017). Moreover, even though modern humans and apes show differences in spatial arrangements, size ratios, and degrees of sexual dimorphism of their

teeth, they nevertheless share a pattern of maxillomandibular covariation (Stelzer et al., 2017).

Modern humans differ from apes in having a parabolic arcade with small canines in both females and males (e.g., Angle, 1899; Broomell, 1902; Le Gros Clark, 1950; Schwartz, 1995). Extant apes share long postcanine tooth rows and diastemata in both upper and lower arcades to accommodate large canines (e.g., Angle, 1899; Hellman, 1919, 1942). There are, however, attributes that characterize every particular taxon. *Gorilla* shows long, parallel tooth rows that appear U-shaped and the anterior teeth are small relative to the postcanine dentition. *Pan* has shorter tooth rows and relatively large anterior teeth. *Pongo* can have more rounded arcades and falls somewhere in between *Gorilla* and *Pan*. In *Hylobates*, the incisal region extends anteriorly with long and straight tooth rows and a V-shaped dental arcade (Angle, 1899; Hellman, 1919, 1942; Remane, 1921; Stelzer et al., 2017). The

* Corresponding author.

E-mail address: stefanie_stelzer@eva.mpg.de (S. Stelzer).

arcade morphology of extinct hominin taxa differs from extant hominoids and can be characteristic at the genus or species level, including the derived shapes found in *Kenyanthropus*, *Paranthropus*, and *Homo rudolfensis* (Rak, 1983; McCollum, 1999; Spoor et al., 2010, 2015; Leakey et al., 2012). Maxillae and mandibles are abundant in the hominin fossil record, taxonomically diagnostic, and have frequently been used as type specimens to describe species (Schoetensack, 1908; Leakey et al., 1964, 1995; Groves and Mazak, 1975; Johanson et al., 1978; Asfaw et al., 1999; Haile-Selassie et al., 2015). However, in the fossil record, upper and lower jaws of the same individual are rarely jointly preserved. When it comes to attributing non-associated fossil specimens, it is sometimes unclear how different a maxilla of one specimen and a mandible of another can be to fall within the variation of a single species or how different they have to be to preclude that they belong to the same species, and how this should be assessed (e.g., Wood, 1992; Rightmire, 1993; Leakey et al., 2012).

It has been shown previously that hominoids share a common pattern and high-levels of covariation between the upper and lower dental arcades (Spoor et al., 2015; Stelzer et al., 2017). This information can be used to predict a mandibular arcade from a maxilla and vice versa (Spoor et al., 2015) and thereby facilitates the quantitative comparison of non-associated upper and lower jaws. To discuss potential species affinities of two fossils quantitatively, one can compare the quantified difference between a dental arcade of one fossil and the predicted arcade based on the complementary arcade shape of a second fossil to the amounts of within-taxon and between-taxon differences of upper or lower jaws in extant species. When the difference between two tested arcades falls within the range of extant intraspecific variation, taxonomic interpretations are not straightforward, given the fact that two different species can exhibit overlapping variation in this feature but not in others. However, such a finding can be consistent with conspecificity and, together with other features and analyses, it can help to interpret fossils. When the differences between two tested arcades are larger than the differences within an extant species, conspecificity of two fossils can be ruled out because we assume that extinct species (generally) do not exceed the range of variation seen in extant species. Building upon the above-mentioned landmark-based analyses, we extend our earlier work to further discuss possibilities and limitations of this methodology. In particular, we examine levels of dental arcade shape variation within and between taxa on both the species and genus level.

The first goal of this study is to explore the limitations of our reference sample caused by the patterns of variation within and between extant taxa that the interpretation of differences in two fossils relies on. Our reference group compositions enable us to study different levels of taxonomic relationships, including intra-specific, interspecific, intrageneric, and intergeneric variation. In the case of our human and chimpanzee samples, within-taxon differences are intraspecific, because each taxon includes only one species, i.e., *Homo sapiens* and *Pan troglodytes*, respectively. Gorillas, orangutans, and gibbons include multiple species; the variation within these taxa is intrageneric. The variation between species of each of these genera is interspecific, while the differences among humans, great apes, and gibbons are intergeneric.

Interpretations of the difference between a predicted shape of one fossil and another specimen and implications on genus or species affinities between them are only relevant if the predicted shape represents a realistic reconstruction in the first place. Hence, the second goal of this study is to systematically quantify and investigate how accurate predictions of complementary arcades are. To this end, we predict and analyze arcade shapes of matching maxillae and mandibles of the same specimens of

humans, chimpanzees, gorillas, orangutans, and gibbons. There are different approaches to reconstructing/predicting landmark data in geometric morphometrics, including the thin-plate spline interpolation function, multiple multivariate regression, or expectation-maximization algorithms (for detailed descriptions, see Ackermann, 1998; Gunz, 2005; Gunz et al., 2009; Benazzi et al., 2011). Apart from the choice of which computational approach is most appropriate for the respective research question, the choice of reference specimens affects the shape of the reconstruction. Ideally, the reference sample should originate from the same population or species as the target specimen (Zollikofer and Ponce de León, 2005), because using reference specimens of similar shape will produce the most accurate predictions (Gunz et al., 2009; Senck et al., 2015). When studying the fossil record, however, we frequently do not know which taxon the specimen belongs to, or there are not enough reference individuals from the same extinct species to compute reliable regression models. Hence, when the goal of the prediction is to analyze taxonomic affinities of a specimen, predicting similar shapes becomes a problem, because predictions using a *Homo* model create *Homo*-like features and a *Pan* model drives the predictions towards a *Pan*-like shape (Gunz et al., 2009; Neubauer et al., 2012). In this study, we use multiple multivariate regression and three distinct reference samples to predict complementary arcade shapes. In the 'correct model' (i), the multivariate regression is based on a reference sample consisting only of individuals of the same genus or species, respectively, that is to be predicted (e.g., using a human reference sample to predict a human individual). This model simulates the best-case scenario, i.e., when we know the genus, or species, of the specimen that we want to predict. The 'pooled model' (ii) includes all specimens of all genera. By providing a wider range of morphological variation, it will be the model to choose if we do not know the taxon of the specimen that is to be predicted. The 'exclusion model' (iii) simulates the worst-case scenario, i.e., an absence of morphology in the reference sample by using all specimens except the individuals of the correct taxon. We quantify the accuracy of these predictions by computing the shape difference between the original and the predicted morphology. We expect the correct model to result in the most accurate predictions. Ideally, the pooled model should not deviate much from the correct model, but we expect the differences between the actual data and the predictions to be larger. The exclusion model will lead to larger differences between the actual data and the predictions, especially in *Homo*, where arcade shape differs the most from every other extant genus of the reference sample (Stelzer et al., 2017). The exclusion model exemplifies a worst-case scenario, especially for predicting modern human jaws from an ape-only reference sample.

In the third part of this study, we investigate the aforementioned aspects when dealing with fossils. To determine whether the extant hominoid model can be applied to fossils, we use two individuals that preserve both the upper and lower jaw: KNM-WT 15000 (*Homo erectus* sensu lato; Brown et al., 1985; Walker and Leakey, 1993) and Sts 52 (*Australopithecus africanus*; Broom et al., 1950). To assess how accurate the predictions are on an individual level, we predict complimentary arcades for the two fossil maxillae and mandibles, and then compare the predictions to the actual fossil arcades like we have done for the extant sample, with the difference that *H. erectus* and *A. africanus* are not part of the reference sample. The fossil specimens therefore exemplify a real case scenario for the exclusion model. Finally, we also predict complementary arcades for two isolated specimens attributed to the same species, *Paranthropus boisei*, but belonging to different individuals: the OH 5 maxilla (Leakey, 1959; Tobias, 1967) and the Peninj mandible (Leakey and Leakey,

Download English Version:

<https://daneshyari.com/en/article/8887353>

Download Persian Version:

<https://daneshyari.com/article/8887353>

[Daneshyari.com](https://daneshyari.com)