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Geometric morphometric analysis of mandibular shape diversity in *Pan*

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ABSTRACT

The aim of this research is to determine whether geometric morphometric (GM) techniques can provide insights into how the shape of the mandibular corpus differs between bonobos and chimpanzees and to explore the potential implications of those results for our understanding of hominin evolution. We focused on this region of the mandible because of the relative frequency with which it has been recovered in the hominin fossil record. In addition, no previous study had explored in-depth three-dimensional (3D) mandibular corpus shape differences between adults of the two *Pan* species using geometric morphometrics. GM methods enable researchers to quantitatively analyze and visualize 3D shape changes in skeletal elements and provide an important compliment to traditional two-dimensional analyses.

Eighteen mandibular landmarks were collected using a Microscribe 3DX portable digitizer. Specimen configurations were superimposed using Generalized Procrustes analysis and the projections of the fitted coordinates to tangent space were analyzed using multivariate statistics. The size-adjusted corpus shapes of *Pan paniscus* and *Pan troglodytes* could be assigned to species with approximately 93% accuracy and the Procrustes distance between the two species was significant. Analyses of the residuals from a multivariate linear regression of the data on centroid size suggested that much of the shape difference between the species is size-related. Chimpanzee subspecies and a small sample of *Australopithecus* specimens could be correctly identified to taxon, at best, only 75% of the time, although the Procrustes distances between these taxa were significant. The shape of the mandibular symphysis was identified as especially useful in differentiating *Pan* species from one another. This suggests that this region of the mandible has the potential to be informative for taxonomic analyses of fossil hominoids, including hominins. The results also have implications for phylogenetic hypotheses of hominoid evolution.

Introduction

As the closest extant relatives of humans, great apes are often viewed as the most appropriate models for the extent and pattern of morphological variation to be expected in early fossil hominin species (LeGros Clark, 1964; Wolpoff, 1977; Kimbel and White, 1988; Wood et al., 1991; Daegling, 1993; Shea et al., 1993; Richmond and Jungers, 1995; Lockwood et al., 1996; Uchida, 1996; Lockwood, 1999; Silverman et al., 2001; Guy et al., 2003, 2008; Harvati, 2003a; Robinson, 2003; Harvati et al., 2004; Skinner et al., 2006; Lague et al., 2008; but see Jolly, 2001, 2009; Taylor, 2006 and references therein). Although some recent, and many earlier, studies suggested that all great ape species other than *Pan paniscus* could be split into two or more species (Groves, 1986, 2000, 2001, 2003; Morin et al., 1994; Ruvolo et al., 1994; Grine et al., 1996; Muir et al., 1998, 2000; Albrecht et al., 2003; Brandon-Jones et al., 2004; Thalmann et al., 2007; Bradley, 2008), *Pan* is currently the only extant great ape genus that researchers agree has multiple species (Badrian and Badrian, 1984; Thomson-Handler et al., 1984; Kano, 1992; Morin et al., 1994; Horai et al., 1995; Takahata et al., 1996; Burrows and Ryder, 1997; Gagneux et al., 1999; Kaessmann et al., 1999; de Waal, 2001; Stone et al., 2002; Yu et al., 2003). Thus, this taxon is valuable as a comparative model for assessing the taxonomic homogeneity of putative species in the hominin fossil record.

There have been many studies documenting craniodental and postcranial differences between the two *Pan* species (Johanson, 1974; Cramer and Zihlman, 1976; Cramer, 1977; Zihlman and Cramer, 1978; Corruccini and McHenry, 1979; McHenry and Corrucini, 1981; Shea, 1983a,b,c, 1984, 1985; Kinzey, 1984; Laitman and Heimbuch, 1984; Shea and Coolidge, 1988; Groves et al., 1992; Uchida, 1992, 1996; Shea et al., 1993; Braga, 1995; Lockwood et al., 2002, 2004; Guy et al., 2003; Pilbrow, 2006; Skinner et al., 2008, 2009; Singleton et al., 2011). Fewer studies have published data on differences between *P. paniscus* and *Pan troglodytes* in their mandibular morphology (Andrews, 1978;

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Brown, 1989; Taylor, 2002; Taylor and Groves, 2003; Schmittbuhl et al., 2007; Boughner and Dean, 2008; Lague et al., 2008; Zihlman et al., 2008). Most of the more recent analyses have used multivariate methods to examine whether the mandibular shapes of these species could be significantly differentiated from one another (Taylor, 2002; Taylor and Groves, 2003; Schmittbuhl et al., 2007; Boughner and Dean, 2008; Lague et al., 2008). However, only three of these investigations included all three commonly recognized subspecies of chimpanzees in their samples (Taylor, 2002; Taylor and Groves, 2003; Schmittbuhl et al., 2007). Sampling all three subspecies provides a more thorough documentation of the range of variation in *P. troglodytes* and improves our confidence in any differences found between chimpanzees and bonobos.

Two of the three studies including all three chimpanzee subspecies described the differences between the two *Pan* species in their mandibular morphology as less extensive than the differences in their cranial shapes. These analyses presented data on 13 (Taylor, 2002) and 17 (Taylor and Groves, 2003) exclusively mandibular linear dimensions scaled to size, with over half of the measurements having at least one of their end points on the ramus. In the third study, Schmittbuhl et al. (2007) explored differences among extant hominoid taxa, including between *P. paniscus* and *P. troglodytes*, in the mean outline shapes of their entire mandibles using elliptical Fourier techniques. However, since complete mandibles are rarely found in the hominoid fossil record and the vast majority of specimens lack rami, it is useful to explore whether the morphology of the mandibular corpus on its own results in a similar or reduced ability to discriminate among hominoid species (Robinson, 2003; Lague et al., 2008). Moreover, the results of Taylor and Groves (2003) suggest that this region of the mandible may be especially important in differentiating bonobo and chimpanzee mandibles given that most of the significant differences they found between these two taxa were measurements taken on the mandibular corpus. Lague et al.'s (2008) analysis included eight linear measurements scaled to the geometric mean that are found on the more commonly preserved mandibular corpus to explore how effective these data were at grouping extant hominoid specimens in the correct genus, species, and subspecies. In the other recent study of *Pan* mandibular morphology using multivariate methods, Boughner and Dean (2008) focused on documenting ontogenetic changes in the three-dimensional (3D) shape of the mandible in *Pan* using geometric morphometric (GM) techniques and, consequently, they included only a small sample of adults for the two species.

This investigation builds on these studies by exploring differences between the two *Pan* species in the three-dimensional shape of the mandibular corpus using geometric morphometric techniques. Three-dimensional geometric morphometric methods have been used to quantify variation in modern human mandibular morphology, to explore differences among fossil hominin mandibles, and to investigate the ontogenetic development of the mandible in *Pan* (Rosas and Bastir, 2004; Oettlé et al., 2005; Nicholson and Harvati, 2006; Boughner and Dean, 2008), but have not been employed, as of yet, to examine in depth differences between adults of the two *Pan* species in their mandibular shapes. One of the advantages of using 3D GM techniques is that it enables researchers to document shape differences in morphological features that have previously only been qualitatively described, often because they have been difficult to accurately quantify using traditional instruments (Dean, 1993; Harvati, 2001, 2003b; Robinson, 2003; Rosas and Bastir, 2004; Nicholson and Harvati, 2006). For example, the sizes of the symphyseal transverse tori have been assessed qualitatively in most studies of extant hominoids by noting how far they project posteriorly relative to the tooth row (Aitchison, 1965; Brown, 1989, 1997; Singleton, 2000). However, the positions of the tori relative to the dentition are strongly influenced by a number of factors, including the inclination of the symphysis. Accounting for symphyseal inclination when quantifying the size of the tori is difficult using standard techniques (Daegling, 1993; Daegling and Jungers, 2000; Robinson, 2003). GM methods provide one possible means of documenting variation in these kinds of morphological features.

The primary questions to be addressed using these data were: (1) How effectively can the mandibular corpora of *P. paniscus* and *P. troglodytes* and those of the three *P. troglodytes* subspecies be differentiated from one another using the 3D shape data derived from GM analyses and how does this compare to previous multivariate studies of these taxa? (2) What features on the mandibular corpus are most useful for distinguishing *Pan* species from one another? (3) Are shape differences between the two *Pan* species and three *P. troglodytes* subspecies related to differences in the sizes of their mandibular corpora?

Materials and methods

Sample

The sample for this study was comprised of 126 mandibular specimens of *P. paniscus* and all three commonly recognized chimpanzee subspecies, *Pan troglodytes schweinfurthii, Pan troglodytes troglodytes* and *Pan troglodytes verus* (Table 1). Males and females were not sampled equally because at most of the museums visited all available specimens were digitized. Data were collected only on adult and wild-shot specimens, as determined by fully erupted permanent dentition, museum tags, and catalog information. Specimens showing obvious abnormalities or substantial resorption due to antemortem tooth loss were excluded since those factors would alter the shape of the mandibular corpus. These restrictions meant that, despite visiting the collections at nine museums, only six male bonobos could be included in the sample. In addition, four *Australopithecus afarensis* and three

Table 1
Number of specimens for each taxon, name of the localities where the hominin specimens are derived from, and institutions where the specimens are housed.

Mandibular specimens		
Taxon(locality)	Museums	Sample size
Pan paniscus	AMNH, BMNH, MCZ, MRAC	23 (6M, 17F)
Pan troglodytes schweinfurthii	AMNH, BMNH, MRAC, NMNH	29 (21 M, 8F)
Pan troglodytes troglodytes	AMNH, NNM, PCM, ZMB	47 (25M, 22F)
Pan troglodytes verus	AMNH, BMNH, NMNH, NNM, PMH	27 (13M, 14F)
Australopithecus afarensis (Maka)	NME	1 (MAK-VP 1/12)
Australopithecus afarensis (Hadar)	NME	3 (AL 417-1a, 437-1, 438-1g)
Australopithecus africanus (Sterkfontein)	TM, WITS	2 (Sts 7, 52)
Australopithecus africanus (Makapansgat)	TM	1 (MLD 2)

Sex, or specimen number in the case of the fossil hominin specimens, is indicated in parentheses (M = males, F = females). Abbreviations for institutions: AMNH – American Museum of Natural History; BMNH – British Museum of Natural History; MCZ – Museum of Comparative Zoology, Harvard; MRAC – Musée Royal de l'Afrique Centrale, Tervuren; NME – National Museum of Ethiopia; NMNH – National Museum of Natural History (Smithsonian); NNM – Nationaal Natuurhistorisch Museum, Leiden; PCM – Powell-Cotton Museum, Birchington, Kent; PMH – Peabody Museum, Harvard; TM – Transvaal Museum; WITS – University of the Witswatersraand; ZMB – Zoologische Museum, Berlin.