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Patterns of mandibular variation in *Pan* and *Gorilla* and implications for African ape taxonomy

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Abstract

Pan and *Gorilla* taxonomy is currently in a state of flux, with the number of existing species and subspecies of common chimpanzee and gorilla having been recently challenged. While *Pan* and *Gorilla* systematics have been evaluated on the basis of craniometric and odontometric data, only a handful of studies have evaluated multivariate craniometric variation within *P. troglodytes*, and none have evaluated in detail mandibular variation in either *P. troglodytes* or *Gorilla gorilla*. In this paper, we examine ontogenetic and adult mandibular variation in *Pan* and *Gorilla*. We test the hypothesis that patterns and degrees of mandibular variation in *Pan* and *Gorilla* closely correspond to those derived from previous analyses of craniometric variation. We then use these data to address some current issues surrounding *Pan* and *Gorilla* taxonomy. Specifically, we evaluate the purported distinctiveness of *P.t. verus* from the other two subspecies of *Pan troglodytes*, and the recent proposals to recognize Nigerian gorillas as a distinct subspecies, *Gorilla gorilla diehli*, and to acknowledge mountain and lowland gorillas as two separate species. Overall, patterns and degrees of multivariate mandibular differentiation parallel those obtained previously for the cranium and dentition. Thus, differences among the three conventionally recognized gorilla subspecies are somewhat greater than among subspecies of common chimpanzees, but differences between *P. paniscus* and *P. troglodytes* are greater than those observed between any gorilla subspecies. In this regard, the mandible does not appear to be more variable, or of less taxonomic value, than the face and other parts of the cranium. There are, however, some finer differences in the pattern and degree of morphological differentiation in *Pan* and *Gorilla*, both with respect to cranial and dental morphology, and in terms of the application and manner of size adjustment. Mandibular differentiation supports the conventional separation of bonobos from chimpanzees regardless of size adjustment, but size correction alters the relative alignment of taxa. Following size correction, intergroup distances are greatest between *P.t. verus* and all other groups, but there is considerable overlap amongst chimpanzee subspecies. Amongst gorillas, the greatest separation is between eastern and western gorillas, but adjustment relative to palatal vs. basicranial length results in a greater accuracy of group classification for *G.g. gorilla* and *G.g. graueri*, and more equivalent intergroup distances amongst all gorilla groups. We find no multivariate differentiation of the Nigerian gorillas based on mandibular morphology, suggesting that the primary difference between Nigerian and other western lowland gorillas lies in the nuchal region. Though intergroup distances are greatest between *P.t. verus* and other chimpanzee subspecies, the degree of overlap amongst all three groups does not indicate a markedly

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greater degree of distinction in mandibular, as opposed to other morphologies. Finally, mandibular differentiation corroborates previous craniodental studies indicating the greatest distinction amongst gorillas is between eastern and western groups. Thus, patterns and degrees of mandibular variation are in agreement with other kinds of data that have been used to diagnose eastern and western gorillas as separate species.

Introduction

In the early part of the 20th century, many species of chimpanzee were commonly recognized, until Schwarz (1929, 1934) combined them into one, which he called *Pan satyrus*, and in his 1929 paper described a new subspecies, *Pan satyrus paniscus*. Coolidge (1933) was the first to recognize Schwarz's *paniscus* as a full species, though the significance of this step was obscured somewhat by his elevation of *Pan satyrus schweinfurthii* to specific rank as well. Schwarz (1934) disagreed, reaffirming that all chimpanzees belong to a single species. Since that date, there has been an increasing consensus that *Pan paniscus* should be given full species rank; as long ago as 1929 the name *satyrus* was suppressed by the International Commission on Zoological Nomenclature (1929), and finally in 1988 the Commission ruled that the prior available name for non-*paniscus* chimpanzees is *Pan troglodytes* Blumenbach, 1775.

The number of recognized subspecies of *P. troglodytes* is controversial: either three or four are now recognized (Morin et al., 1994; Gonder et al., 1997; Gagneux et al., 1999; Groves, 2001). Groves et al. (1992) warned that, although the then-traditional three-subspecies model was adequate for most analytic purposes, there were indications that, as far as craniometrics were concerned, divisions within some of the recognized subspecies may be at least as cogent as any that exist between them. Morin et al. (1994), on the basis of mtDNA sequencing, even proposed that West African chimpanzees constitute a distinct species, *Pan verus*.

Two subspecies of *Gorilla* were accepted for much of the 20th century (Coolidge, 1929). Vogel (1961), however, recognized two species, western *Gorilla gorilla* and eastern *G. beringei*, and awarded the latter two subspecies (*G.g. beringei* and *G.g. graueri*). Groves (1967) recognized *gorilla, graueri*, and *beringei* as three equivalent subspecies within a single species, and this became standard for another quarter-century. *Gorilla* systematics, like that of *Pan*, is today undergoing an appreciable amount of change. Some have resurrected the idea that the western and eastern gorillas are sufficiently genetically (Ruvolo et al., 1994) and morphologically (Groves, 2001) distinct to be recognized as separate species, while others have advocated recognition of one or two additional subspecies (Sarmiento et al., 1996; Oates et al., 2003; Stumpf et al., 2003).

Common chimpanzees (*Pan troglodytes*) live in geographically isolated populations, but are distributed broadly and almost continuously across central Africa, from Senegal and Gambia in the West to Uganda and Tanzania in the east (Groves, 2001). Bonobos (*Pan paniscus*), restricted to the equatorial forest of Zaïre (now called Democratic Republic of Congo (DRC)), are considerably less widespread in distribution than chimpanzees (Groves, 2001). Gorillas are also geographically isolated but their distribution across central Africa is more fragmented. Western gorillas (*Gorilla gorilla*) chiefly inhabit the western Congo Basin, with small and fragmented populations documented as far north as the Cross River along the edge of the Cameroon Highlands (Harcourt et al., 1989), and are separated from the eastern gorillas (*Gorilla beringei*) of Rwanda, Uganda and DRC by approximately 1000 km (Schaller, 1963). The eastern mountain gorillas (*G.g. beringei*) are confined to the Virunga mountain region of DRC/Rwanda/Uganda borders, and so remain geographically isolated from populations of both western and eastern lowland gorillas (*G.g. graueri*). The gorillas of the Bwindi Impenetrable Forest, situated approximately 25 km north of the Virunga mountains in Uganda, comprise a similarly small and fragmented population (Goldsmith, 2003), which may or may not constitute a separate subspecies.

There have been a number of detailed evaluations of craniometric (Fenart and Deblock, 1973; Cramer, 1974; 1977; Shea, 1983a,b,c, 1984, 1985) and odontometric (Mahler, 1973; Johanson, 1974; Kinzey, 1984; Uchida, 1996) variation in *Pan*, but far fewer investigations of craniometric variation within *P. troglodytes*. Shea and Coolidge (1988) conducted a thorough multivariate examination of craniometric variation within *P. troglodytes*, based on 17 linear dimensions of the cranium obtained from 360 adult crania. Their results revealed notable differences amongst the three geographic populations, but a markedly greater degree of separation between *P. paniscus* and *P. troglodytes*, from which they concluded that their analysis supported the tri-subspecies classification of *P. troglodytes*; but the degree of craniometric variation among the three chimpanzee subspecies was not as marked as that demonstrated for other ape taxa, such as *Gorilla* or *Pongo* (e.g., Groves, 1967, 1970a,b; Jacobshagen, 1979). In an extension of their earlier analysis, Shea et al., (1993) found that the degree of between-population differentiation in *Pan* decreased further following allometric size-correction, and that size correction altered the morphometric proximity among taxa. Nevertheless, their earlier claims for a greater degree of between-species vs. within-species craniometric differentiation remained upheld, as did their support for the two-species classification of *Pan*, and (at least) three subspecies within *P. troglodytes* (see also Groves et al., 1992).

Studies of dental variability (Mahler, 1973; Johanson, 1974; Uchida, 1996) have corroborated that the greatest morphological distinctions are between bonobos and chimpanzees, but there has been less agreement as to the nature and degree of subspecies variation. Johanson (1974), for example, found no size or proportion differences in the dentition amongst chimpanzee subspecies, whereas Uchida (1996) observed significant subspecies differences in linear dental dimensions and molar cusp areas. Notably, Uchida (1996) found clear distinctions between *verus* and the other two chimpanzee subspecies in both upper and lower molar cusp proportions, though with admittedly small samples.

There have been numerous and detailed studies of craniometric variation among gorilla subspecies. Coolidge (1929) provided the first systematic and comprehensive evaluation of craniometric variation in *Gorilla*, bringing some order into what had become total chaos. Based on univariate analyses of 17 cranial and 9 mandibular dimensions measured on 203 skulls, Coolidge (1929) concluded that the most notable and systematic differences in skull morphology were in palatal length and, to a lesser degree, cranial width between eastern ("coast") and mountain gorillas. He thus proposed a single species of *Gorilla* comprising two subspecies, *G.g. gorilla* and *G.g. beringei*, attributing much of the previously recognized differences among gorilla populations to individual variation; the only major demurral from this scheme was an early proposal to recognize the two subspecies as full species (Schultz, 1934). Coolidge's scheme was widely adopted, despite the demonstration by Haddow and Ross (1950) that there had been some irregularities in his statistical methodology.

Following the work of Coolidge, Groves (1967, 1970a,b) and Groves and Stott (1979) addressed the systematic relationships among eastern gorillas, building upon the work of Vogel (1961), who showed that eastern lowland gorillas differed from Virunga mountain gorillas in displaying less flaring of the lower jaws and a lower ascending ramus; the differences were greater among females than among males. Groves (1967, 1970a) subsequently analyzed 30 cranial and 15 mandibular dimensions on 747 skulls of adult gorillas. He demonstrated that the degree of multivariate differentiation between *G.g. gorilla* and *G.g. beringei* was similar to the degree of difference between *G.g. beringei* (of the Virunga Volcanoes) and the collection of gorilla demes distributed at lower altitudes within eastern Zaïre. Groves (1967, 1970a) therefore separated these demes into a distinct subspecies, *G.g. graueri*, retaining only the Virunga mountain gorillas within *G.g. beringei*. Patterns and degrees of dental variation have tended to support three distinct subspecies, with the greatest differences observed between *G.g. gorilla* and the two eastern subspecies, particularly (but not always) *G.g. beringei*. A number of investigators have subsequently evaluated (Casimir, 1975; Groves and Stott, 1979; Uchida, 1996, 1998) and re-evaluated (Albrecht et al., 2003; Leigh et al., 2003; Stumpf et al., 2003) gorilla systematics on the basis of craniomandibular variation, either corroborating or slightly modifying Groves' three-subspecies model.

In this paper we extend the work of previous investigators by evaluating the degree and patterning of intraspecific and interspecific mandibular variation within and between *Pan* and *Gorilla*. We test the hypothesis that patterns and degrees of mandibular variation within and between these two African ape genera generally accord with those previously established for craniodental variation (Mahler, 1973; Johanson, 1974; Shea and Coolidge, 1988; Shea et al., 1993; Uchida, 1996, 1998). Thus, we predict that degree of mandibular differentiation will be greatest between *P. paniscus* and *P. troglodytes* and least between subspecies of *P. troglodytes* or among the three gorilla groups. We further predict a greater degree of mandibular differentiation amongst gorillas than between any chimpanzee subspecies. We test these predictions using both raw and allometrically adjusted data. Finally, we apply patterns and degrees of mandibular variation, together with previously well-established patterns and degrees of craniodental differentiation, to address some current issues surrounding African ape systematics. Specifically, we are interested in whether degrees and patterns of mandibular variation provide support for 1) the purported distinctiveness of *P.t. verus* from the other two subspecies of *Pan troglodytes* based on metric (Shea et al., 1993) and nonmetric (Braga, 1995a,b) differences in cranial morphology, behavior (Doran and Hunt, 1994; Boesch, 1996), and molecular genetics (Gagneux et al., 1999); 2) the recognition of Nigerian gorillas as a distinct subspecies, *Gorilla gorilla diehli* (Sarmiento and Oates, 2000; Oates et al., 2003; Stumpf et al., 2003); and 3) the recognition of mountain and lowland gorillas as two separate species on the basis of general morphology (they are diagnosably different: Groves, 2000), dental characteristics (Uchida, 1998) and genetic differentiation (Garner and Ryder, 1996). We have insufficient mandibular material to test the recently proposed resurrection of *Pan t. vellerosus* as a distinct subspecies (Gonder et al., 1997; Gagneux et al., 1999), or the possibility of a separate subspecies of gorilla in the Bwindi Impenetrable Forest (Sarmiento et al., 1996); nor will we at this time test the possibility that further splitting may be warranted within *Pan troglodytes* (Groves et al., 1992; Groves, in preparation).

There are several reasons why an analysis of mandibular variation in these taxa is warranted. First, though there have been studies of within and between group variation in both *Pan* and *Gorilla*, the primary focus of these studies has been on cranial and dental variation, with less attention paid to the mandible, except for the forty-year-old study by Vogel (1961). The multivariate studies of craniometric variation in *Pan* (Shea and Coolidge, 1988; Shea et al., 1993), for example, did not include mandibular dimensions, and while mandibular dimensions have been incorporated in some studies of variation in *Gorilla* (Groves, 1970a), it seems safe to say that exploration of mandibular variation has not been comprehensive within this group. Although it is logical to assume structural and functional integration of the cranium and mandible, different, if overlapping, functional domains between the cranium and mandible suggest these morphological units need not be subject to precisely the same set of developmental constraints. Differences in patterns of cranial, mandibular and dental allometry have been demonstrated in several primate taxa (Cochard, 1985; Cole, 1992; Ravosa, 1992; Daegling, 1996; Taylor, 2002). Furthermore, several investigators (Wood and Lieberman, 2001; Plavcan, 2002) have shown that patterns and degrees of variation differ regionally, even among components of the cranium and mandible, suggesting that the mandible may be more or less free to vary than the cranium. As a matter of practicality, the differential preservation of mandibles in the fossil record in general, and the relatively recent accumulation of hominoid and hominid fossil mandibles in particular, mandates a critical examination of mandibular differentiation between and within these two genera.

Second, we analyze both raw data, and data size-adjusted using ontogenetic allometry. This is important, because, in comparisons between *Pan* species, Shea et al. (1993) showed that allometric size adjustment altered the relative morphological proximity of *Pan* taxa to each other. In their study, *P. paniscus* was found to align most closely with *P.t. schweinfurthii*, in contradistinction to the unadjusted data, which aligned *P. paniscus* most closely with *P.t. verus*. In their within-species analysis, these authors further demonstrated that allometric size adjustment substantially decreased the degree of morphological divergence found to exist between *P.t. troglodytes* and *P.t. schweinfurthii* based on the nonadjusted data, suggesting that "the primary differences driving the divergence of *P.t. troglodytes* and *P.t. schweinfurthii* in the non-size-corrected analysis are due to size and allometric factors". With the exception of the study by Shea et al. (1993) on *Pan*, we are aware of no other detailed studies of craniometric variation in an African ape on allometrically size-adjusted data (but see Stumpf et al. [2003] for an evaluation of gorilla cranial variation using static adult size correction). Significant localized differences in facial size amongst gorilla subspecies (Taylor, 2003) suggest that allometric size adjustment may have an important impact on the outcome of studies of gorilla mandibular variation. Thus, allometric size adjustment should help to clarify the patterning and degree of mandibular differentiation in both *Pan* and *Gorilla*.

Finally, understanding patterns and degrees of within vs. between-species morphological variation provides an important framework for evaluating and interpreting the functional, adaptive and evolutionary significance of such patterns at higher taxonomic levels and in the fossil record. This seems especially critical in light of the current taxonomic restructuring that has been justified by investigators on morphological (Groves, 2001; Stumpf et al., 2003) as well as genetic (Ruvolo et al., 1991) grounds. A thorough and comprehensive look at mandibular variation should provide a more complete picture of intra- and inter- specific morphological variation in these taxa, and be incorporated into the entire evidentiary framework for evaluating systematic relationships within and among extant and fossil apes.

Materials and methods

Samples

Two sets of data are used in this study. One dataset comprises a mixed-sex, ontogenetic and adult series of 669 crania and mandibles: 230 skulls of *Gorilla* and 439 of *Pan* (data collected by A.B. Taylor). We do not incorporate CPG's substantial dataset of chimpanzees because the majority of measurements are of the cranium rather than the mandible. The *Pan* adult sample includes 26 *P. paniscus*, 28 *P.t. schweinfurthii*, 79 *P.t. troglodytes* and 56 *P.t. verus*. Adult samples for the three conventionally (*sensu* Groves, 1967) recognized subspecies of *Gorilla* include 27 *G.g. beringei*, 60 *G.g. gorilla* and 36 *G.g. graueri*. All of the eastern mountain gorilla material derives from the Virunga volcano region and so excludes any individuals from the Bwindi Impenetrable Forest that may represent a distinct gorilla subspecies (Sarmiento et al., 1996). Likewise, the entire sample of *P.t. verus* originates from Liberia, and therefore does not contain any putative *P.t. vellerosus* from Nigeria and adjacent parts of west Cameroon (Gonder et al., 1997). While most samples are smaller (though some larger), than those incorporated in previous studies of African ape cranial (e.g., Groves, 1970a; Shea and Coolidge, 1988; Shea et al., 1993) and dental (e.g., Mahler, 1973; Johanson, 1974) variation, we believe the samples are sufficient to provide a reasonable "yardstick" (Albrecht and Miller, 1993; Albrecht et al., 2003) for establishing the overall patterning of mandibular variation within and between populations, and for comparing the patterns and degrees of mandibular variation between and among species/subspecies. Gorillas, in particular, though highly variable as a genus, appear to exhibit similar levels of cranial variability across subspecies (Albrecht et al., 2003). Locality information, which is critical in this type of analysis, was derived from museum records and only specimens of known, unambiguous provenance were incorporated.

We also employ Groves' (1967, 1970a) well-known and extensive dataset of adult gorillas. Groves measured mandibular (and cranial) dimensions for the three traditionally recognized gorilla subspecies, as well as the gorillas of the

Table 1
Mandibular measurements

Taylor
Condylion—incision (MANDIBLEN)
Gonion—incision (OCCLUSALLEN)
Condylion—gonion (RAMUSHT)
Coronoid—inferior mandible (ANTRAMALHT)
Condylion laterale—condylion laterale (BICONBRE)
Occlusal plane of M2—superior condyle (CONDYLEHT)
Anterior margin of ramus—posterior margin of ramus (RAMUSWD)
M_1 mandibular corpus width (M1CPWD)
M_2 mandibular corpus width (M2CPWD)
M_1 mandibular corpus height (M1CPDP)
M_2 mandibular corpus height (M2CPDP)
Symphyseal width (SWD)
Symphyseal height (SDP)
Condylar length (CONLEN)
Condylar width (CONWD)
Condylion—coronoid (TEMPINS)
Lateral I_2—lateral I_2 (INCISORLEN)

Groves
Bicondylar breadth (condylion laterale—condylion laterale)
Condylar width (mediolateral width of condyle)
Jaw length (greatest length of mandible from symphysis to intercondylar line in median plane)
Sigmoid notch width
Sigmoid notch depth
Ramal height (ascending ramal height from inferior margin of ramus to coronoid process)
Ramal breadth (ascending ramal breadth at right angles to ramal height, wherever greatest)
Bigonial breadth (gonion—gonion wherever greatest)
Mandibular toothrow length (alveolus of P3—alveolus of M3)
Jaw breadth (outside of M_2—outside of M_2)
Projected length from infradentale to posterior margin of inferior transverse torus
Jaw depth (greatest depth of mandibular body)
P2 alveolus—foramen mentale
Canine alveolus—foramen mentale
Nearest point on any alveolar margin to foramen mentale

Cross-River region along the Nigerian-Cameroon border, which, it has been recently suggested, represent a distinct subspecies, *Gorilla gorilla diehli* Matschie (Sarmiento and Oates, 2000; Groves, 2001; Oates et al., 2003). The mixed-sex samples include 350 *G.g. gorilla*, 67 *G.g. graueri*, 26 *G.g. beringei*, and 13 of the recently resurrected *G.g. diehli*. As roughly only 5% of our combined samples of gorilla mandibles overlap, and comparable measurements between our samples are few, we analyze this dataset separately.

Measurements

Taylor's data include a maximum of 17 linear dimensions of the mandible obtained on ontogenetic series of *Pan* and *Gorilla* (Table 1). Groves' data for *Gorilla* comprise 15 mandibular dimensions obtained on adults (Table 1). These two sets of mandibular measurements, though not exhaustive, are believed to adequately represent mandibular variation. For more details on measurement definitions and sources see Groves (1967, 1970a; Taylor, 2002, 2003).

Statistical analyses

Multiple methods of analysis were utilized in this investigation. Using Taylor's data, significant differences in mandibular size and shape (proportions) were evaluated using one-way analysis of variance (ANOVA). These tests were performed within *Pan* and *Gorilla*, separately by sex, and the conventional Bonferroni adjustment applied to protect against Type I errors associated with multiple pairwise comparisons. Because proportions often violate distributional assumptions, the arcsine (or angular) transformation was applied to mandibular proportions before subjecting the data to statistical testing (Sokal and Rohlf, 1995). These statistical analyses were completed using SYSTAT (version 8.0) and results judged statistically significant at $P<0.05$.

To evaluate the influence of ontogeny on within- and between- group mandibular differentiation, regression analysis was performed on $\log_{10}$-transformed data to describe scaling trajectories. In all bivariate comparisons, basicranial length (basion to nasion) is used as the independent variable. Basicranial length is suitable in this case, since the purpose here is to assess the patterning and degree of variation in the mandible as a consequence of differences in relative growth and size (Smith, 1993), and not to evaluate the relationship between mandibular variation and diet (Bouvier, 1986). Logically, ordinary least squares (OLS) regression applies when one variable is used to scale another, and this, plus analysis of covariance (ANCOVA), together provide the most robust technique. However, error in both the dependent and independent variables, and some lower correlation coefficients, particularly for *G.g. beringei* and *P.t. verus*, argue for reduced major axis regression (RMA; Clarke, 1980). Therefore, we present RMA regression statistics, but consider scaling trajectories to be significantly ($P<0.05$) different between groups only if both OLS and RMA results were concordant. We generated OLS regressions and applied ANCOVA to test for differences in OLS slopes and y-intercepts using SYSTAT (version 8.0). RMA regression coefficients were generated using the NONLIN module in SYSTAT and differences in RMA slopes evaluated using a statistical program written by Tim Cole. We applied the "Quick Test" of Tsutakawa and Hewett (1977) to test for elevation differences, also using the NONLIN module in SYSTAT. We note that high correlation coefficients ($r \geq 0.90$) in many cases resulted in only minor differences in regression coefficients, and relatively few instances in which both techniques did not yield similar results.

Within *Pan* and *Gorilla*, the patterning and degree of multivariate differentiation among groups was assessed and displayed graphically using Canonical variates or Discriminant Function analysis (CVA or DFA) and generalized distances (Mahalanobis D^2); CVA was also used to evaluate which variables were particularly influential in effecting group separation. CVA is particularly suited to this type of analysis because it partitions groups by maximizing between-group variance while minimizing within-group variance. CVA produces multiple canonical axes—linear functions of variables that are orthogonal to each other. The first axis contains linear functions of variables that produce the greatest degree of separation, and is followed by additional linear combinations of variables that are uncorrelated with the first and subsequent axes, and which produce successively less separation. The total number of axes produced will either be equal to the number of variables in the analysis, or one less than the number of groups. Much of the variance that accounts for group separation is typically contained within the first two or three axes (Oxnard, 1972, 1983). CVA has been used for similar types of studies by numerous investigators (Groves, 1967, 1970a; Albrecht, 1978, 1980; Reyment et al., 1984; Oxnard, 1987; Albrecht and Miller, 1993), and so has the added advantage of facilitating comparison of our results with findings of within vs. between-group craniometric variation in *Pan* and *Gorilla* derived from the same multivariate methods (e.g., Groves, 1967, 1970a; Shea and Coolidge, 1988; Shea et al., 1993; Uchida, 1996). In analyses of *Pan* and *Gorilla*, we excluded MANDIBLEN, ANTRAMALHT, M1CPWD, M1CPDP and CONDYLEHT to reduce the undesirable effects of multicollinearity (see Table 1 for variable names and abbreviations). INCISORLEN was additionally excluded because of an unacceptable reduction in sample size. Therefore, CVAs were performed on 11 of the original 17 variables. We note that CVAs performed on the entire set of 17 variables reduced sample sizes, particularly for *P.t. verus*, and were accompanied by an increase in the percentage correctly classified, but marginally affected the generalized distances and relative alignment of taxa. Given the importance of capturing as much variation as possible within each taxon, we deemed it more important to maximize sample sizes at the expense of a few variables. All CVAs were performed using SPSS (version 10.0).

Following Shea et al., (1993), CVAs for *Pan* and *Gorilla* are carried out on raw data, and on adult mandibular values size-adjusted by deriving residuals relative to least-squares bivariate regressions, again using basicranial length as the independent variable. As gorillas differ significantly in facial size (Taylor, 2003), residuals are also derived relative to OLS bivariate regressions using palatal length as the independent variable in order to evaluate the effect of adjustment for facial size on multivariate differentiation. Ontogenetic size adjustment for *Pan* was accomplished by deriving residuals from regressions of all *P. paniscus* and *P. troglodytes* combined (in other words, from a single *Pan* regression line). Residuals for *Gorilla* were similarly derived using a single *Gorilla* regression line. Small ontogenetic samples of *G.g. beringei* and *P.t. verus* precluded separation of the sexes; therefore, CVAs are performed on males and females combined, which also reduces size effects. Finally, we performed a CVA on raw mandibular values using Groves' data in order to evaluate the distinctiveness of the Nigerian gorillas. For all CVAs, accuracy of group classification is based on cross-validation in which each case is classified by the functions derived from all cases excluding that one. Accuracy of group classification is based on unequal sample sizes. We test for significant discriminant functions using Wilks' Lambda, a robust measure of group differences over multiple variables (Olson, 1974). All statistical analyses were carried out by ABT.

Results

Between-group differences in mandibular size and shape

Pan

Descriptive statistics for both *Pan* and *Gorilla* are provided in the Appendix. In same-sex pairwise comparisons of mean linear dimensions between taxa, the majority of significant differences in adult mandibular size occur between *P. troglodytes* and *P. paniscus*, with *P. paniscus* being markedly smaller (Table 2). These results are entirely concordant with the well-established pattern of relatively smaller cranial (Shea, 1983a,b,c, 1984) and dental (Mahler, 1973; Johanson, 1974; Kinzey, 1984; Uchida, 1996) size in *P. paniscus*. Amongst chimpanzee subspecies, *P.t. verus* differs consistently from the other two taxa in having an absolutely wider symphysis. In addition, *P.t. verus* has an absolutely shorter posterior ramal height as compared to *P.t. troglodytes*. Interestingly, there are no species or subspecies differences in condylar length.

In same-sex comparisons, adult shape differences occur with greatest frequency between bonobos and common chimpanzees (Table 3). These include consistent differences in M_1 and M_2 corpus width and symphyseal height. We find additional proportion differences related to mandibular shape (e.g., corpus height, gonion-incision, condyle-incision), symphyseal shape (i.e., symphyseal width), and jaw height (i.e., posterior ramal height) in multiple pairwise comparisons between *P. troglodytes* and *P. paniscus*. A number of shape differences occur in only one or the other sex.

Among *P. troglodytes* subspecies, differences least often occur between *P.t. troglodytes* and *P.t. verus*, and most often between *P.t. schweinfurthii* and *P.t. verus.* (Table 3) *P.t. verus*, in particular, has a relatively wider symphysis than the other two subspecies, and compared to male *P.t. schweinfurthii*, male *P.t. verus* have a relatively narrower ramus, shorter mandible, and shorter condylar and ramal heights. As there are no subspecies differences in basicranial length (Table 2), both absolute and relative size differences in mandibular dimensions account for these proportion differences.

Gorilla

In same-sex comparisons, differences in mandibular size occur with greater frequency in *Gorilla gorilla* than in *Pan troglodytes*, but no between-group comparisons approach the frequency of differences observed between *P. paniscus* and any subspecies of chimpanzee (Tables 2 and 4). The highest frequency of size differences occurs

Table 2
Results of same-sex pairwise comparisons for statistical differences in mean linear dimensions between taxa in *Pan*[1,2]

	PTT/PTS		PTT/PTV		PTS/PTV		PTT/PP		PTS/PP		PTV/PP	
Variable (mm)	M	F	M	F	M	F	M	F	M	F	M	F
Basicranial length	NS	NS	NS	NS	NS	NS	*	*	*	*	*	*
Palatal length	NS	NS	NS	NS	NS	NS	*	*	*	*	*	*
M_1 Corpus height	NS	NS	NS	NS	NS	NS	*	*	*	*	*	*
M_2 Corpus height	NS	NS	NS	NS	NS	NS	*	*	*	*	*	*
M_1 Corpus width	NS	NS	NS	NS	NS	NS	*	*	*	*	*	*
M_2 Corpus width	NS	NS	NS	NS	NS	NS	*	*	*	*	*	*
Symphyseal height	NS	NS	NS	NS	NS	NS	*	*	*	*	*	*
Symphyseal width	NS	NS	*	*	*	*	*	*	*	NS	*	*
Incisor cord length	*	NS	NS	NS	*	NS	*	*	*	*	*	*
Bicondylar breadth	NS	NS	NS	NS	NS	NS	*	*	*	*	*	*
Condylar length	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Condylar width	NS	NS	NS	NS	NS	NS	*	*	*	*	*	*
Condyle-incision	NS	NS	NS	NS	NS	NS	*	*	*	*	*	*
Gonion-incision	NS	NS	NS	NS	NS	NS	*	*	*	*	*	*
Condyle-coronoid	NS	*	*	NS	NS	NS	*	*	*	*	*	*
Ramal width	NS	NS	*	NS	NS	NS	*	*	*	*	*	*
Anterior ramal height	NS	NS	NS	NS	NS	NS	*	*	*	*	*	*
Posterior ramal height	NS	NS	*	*	*	NS	*	*	*	*	*	*
Condylar height	NS	NS	*	NS	NS	NS	*	*	*	*	NS	*

*, $P<0.05$; NS, not significant.

[1] Results based on Bonferroni-adjusted one-way ANOVAs by taxon.

[2] PTT, *Pan t. troglodytes*; PTS; *Pan t. schweinfurthii*; PTV, *Pan t. verus*; PP, *Pan paniscus*.

in comparisons between *G.g. gorilla* and *G.g. beringei*. *G.g. beringei* is consistently larger than *G.g. gorilla* in most mandibular dimensions, the exceptions being symphyseal height, condylar length, condyle-coronoid distance, and incisor cord length (in same sex comparisons Uchida (1996) found no differences in upper incisor cord lengths). *G.g. graueri* has absolutely wider corpora at M_1, higher symphyses, longer jaws (condyle–incision, gonion–incision), higher posterior rami and longer incisor cords as compared to *G.g. gorilla*; in addition, *G.g. graueri* males have absolutely higher mandibular corpora, wider mandibular rami and higher condyles. As expected, both *beringei* and *graueri* have longer palates as compared to *G.g. gorilla* (Coolidge, 1929; Uchida, 1996; Taylor, 2003). There are fewest differences between the two eastern gorillas; male and female *G.g. beringei* exhibit wider symphyses and condyles, and higher posterior rami and condyles.

Adult shape differences occur predominantly in comparisons between the Virunga mountain and western lowland subspecies (Table 5), consistent with previous findings of adult differences in mandibular proportions relative to jaw length (Taylor, 2002, 2003). *G.g. beringei* consistently have relatively wider mandibular symphyses, and wider and higher condyles, as compared to *G.g. gorilla* and *G.g. graueri.* *G.g. gorilla* have shorter mandibles (gonion-incision) as compared to the two eastern gorilla subspecies. Females show more proportion differences as compared to males, as Vogel (1961) also demonstrated.

Scaling patterns in the mandible

Pan

Bivariate regressions show moderate to high correlations except in *P.t. verus*, for which non-adult samples are relatively small and, probably as a consequence, more than 50% of the slopes are not significantly different from zero (Table 6). However, there may be other reasons for the comparatively low correlations observed in *verus*

Table 3
Results of same-sex pairwise comparisons for statistical differences in mean shape ratios between adult taxa in *Pan*[1,2]

	PTT/PTS		PTT/PTV		PTS/PTV		PTT/PP		PTS/PP		PTV/PP	
vs. Basicranial length	M	F	M	F	M	F	M	F	M	F	M	F
M_1 Corpus height	NS	NS	NS	NS	NS	NS	*	*	*	NS	*	NS
M_2 Corpus height	NS	NS	NS	NS	NS	NS	NS	NS	*	NS	NS	NS
M_1 Corpus width	NS	NS	NS	NS	NS	NS	*	*	*	*	*	*
M_2 Corpus width	NS	NS	NS	NS	NS	NS	*	*	*	*	*	*
Symphyseal height	*	*	NS	NS	NS	NS	*	*	*	*	*	*
Symphyseal width	NS	NS	*	*	*	*	*	NS	*	NS	*	*
Incisor cord length	NS	NS	NS	NS	NS	NS	NS	*	NS	NS	NS	*
Bicondylar breadth	NS	NS	NS	NS	NS	NS	NS	*	NS	NS	NS	NS
Condylar length	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	*
Condylar width	*	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Gonion-incision	*	NS	NS	NS	*	NS	NS	*	*	*	NS	NS
Condyle-incision	NS	NS	NS	NS	*	NS	*	*	*	*	*	NS
Condyle-coronoid	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Ramal width	NS	NS	NS	NS	*	NS	NS	NS	*	NS	NS	NS
Anterior ramal height	NS	NS	NS	NS	*	NS	NS	*	NS	NS	NS	NS
Posterior ramal height	NS	NS	*	NS	*	NS	NS	*	*	*	NS	NS
Condylar height	NS	NS	NS	NS	*	NS	NS	*	NS	NS	NS	NS

*, $P<0.05$; NS, not significant.

[1] The arcsine transformation was applied to shape proportions and results based on Bonferroni-adjusted one-way ANOVAs by taxon.

[2] PTT, *Pan t. troglodytes*; PTS; *Pan t. schweinfurthii*; PTV, *Pan t. verus*; PP, *Pan paniscus*.

(see Discussion below). Shape clearly changes during growth in males and females, but there are few differences between the sexes and scaling patterns are similar in bonobos and chimpanzees (Table 6). We note that for bonobos, in particular, slope differences between the sexes are eliminated when analyses are performed on trajectories excluding the youngest dental stages (i.e., mandibles with only deciduous dentition), suggesting these differences are likely accounted for by disproportionate sampling at younger stages. All taxa exhibit strong positive allometry of mandibular height dimensions, including M_1 corpus and symphyseal heights, and anterior, posterior and condylar heights. Condylar dimensions, jaw length (gonion-incision and condyle-incision) and ramal width are also strongly positively allometric. Bicondylar breadth and symphyseal width tend to hover around isometry or scale with slight negative allometry. Slopes for corpus width at M_1 and M_2 are typically not significantly different from zero, and the correlation coefficients are notably low in the few instances in which these slopes are significant. Slopes for corpus height at M_2 are lower, sometimes substantially, than those for corpus height at M_1.

In same-sex pairwise comparisons between species and subspecies of *Pan*, there are a number of significant departures from ontogenetic scaling of the mandible (Table 7). However, of 262 possible pairwise comparisons (408 less the 146 slopes/y-intercepts not tested because the slopes did not depart significantly from zero), only about 15% reflect significant differences in ontogenetic trajectories between *Pan* species and subspecies. The greatest number of departures from ontogenetic scaling of mandibular dimensions occurs between *P. paniscus* and *P.t. schweinfurthii*.

Gorilla

Correlation coefficients for bivariate regressions are moderately high excepting *G.g. beringei*; sample size is likely an issue here (Table 8). Scaling trends are remarkably similar in *Gorilla* and *Pan*. Although scaling differences between the sexes are few, slopes tend to be higher for females as compared to males (cf. Daegling, 1996), suggesting that

Table 4
Results of same-sex pairwise comparisons for statistical differences in mean linear dimensions between taxa in *Gorilla*[1,2]

	GGG/GGGR		GGG/GGB		GGGR/GGB	
Variable (mm)	M	F	M	F	M	F
Basicranial length	NS	NS	NS	NS	NS	NS
Palatal length	*	*	*	*	NS	NS
M_1 Corpus height	*	NS	*	*	NS	NS
M_2 Corpus height	*	NS	*	*	NS	NS
M_1 Corpus width	*	*	*	*	NS	*
M_2 Corpus width	NS	NS	*	*	NS	*
Symphyseal height	*	*	*	NS	NS	NS
Symphyseal width	NS	NS	*	*	*	*
Bicondylar breadth	NS	NS	*	*	NS	NS
Condylar length	NS	NS	NS	NS	NS	NS
Condylar width	NS	NS	*	*	*	*
Condyle-incision	*	*	*	*	NS	NS
Gonion-incision	*	*	*	*	NS	NS
Condyle-coronoid	NS	NS	NS	NS	NS	NS
Ramal width	*	NS	*	*	NS	NS
Anterior ramal height	NS	NS	*	*	NS	*
Posterior ramal height	*	*	*	*	*	*
Condylar height	*	NS	*	*	*	*
Incisor cord length	*	*	*	NS	NS	NS

*, $P<0.05$; NS, not significant.

[1] Results based on Bonferroni-adjusted one-way ANOVAs by taxon.

[2] GGG, *Gorilla g. gorilla*; GGGR, *Gorilla g. graueri*; GGB, *Gorilla g. beringei*.

rates of shape change occur relatively faster in females. Taken in conjunction with the differential extension of males along a common trajectory with females, this suggests that females achieve adult mandibular growth earlier than do males. These results are consistent with the high rates and early cessation of growth in adult body weight in females as compared to males, who experience prolonged growth rates relative to females (Leigh and Shea, 1995, 1996). Gorilla subspecies show a greater percentage (19%) of departures from ontogenetic scaling of mandibular proportions than is observed in comparisons between chimpanzee subspecies (16%). The greatest number occurs between the eastern and western lowland gorillas (Table 9).

Multivariate mandibular differentiation

Pan

Based on the non size-adjusted CVA, sexes combined, mandibular dimensions completely separate *P. paniscus* from *P. troglodytes* (Table 10a and Fig. 1a), mirroring the univariate results presented earlier. These findings are consistent with Cramer's (1977) observation that mandibular length alone achieves a clean separation of adult bonobos from chimpanzees, and accord with previous results for the cranium (e.g., Shea and Coolidge, 1988; Shea et al., 1993). The first ($\chi^2 = 309.4$; df = 33, $P<0.001$) and second ($\chi^2 = 114.0$; df = 20; $P<0.001$) discriminant functions are significant. The variables most important in effecting species differentiation along the first canonical variates axis include width of the corpus, symphyseal height, jaw length and ramal height. Intergroup centroid distances indicate that *P. paniscus* is morphologically most distinct from *P.t. troglodytes* and least distinct from *P.t. schweinfurthii* (Table 10b). Overlap is evident amongst the three chimpanzee subspecies, particularly between *schweinfurthii* and *troglodytes*, while *verus* and *schweinfurthii* remain more distinct from each other along Axis 2. Symphyseal width shows the highest correlation with the second canonical

Table 5
Results of same-sex pairwise comparisons for statistical differences in mean shape ratios between adult taxa in *Gorilla*[1,2]

	GGG/GGGR		GGG/GGB		GGGR/GGB	
vs. Basicranial length	M	F	M	F	M	F
M_1 Corpus height	NS	NS	NS	NS	NS	NS
M_2 Corpus height	NS	NS	NS	NS	NS	NS
M_1 Corpus width	NS	*	*	*	NS	*
M_2 Corpus width	NS	NS	NS	*	NS	NS
Symphyseal height	*	*	NS	NS	NS	NS
Symphyseal width	NS	NS	*	*	*	*
Incisor cord length	NS	*	NS	NS	NS	NS
Bicondylar breadth	NS	NS	NS	NS	NS	NS
Condylar length	NS	*	NS	NS	NS	NS
Condylar width	NS	NS	*	*	*	*
Gonion-incision	*	*	*	*	NS	NS
Condyle-incision	*	*	*	NS	NS	NS
Condyle-coronoid	NS	NS	NS	NS	NS	NS
Ramal width	NS	NS	NS	*	NS	NS
Anterior ramal height	NS	NS	NS	*	NS	*
Posterior ramal height	NS	NS	NS	NS	NS	NS
Condylar height	NS	NS	*	*	*	*

*, $P<0.05$; NS, not significant.
[1] Results based on Bonferroni-adjusted one-way ANOVAs by taxon.
[2] GGG, *Gorilla g. gorilla*; GGGR, *Gorilla g. graueri*; GGB, *Gorilla g. beringei*.

axis. The relative morphological distinctiveness of *P.t. verus* from the other chimpanzee subspecies is reflected in the intergroup centroid distances. These findings again accord with those previously obtained for the cranium (Shea et al., 1993; Braga, 1995a,b), though lower integroup distances between all chimpanzee subspecies are observed in Shea et al.'s (1993) study.

Exclusion of bonobos from the CVA produces greater overlap amongst chimpanzee subspecies (Fig. 1b), as Shea et al. (1993) also observed, along with a negligible drop in the intergroup centroid distances (not shown). The distinction diminishes between *verus* and the other two subspecies, but the greatest overlap is still apparent between *troglodytes* and *schweinfurthii*, with a slight shift of *verus* to the right along Axis 1. The first discriminant function is significant ($\chi^2 = 111.2$; df = 22, $P<0.001$), and symphyseal width remains the most highly correlated with the first canonical variates axis.

Size adjustment for *Pan* using basicranial and palatal lengths yielded virtually identical results; therefore, only those for basicranial length are presented (Tables 10a-b). Accuracy of group classification decreases in all groups following ontogenetic size adjustment, though decrease in intergroup distances is greatest between *P. paniscus* and *P. troglodytes*. However, it must be remembered that we completed the CVAs on a subset of 11 variables and accuracy of group classification is based on unequal sample sizes. In CVAs in which all 17 variables were entered into the analysis, both raw and size-adjusted results yielded 100% correct classification of bonobos; this analysis, however, also reduced the *P.t. verus* sample size from 43 to 32. Importantly, analyses performed assuming equal sample sizes also resulted in higher percentages of correct classification for all taxa, but only 100% accuracy for bonobos.

Apart from intergroup distances, size adjustment alters the relative alignment of one subspecies to another: though *P. paniscus* remains most closely aligned with *P.t. schweinfurthii*, size correction now places *paniscus* furthest from *P.t. verus* (Table 10b and Fig. 2a). Amongst the three subspecies, *P.t. troglodytes* and *P.t. schweinfurthii* remain most closely aligned with each other

Table 6
Reduced major axis regression statistics for *Pan* separately by taxon and sex[1–3]

	P. paniscus					*P.t. troglodytes*					*P.t. schweinfurthii*					*P.t. verus*				
vs. Basicranial length	k	y	CI	r	n	k	y	CI	r	n	k	y	CI	r	n	k	y	CI	r	n
Bicondylar breadth	1.15	−0.25	±0.12	0.95	43	1.04	−0.06	±0.09	0.93	87	1.08	−0.13	±0.11	0.96	34	1.01	0.01	±0.37	0.58	29
	1.02	0.00	±0.11	0.96	33	1.06	−0.09	±0.11	0.92	62	1.07	−0.10	±0.11	0.95	41	**1.03**	−0.02	±0.43	0.32	34
Gonion-incision	1.55	−1.02	±0.16	0.95	40	1.50	−0.92	±0.11	0.95	84	1.52	−0.97	±0.15	0.96	35	**1.11**	−0.16	±0.48	0.37	30
	1.45	−0.83	±0.12	0.98	31	1.41	−0.76	±0.10	0.96	62	1.54	−1.00	±0.13	0.97	42	1.19	−0.30	±0.33	0.70	34
Condyle-incision	1.48	−0.82	±0.12	0.97	41	1.48	−0.81	±0.10	0.95	89	1.50	−0.85	±0.13	0.97	35	**1.00**	0.13	±0.44	0.36	30
	1.38	−0.62	±0.09	0.99	31	1.40	−0.66	±0.10	0.96	62	1.51	−0.86	±0.11	0.98	41	1.09	−0.05	±0.35	0.58	35
M_1 Corpus height	1.83	−2.18	±0.26	0.92	36	1.65	−1.85	±0.18	0.89	87	1.86	−2.24	±0.30	0.91	31	1.70	−1.94	±0.73	0.39	30
	1.54	−1.67	±0.24	0.93	28	1.76	−2.08	±0.17	0.93	59	1.84	−2.21	±0.21	0.94	41	1.80	−2.17	±0.63	0.51	35
M_2 Corpus height	2.11	−2.73	±0.77	0.63	26	1.77	−2.10	±0.31	0.75	65	1.70	−1.97	±0.47	0.86	17	**0.87**	−2.30	±0.82	0.36	30
	1.38	−1.35	±0.44	0.84	16	1.52	−1.61	±0.27	0.84	44	1.86	−2.27	±0.43	0.83	28	1.83	−2.25	±0.61	0.56	35
M_1 Corpus width	**0.68**	−0.26	±0.28	0.19	34	0.83	−0.51	±0.20	0.37	87	**0.68**	−0.20	±0.30	0.34	31	**1.29**	−1.43	±0.68	0.08	30
	0.56	−0.02	±0.25	0.35	28	0.65	−0.14	±0.14	0.67	59	0.77	−0.36	±0.24	0.54	41	**1.53**	−1.90	±0.64	0.30	35
M_2 Corpus width	**1.59**	−1.99	±0.80	0.09	26	**1.09**	−1.01	±0.30	0.22	65	**1.06**	−0.95	±0.73	0.10	17	**1.59**	−1.99	±0.73	0.02	30
	1.09	−1.04	±0.70	0.44	16	0.77	−0.37	±0.23	0.57	42	**1.06**	−0.93	±0.55	0.19	28	1.36	−1.55	±0.52	0.42	35
Symphyseal height	1.43	−1.24	±0.11	0.97	43	1.57	−1.50	±0.14	0.92	91	1.54	−1.43	±0.16	0.95	36	**1.41**	−1.17	±0.63	0.34	30
	1.22	−0.86	±0.13	0.96	33	1.46	−1.29	±0.12	0.95	62	1.72	−1.77	±0.17	0.95	42	1.77	−1.89	±0.54	0.63	35
Symphyseal width	1.13	−1.05	±0.18	0.87	43	1.02	−0.82	±0.17	0.71	90	1.12	−1.05	±0.24	0.81	36	**1.64**	−2.02	±0.80	0.21	30
	0.81	−0.44	±0.21	0.75	33	1.17	−1.11	±0.18	0.82	62	1.19	−1.14	±0.20	0.85	42	1.51	−1.77	±0.58	0.42	35
Incisor cord length	0.88	−0.34	±0.16	0.86	38	1.07	−0.67	±0.15	0.82	79	0.96	−0.47	±0.20	0.86	31	**0.88**	−0.29	±0.56	0.04	19
	0.79	−0.17	±0.15	0.90	28	1.10	−0.73	±0.18	0.83	57	1.02	−0.59	±0.17	0.88	40	**1.16**	−0.86	±0.60	0.24	26
Condylar length	2.07	−3.04	±0.29	0.90	43	2.10	−3.15	±0.25	0.85	90	1.43	−1.84	±0.33	0.78	36	**3.52**	−6.00	±2.10	0.15	29
	2.17	−3.24	±0.39	0.88	33	1.92	−2.82	±0.24	0.88	62	1.51	−1.98	±0.31	0.80	42	**3.02**	−5.03	±1.27	0.80	35
Condylar width	1.81	−2.22	±0.21	0.93	43	1.86	−2.35	±0.19	0.89	90	1.59	−1.80	±0.20	0.92	36	**2.17**	−2.96	±0.98	0.34	29
	1.75	−2.11	±0.25	0.93	33	1.58	−1.81	±0.16	0.92	62	1.68	−1.97	±0.20	0.93	42	2.13	−2.91	±0.76	0.50	35
Condylar joint height	1.30	−0.96	±0.30	0.79	36	1.68	−1.68	±0.23	0.81	83	1.77	−1.85	±0.33	0.88	31	**2.61**	−3.56	±1.40	0.23	30
	1.59	−1.49	±0.22	0.94	28	1.57	−1.46	±0.25	0.83	59	2.01	−2.31	±0.22	0.94	41	**2.52**	−3.40	±1.34	0.13	35
Anterior ramal height	1.61	−1.39	±0.19	0.93	42	1.65	−1.46	±0.15	0.91	89	1.69	−1.54	±0.21	0.94	36	**1.64**	−1.46	±0.86	0.08	25
	1.54	−1.24	±0.17	0.96	33	1.51	−1.21	±0.14	0.94	62	1.75	−1.65	±0.20	0.93	42	1.65	−1.50	±0.63	0.42	28
Posterior ramal height	1.61	−1.34	±0.16	0.95	43	1.64	−1.39	±0.12	0.94	87	1.77	−1.65	±0.18	0.96	36	1.96	−2.04	±0.92	0.41	25
	1.62	−1.36	±0.13	0.98	33	1.64	−1.41	±0.16	0.93	62	1.89	−1.87	±0.15	0.97	42	**1.51**	−1.17	±0.69	0.35	28
Condyle-coronoid	2.05	−2.45	±0.21	0.95	41	1.74	−1.88	±0.17	0.92	88	1.94	−2.29	±0.22	0.95	36	**2.11**	−2.62	±1.01	0.24	30
	1.79	−1.99	±0.22	0.95	33	1.88	−2.17	±0.20	0.92	62	2.22	−2.84	±0.24	0.94	41	1.93	−2.28	±0.77	0.37	35
Ramal width	1.57	−1.48	±0.16	0.95	43	1.58	−1.50	±0.12	0.94	90	1.49	−1.31	±0.16	0.95	36	**1.42**	−1.19	±0.76	0.06	30
	1.48	−1.30	±0.14	0.97	33	1.66	−1.65	±0.11	0.97	62	1.68	−1.68	±0.16	0.95	42	1.55	−1.44	±0.42	0.70	35

[1] Data for females presented on the first line, data for males presented on the second line; k, slope; y, RMA modified intercept; CI, 95% confidence intervals for slopes; r, correlation coefficient.

[2] Boldfaced values indicate the slope is not significantly different from zero; therefore, differences in slopes and OLS y-intercepts/RMA elevations not tested.

[3] Underlined slope or y-intercept is significantly different between the sexes at $P<0.05$; if slope significantly different, the y-intercept is not tested.

Table 7
Results of same-sex pairwise significance tests for differences in slopes or y-intercepts between species/subspecies of *Pan*[1–3]

	PP/PTT				PP/PTV				PP/PTS				PTT/PTS				PTT/PTV				PTS/PTV			
	Males		Females		Males		Females		Males		Females		Males		Females		Males		Females		Males		Females	
vs. basicranial length	k	y	k	y	k	y	k	y	k	y	k	y	k	y	k	y	k	y	k	y	k	y	k	y
M_1 corpus height	NS	NS	NS	NS	NS	NS	NS	NS	*	—	NS	NS	NS	*	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
M_2 corpus height	NS	NS	NS	NS	NS	NS	¥	—	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	¥	—	NS	NS	¥	—
M_1 corpus width	¥	—	¥	—	¥	—	¥	—	¥	—	¥	—	NS	NS	NS	NS	¥	—	¥	—	¥	—	¥	—
M_2 corpus width	¥	—	¥	—	¥	—	¥	—	¥	—	¥	—	¥	—	¥	—	¥	—	¥	—	¥	—	¥	—
Symphyseal height	*	—	NS	NS	NS	*	¥	—	*	—	NS	*	NS	*	NS	NS	NS	*	¥	—	NS	NS	¥	—
Symphyseal width	*	—	NS	NS	NS	NS	¥	—	*	—	NS	NS	NS	NS	NS	NS	NS	NS	¥	—	NS	NS	¥	—
Incisor cord length	NS	NS	NS	NS	¥	—	¥	—	NS	NS	NS	*	NS	NS	NS	NS	¥	—	¥	—	¥	—	¥	—
Bicondylar breadth	NS	NS	NS	*	¥	—	NS	NS	NS	NS	NS	NS	NS	*	NS	NS	¥	—	NS	NS	¥	—	NS	NS
Condylar length	NS	NS	NS	*	¥	—	¥	—	*	—	*	—	NS	*	*	—	¥	—	¥	—	¥	—	¥	—
Condylar width	NS	NS	NS	*	NS	NS	¥	—	NS	NS	NS	NS	NS	*	NS	*	NS	NS	¥	—	NS	*	¥	—
Gonion-incision	NS	NS	NS	NS	NS	NS	¥	—	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	¥	—	*	—	¥	—
Condyle-incision	NS	NS	NS	NS	NS	NS	¥	—	*	—	NS	NS	NS	*	NS	NS	NS	NS	¥	—	*	—	¥	—
Condyle-coronoid	NS	NS	NS	NS	NS	NS	¥	—	*	—	NS	*	*	—	NS	NS	NS	NS	¥	—	NS	*	¥	—
Ramal width	*	—	NS	NS	NS	NS	¥	—	*	—	NS	NS	NS	*	NS	NS	NS	NS	¥	—	NS	*	¥	—
Anterior ramal height	NS	NS	NS	NS	NS	NS	¥	—	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	¥	—	NS	*	¥	—
Posterior ramal height	NS	NS	NS	NS	¥	—	NS	NS	*	—	NS	NS	NS	NS	NS	NS	¥	—	NS	NS	¥	—	NS	NS
Condylar joint height	NS	NS	NS	NS	¥	—	¥	—	*	—	*	—	*	—	NS	NS	¥	—	¥	—	¥	—	¥	—

[1] *, OLS and RMA regression coefficients significantly different at $p<0.05$; —, If slope significantly different, differences in OLS y-intercept/RMA elevation not tested. NS, not significant.

[2] PTT, *Pan t. troglodytes*; PTS, *Pan t. schweinfurthii*; PTV, *Pan t. verus*. PP, *Pan paniscus*

[3] ¥, Slope does not depart significantly ($P > 0.05$) from zero; —, differences in OLS y-intercept/RMA elevation not tested.

following size-correction, and *P.t. verus* is now most distinct from *P.t. schweinfurthii* (Table 10b). In the regression-corrected CVA excluding bonobos, we observe an increase in subspecies overlap akin to the unadjusted CVA, and the intergroup distances again drop slightly, but intergroup distances remain greatest between *verus* and the other two subspecies (Fig. 2b).

Gorilla

In the analysis of the unadjusted data for the three gorilla groups, accuracy of group classification ranges between 63% and 86% (Table 11a). There is overlap among taxa, though less overlap than was observed amongst the three subspecies of *P. troglodytes* (Fig. 3a). Intergroup distances are greatest between eastern and western gorilla groups (Table 11b). Accuracy of group classification is generally higher in *G. gorilla* than *P. troglodytes*, but not higher than in *P. paniscus*. Judging from the classification matrix and intergroup centroid distances (Tables 11a-b), *G.g. beringei* appears the most distinctive along Axis 1, whereas Axis 2 separates *G.g. graueri* and *G.g. gorilla* (Fig. 3a). The first ($\chi^2 = 116.6$; df = 22; $P<0.001$) and second ($\chi^2 = 24.5$; df = 10; $P<0.01$) discriminant functions are significant. The variables most highly correlated with the first canonical discriminant function are ramal height, condylar width, and symphyseal width. Symphyseal height is the most highly correlated with the second discriminant function.

Ontogenetic size adjustment based on basicranial length results in a drop in accuracy of group classification for *G.g. beringei* and *G.g. gorilla* and a negligible improvement for *G.g. graueri* (Table 11c and Fig. 3b). There is a corresponding drop in intergroup distances between *G.g. beringei* and the other two gorilla groups, and the relative alignment of taxa changes such that *graueri* is somewhat more distinct from *beringei* than is *G.g. gorilla* (Table 11d). Size adjustment using palatal

Table 8
Reduced major axis regression statistics for *Gorilla* separately by taxon and sex$^{1–3}$

	G.g. gorilla					*G.g. graueri*					*G.g. beringei*				
vs. Basicranial length	k	y	CI	r	n	k	y	CI	r	n	k	y	CI	r	n
Bicondylar breadth	1.04	−0.04	±0.08	0.96	56	0.98	0.08	±0.15	0.94	25	1.70	−1.38	±1.32	0.62	9
	0.90	0.23	±0.07	0.97	55	0.90	0.25	±0.19	0.90	21	1.03	−0.03	±0.24	0.93	15
Gonion-incision	1.50	−0.94	±0.11	0.96	56	1.47	−0.85	±0.17	0.97	24	0.46	1.21	±0.41	0.86	9
	1.36	−0.67	±0.07	0.98	50	1.22	−0.34	±0.14	0.97	21	1.46	−0.87	±0.31	0.94	14
Condyle-incision	1.50	−0.89	±0.10	0.97	56	1.34	−0.54	±0.16	0.96	25	0.17	1.86	±0.15	0.85	11
	1.34	−0.57	±0.07	0.98	61	1.18	−0.20	±0.12	0.98	21	1.43	−0.74	±0.27	0.95	15
M_1 Corpus height	2.05	−2.69	±0.30	0.87	52	1.82	−2.20	±0.33	0.91	25	1.84	−2.24	±0.62	0.91	12
	1.66	−1.90	±0.14	0.95	59	1.41	−1.36	±0.29	0.91	21	1.64	−1.86	±0.34	0.93	15
M_2 Corpus height	2.04	−2.68	±0.73	0.41	37	3.21	−5.08	±1.71	0.49	18	1.01	−0.54	±0.77	0.75	11
	1.70	−2.02	±0.37	0.77	42	1.62	−1.84	±0.82	0.49	20	**2.07**	−2.81	±1.41	0.42	14
M_1 Corpus width	0.64	−0.06	±0.22	0.30	52	**0.55**	0.17	±0.32	0.06	25	**1.12**	−1.00	±0.82	0.54	12
	0.49	0.25	±0.13	0.52	59	**0.59**	0.05	±0.32	0.38	21	0.70	−0.17	±0.41	0.53	15
M_2 Corpus width	**0.91**	−0.57	±0.51	0.07	37	**1.43**	−1.62	±0.93	0.03	18	**1.92**	−2.60	±1.97	0.07	11
	0.93	−0.62	±0.38	0.20	41	**0.96**	−0.70	±0.60	0.12	19	**1.65**	−2.17	±1.34	0.21	14
Symphyseal height	1.51	−1.37	±0.14	0.94	56	1.26	−0.83	±0.17	0.95	25	1.09	−0.50	±0.47	0.81	12
	1.38	−1.10	±0.12	0.95	62	1.25	−0.81	±0.21	0.94	21	1.45	−1.25	±0.40	0.90	15
Symphyseal width	1.07	−0.83	±0.15	0.89	56	0.99	−0.65	±0.26	0.82	25	1.27	−1.21	±0.87	0.61	12
	1.10	−0.90	±0.11	0.92	62	1.25	−1.21	±0.40	0.78	21	1.36	−1.41	±0.39	0.89	15
Incisor cord length	1.22	−1.07	±0.20	0.83	54	1.49	−1.61	±0.28	0.91	25	**0.87**	−0.35	±0.91	0.46	8
	0.95	−0.53	±0.16	0.80	57	1.08	−0.82	±0.30	0.84	21	**1.45**	−1.63	±1.28	0.32	11
Condylar length	1.71	−2.47	±0.38	0.68	56	1.94	−2.87	±0.62	0.72	25	**2.39**	−3.80	±2.04	0.27	12
	2.08	−3.23	±0.25	0.89	61	1.80	−2.61	±0.72	0.65	21	1.87	−2.80	±0.53	0.90	15
Condylar width	1.59	−1.78	±0.15	0.94	55	1.30	−1.21	±0.26	0.89	25	2.11	−2.81	±1.06	0.75	12
	1.30	−1.21	±0.14	0.93	51	1.28	−1.19	±0.28	0.89	21	1.28	−1.15	±0.37	0.89	15
Condylar joint height	1.37	−0.97	±0.21	0.86	51	1.26	−0.72	±0.25	0.90	25	1.97	−2.14	±0.80	0.84	12
	1.29	−0.83	±0.13	0.94	49	1.03	−0.29	±0.22	0.91	21	1.56	−1.36	±0.58	0.82	14
Anterior ramal height	1.76	−1.62	±0.16	0.95	55	1.31	−0.70	±0.22	0.93	25	2.10	−2.29	±0.63	0.91	12
	1.61	−1.35	±0.12	0.96	60	1.24	−0.56	±0.26	0.91	21	1.63	−1.39	±0.57	0.83	15
Posterior ramal height	1.74	−1.54	±0.15	0.95	56	1.36	−0.76	±0.18	0.96	25	1.99	−2.02	±0.65	0.89	12
	1.46	−1.00	±0.13	0.95	60	1.13	−0.30	±0.20	0.93	21	1.55	−1.16	±0.43	0.89	15
Condyle-coronoid	2.01	−2.56	±0.19	0.94	55	2.05	−2.61	±0.37	0.92	24	1.99	−2.48	±0.60	0.60	12
	1.99	−2.54	±0.19	0.94	60	1.39	−1.31	±0.45	0.76	20	1.80	−2.19	±0.87	0.87	15
Ramal width	1.71	−1.77	±0.13	0.96	55	1.43	−1.16	±0.24	0.92	25	1.73	−1.79	±0.90	0.90	12
	1.62	−1.58	±0.10	0.97	62	1.25	−0.79	±0.22	0.93	21	1.75	−1.87	±0.93	0.93	14

[1] Data for females presented on the first line, data for males presented on the second line; k, slope; y, RMA modified y-intercept; CI, 95% confidence intervals for slopes; r, correlation coefficient.

[2] Boldfaced values indicate the slope is not significantly different from zero; therefore, differences in slopes and OLS y-intercept/RMA elevation not tested.

[3] Underlined slope or y-intercept is significantly different between the sexes at $P<0.05$; if slope significantly different, the y-intercept is not tested.

length does a notably better job than basicranial length at correctly classifying all three gorilla groups (Table 11c and Fig. 3c), and is better at classifying *G.g. graueri* than the non-size corrected data, but this is only to be expected, considering that palatal length itself is a major—perhaps the major—difference amongst these taxa. With palatal length, the intergroup centroid distances increase between the western and eastern gorillas. The net effect is that the centroids for all three groups are more approximately equidistant from one another than was observed either in the unadjusted data, or in the data size corrected against basicranial length. Regardless of the method of

Table 9
Results of same-sex pairwise significance tests for differences in slopes or y-intercept between gorilla subspecies.[1–3]

	GGG/GGGR				GGG/GGB				GGGR/GGB			
	Males		Females		Males		Females		Males		Females	
vs. Basicranial length	k	y	k	y	k	y	k	y	k	y	k	y
M_1 Corpus height	NS	NS	NS	*	NS	NS	NS	NS	NS	NS	NS	NS
M_2 Corpus height	NS	NS	NS	NS	¥	—	NS	NS	¥	—	NS	NS
M_1 Corpus width	¥	—	¥	—	NS	*	¥	—	¥	—	¥	—
M_2 Corpus width	¥	—	¥	—	¥	—	¥	—	¥	—	¥	—
Symphyseal height	NS	NS	NS	*	NS	NS	NS	NS	NS	NS	NS	*
Symphyseal width	NS	NS	NS	*	NS	NS	NS	*	NS	*	NS	*
Incisor cord length	NS	NS	NS	NS	¥	—	¥	—	¥	—	¥	—
Bicondylar breadth	NS	NS	NS	*	NS	NS	NS	NS	NS	NS	NS	NS
Condylar length	NS	NS	NS	NS	NS	NS	¥	—	NS	NS	¥	—
Condylar width	NS	NS	NS	NS	NS	NS	NS	*	NS	*	NS	NS
Gonion-incision	NS	*	NS	*	NS	NS	NS	NS	NS	NS	NS	*
Condyle-incision	NS	NS	NS	*	NS	NS	NS	*	NS	NS	NS	NS
Condyle-coronoid	*	—	NS	NS	NS	NS	NS	*	NS	NS	NS	NS
Ramal width	*	—	*	—	NS	NS	NS	*	*	—	NS	NS
Anterior ramal height	*	—	*	—	NS	NS	NS	NS	NS	NS	*	—
Posterior ramal height	*	—	*	—	NS	NS	NS	*	NS	NS	NS	*
Condylar height	NS	NS	NS	*	NS	NS	NS	*	NS	*	NS	NS

[1] *, OLS and RMA regression coefficients significantly different at $P<0.05$. —, If slope significantly different, differences in y-intercept/elevation not tested. NS, not significant.

[2] GGG, *Gorilla g. gorilla*; GGGR, *Gorilla g. graueri*; GGB, *Gorilla g. beringei*.

[3] ¥, Slope does not depart significantly ($P > 0.05$) from zero; —, OLS y-intercept/RMA elevation differences not tested.

size correction, the first two discriminant functions remain significant ($P<0.01$).

In our analysis of Groves' mandibular data (sexes combined), the three conventional subspecies range from 50% to 96% correctly classified, while none of the Nigerian gorillas are correctly classified (Table 12a). These analyses were performed on precisely the same specimens as those of Stumpf et al. (2003); however, fewer Nigerian gorillas are included in our analysis simply because crania are more abundant than mandibles. We believe it unlikely, however, that smaller samples account for the absence of any discrimination between Nigerian and other western lowland gorillas, since differences emerge in other analyses involving relatively small samples (e.g., *G.g. beringei*).

The greatest distinction is between the western (*G.g. gorilla*) and eastern (*G.g. graueri* and *G.g. beringei*) gorillas (Table 12b), consistent with previous craniometric analyses (Groves, 1970a; Stumpf et al., 2003) and with the recent proposal (Groves, 2000, 2001) to separate eastern and western gorillas at the species level. The intergroup centroid distances, however, are greatest between *G.g. graueri* and *G.g. gorilla*, and least between *graueri* and *beringei* (Table 12b). These contrast with the non-size corrected results presented earlier (Table 11b), as well as with those of Uchida (1996) for craniodental dimensions, which both indicate a greater distinction between *G.g. beringei* and *G.g. gorilla*. There are a number of reasons why analyses of our respective datasets—even of the same region—might yield a different patterning of results, including different sample sizes, incorporation of different demes, and nominal overlap in mandibular measurements. Finally, the observed intergroup centroid for the Nigerian gorillas and the other western lowland gorillas is the smallest of all D^2 distances (Table 12b), and the two groups completely overlap with no suggestion of separation along either axis (Fig. 4).

Table 10a
Accuracy of group classification for the canonical variates analysis completed on non size-adjusted/size-adjusted data for *Pan*[1,2]

	P. paniscus	*P.t. schweinfurthii*	*P.t. troglodytes*	*P.t. verus*	Total	% Correct
P. paniscus	21/16	0/3	0/1	0/1	21/21	100/76
P.t. schweinfurthii	0/1	13/12	10/9	3/3	26/25	50/48
P.t. troglodytes	1/4	8/7	48/46	9/8	66/65	73/71
P.t. verus	0/0	2/1	9/10	32/30	43/41	74/73

[1] Group classification based on cross-validation analysis in which each case is classified by the functions derived from all cases excluding that case.

[2] The probability of group membership is based on unequal sample sizes.

Table 10b
Intergroup centroid Mahalanobis distances on non size-adjusted/size-adjusted data for *Pan*

	P. paniscus	*P.t. schweinfurthii*	*P.t. troglodytes*	*P.t. verus*
P. paniscus	0.000			
P.t. schweinfurthii	23.8/9.1	0.000		
P.t. troglodytes	33.2/12.1	3.3/4.0	0.000	
P.t. verus	27.5/13.3	7.3/7.8	8.7/7.1	0.000

Discussion

Ontogenetic variation

Overall, bivariate patterns of mandibular growth allometry, like cranial growth allometry (Shea, 1983b), are similar in the African apes. Sex differences in ontogenetic trajectories are negligible in *Pan* and *Gorilla*. Despite nontrivial differences in measurements and shape variables, these results are generally consistent with Daegling's (1996) findings of ontogenetic scaling of the sexes in *Pan* and *Gorilla* for many (though not all) mandibular proportions. The mix of positive and negative allometry, in conjunction with the scaling coefficients, indicates that shape changes during growth, and in similar ways, in gorillas and chimpanzees. As has been suggested elsewhere (Taylor, 2002, 2003), ontogenetic changes in mandibular proportions may reflect functional shifts during growth that are related to changes in mastication and diet; changes in cranial and skeletal proportions during growth should not, as has been suggested (Godfrey et al., 1998), be interpreted as functionally neutral.

The marked differences in mandibular dimensions observed between adult *P. paniscus* and *P. troglodytes* are noticeably diminished when size corrected using ontogenetic allometry, though they are not eliminated (Table 7). Likewise, the number of adult differences in mandibular dimensions amongst gorillas decreases with ontogenetic size correction, but gorilla groups are characterized by more differences in scaling trajectories than are chimpanzee subspecies (Tables 7 and 9). In this regard, the bivariate analyses appear to reasonably reflect the overall patterning of multivariate differentiation within and between *Pan* and *Gorilla*.

In *Pan*, most slopes for *P.t. troglodytes* and *P.t. schweinfurthii* overlap within the 95% confidence intervals, and many (though not all) overlap with bonobos as well, even in cases of statistically significant differences. Our data, such as they are, provide little empirical evidence to suggest that *P.t. verus* follows a trajectory for mandibular growth that differs from other chimpanzees or bonobos (Fig. 5), similar to previous allometric evaluation of cranial variation in *Pan* (Shea and Groves, 1987). Statistical differences in slopes, even when ontogenetic trajectories appear quite similar, have been previously observed (e.g., Shea, 1984, 1985) and may, apart from issues of sampling, reflect underlying genetic correlations (Shea, 1985).

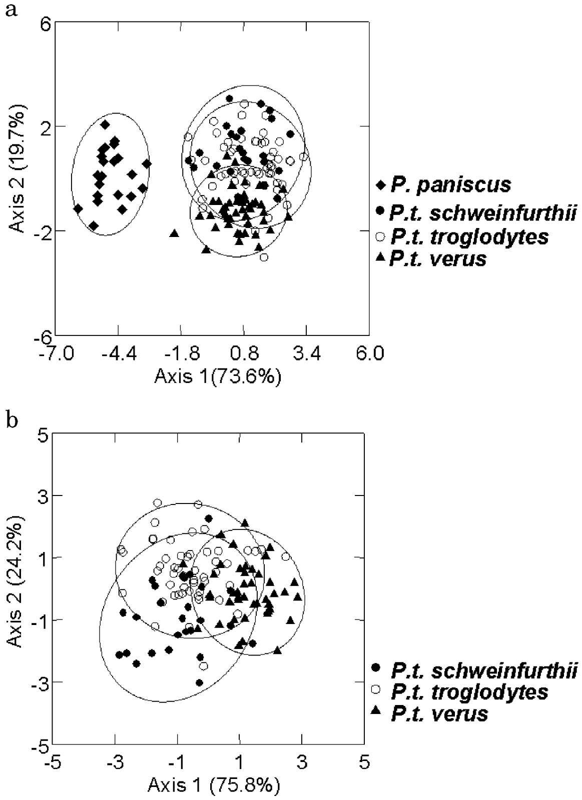

Fig. 1. Plots of non size-adjusted CVAs with 90% confidence ellipses of adult male and female *Pan*. Accuracy of group classification and intergroup distances presented in Tables 10a-b. (a) Note the complete separation of bonobos from all subspecies of *P. troglodytes* along Axis 1. The greatest overlap among chimpanzee subspecies is between *P.t. troglodytes* and *P.t. schweinfurthii*. The greatest distinction is between *P.t. verus* and *P.t. schweinfurthii* along Axis 2. (b). The degree of overlap increases amongst all three chimpanzee subspecies with removal of bonobos. *P.t. verus* remains slightly shifted along Axis 2.

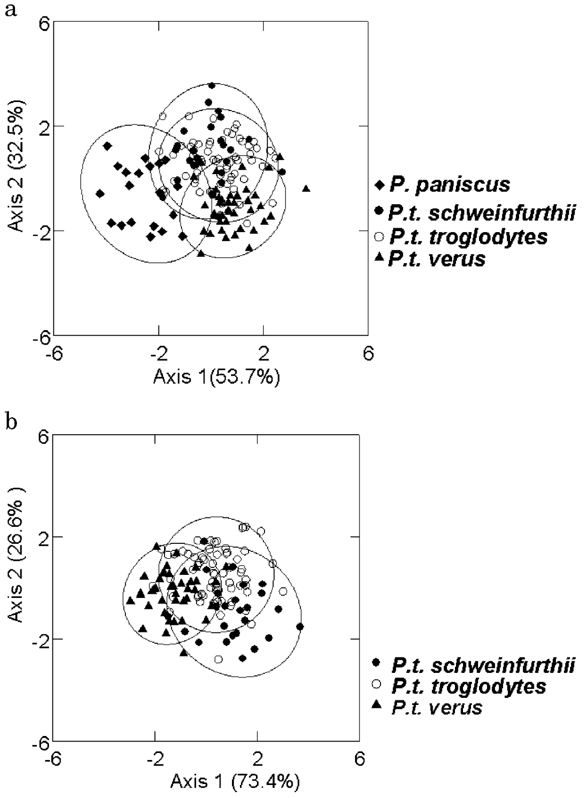

Fig. 2. Plots of allometrically adjusted CVAs with 90% confidence ellipses of adult male and female *Pan*. Accuracy of group classification and intergroup distances are presented in Tables 10a-b. (a) Size adjustment reduces the degree of separation amongst all chimpanzee groups. However, *P. paniscus* remains the most distinctive, followed again by *P.t. verus*. (b) Elimination of bonobos increases the degree of overlap (similar to the non-size corrected results).

We emphasize, however, that patterns of relative mandibular growth cannot be easily compared between *P.t. verus* and sister taxa because many bivariate relationships are characterized by weak or nonsignificant correlations. Slopes can be unduly influenced by small samples of younger developmental stages, coupled with samples heavily weighted towards adults. Nevertheless, we do not observe such low correlations in *G.g. beringei*, which is also represented by relatively few young individuals (though admittedly fewer adults as well). Curvilinear slopes can also affect the correlations, particularly if there is a sharp drop in relative growth at the adult stages. This may be a problem for *verus* because our samples are heavily weighted towards adults, yet where *verus* trajectories show comparable degrees of linearity with other *Pan* subspecies, as demonstrated empirically using Lowess fits, these are not accompanied by correspondingly higher correlations. Thus, attributing this unusual correlational structure to ontogenetic sampling alone may be an over simplification. More variation, and correspondingly lower correlations, could also result from sampling from a broad geographic area, but all *verus* specimens in this study derive from the rather homogenous Liberian collection housed in the

Table 11a
Accuracy of group classification for the canonical variates analysis completed on non size-corrected data for *Gorilla*[1,2]

	G.g. beringei	*G.g. gorilla*	*G.g. graueri*	Total	% Correct
G.g. beringei	18	2	1	21	86
G.g. gorilla	2	38	9	49	78
G.g. graueri	0	11	19	30	63

[1] Group classification based on cross-validation analysis in which each case is classified by the functions derived from all cases excluding that case.

[2] The probability of group membership is based on unequal sample sizes.

Table 11b
Intergroup centroid Mahalanobis distances on non size-corrected data for *Gorilla*

	G.g. beringei	*G.g. gorilla*	*G.g. graueri*
G.g. beringei	0.000		
G.g. gorilla	15.2	0.000	
G.g. graueri	13.2	2.5	0.000

Table 11c
Accuracy of group classification for the canonical variates analysis completed on size-adjusted (basicranial length/palatal length) data for *Gorilla*[1,2]

	G.g. beringei	*G.g. gorilla*	*G.g. graueri*	Total	% Correct
G.g. beringei	10/13	5/2	3/4	18/19	56/68
G.g. gorilla	5/3	26/32	9/8	40/43	65/74
G.g. graueri	0/3	11/5	21/24	32/32	66/75

[1] Group classification based on cross-validation analysis in which each case is classified by the functions derived from all cases excluding that case.

[2] The probability of group membership is based on unequal sample sizes.

Table 11d
Intergroup centroid Mahalanobis distances on size-adjusted (basicranial length/palatal length) data for *Gorilla*

	G.g. beringei	*G.g. gorilla*	*G.g. graueri*
G.g. beringei	0.000		
G.g. gorilla	6.4./7.4	0.000	
G.g. graueri	8.0/6.3	3.2/6.8	0.000

Peabody Museum, Harvard University. It is of interest, therefore, that Schuman and Brace (1955) observed a degree of variability in the dentition of these same Liberian specimens comparable to the degree of variability expressed in some human populations. Our results, along with those of Schuman and Brace, suggest these chimpanzees may possibly be characterized by a greater degree of morphological variability than other populations, and, possibly, other chimpanzees. More complete ontogenetic samples of *verus* alone may resolve the apparent peculiarity of their correlational structure, but no difference in degree of cranial variability amongst chimpanzee subspecies is an interesting null hypothesis that remains to be carefully evaluated.

Gorillas, like chimpanzees, are also ontogenetically scaled for many bivariate relationships. In cases of significant departures from ontogenetic scaling, some slopes overlap, though with less frequency than was observed in *Pan*. Differential sampling in *G.g. beringei*, both across age groups and between sexes, may be a factor here, and partially account for why some departures from ontogenetic scaling are expressed more frequently in females as compared to males. However, Vogel (1961) similarly observed more differences in mandibular proportions between females as compared to males. This does not appear to be the case, however, in comparisons between *Pan* and *Gorilla*, where departures from ontogenetic scaling of mandibular proportions are more consistently expressed in pairwise comparisons between both sexes, and are established relatively early in ontogeny (Daegling, 1996; Taylor, 2002).

One additional pattern worth noting is the systematically low and often nonsignificant correlations between M_1 and M_2 corpus width and cranial (and mandibular: Taylor, 2002, 2003) size during growth across all the African apes (Tables 6 and 8). Similarly low correlations have been observed in other taxa (e.g., *Cebus*: Cole, 1992), and contrast with the observed patterns of growth for the deciduous corpus (i.e., corpus width dimensions obtained at dm_1 and dm_2) in the African apes (Taylor, 2002). In gorillas, deciduous corpus width is significantly correlated with size increase during

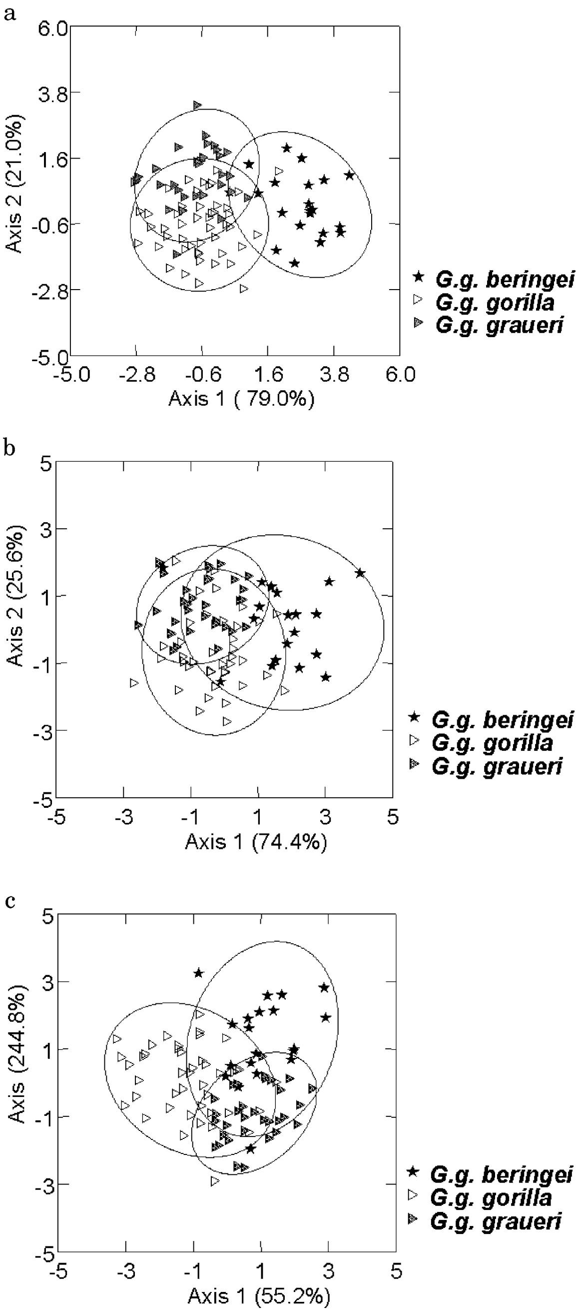

Fig. 3. Plots of CVAs with 90% confidence ellipses of adult male and female *Gorilla*. Accuracy of group classification and intergroup distances are presented in Tables 11a-d. (a) Non size-adjusted CVA of adult male and female *Gorilla*. *G.g. beringei* shows the greatest differentiation along Axis 1; *G.g. gorilla* and *G.g. graueri* are differentiated from each other along Axis 2. Note the greater degree of multivariate differentiation than exhibited by chimpanzee subspecies. (b) Allometrically size-adjusted CVA using basicranial length. Degree of overlap increases amongst all gorilla groups, but *G.g. beringei* remains the most distinct along Axis 1. (c) Allometrically size-adjusted CVA using palatal length. Accuracy of group classification is improved compared to size adjustment using basicranial length, and shifts in intergroup distances result in a more equal three-way relationship among groups. Degree of group separation is greater than that observed in the size adjusted CVA for chimpanzee subspecies.

Table 12a
Accuracy of group classification for the canonical variates analysis completed on Groves' data for *Gorilla*[1,2]

	G.g. gorilla	*G.g. diehli*	*G.g. beringei*	*G.g. graueri*	Total	% Correct
G.g. gorilla	333	2	2	9	346	96
G.g. diehli	10	0	1	2	13	0
G.g. beringei	5	0	13	8	26	50
G.g. graueri	16	0	3	48	67	72

[1] Group classification based on cross-validation analysis in which each case is classified by the functions derived from all cases excluding that case.
[2] The probability of group membership is based on unequal sample sizes.

Table 12b
Intergroup centroid Mahalanobis distances on Groves' data for *Gorilla*

	G.g. gorilla	*G.g. diehli*	*G.g. beringei*	*G.g. graueri*
G.g. gorilla	0.000			
G.g. diehli	1.2	0.000		
G.g. beringei	22.1	7.4	0.000	
G.g. graueri	31.3	6.2	4.9	0.000

growth and positively allometric, whereas in chimpanzees, this relationship is significantly correlated, but isometric (Taylor, 2002).

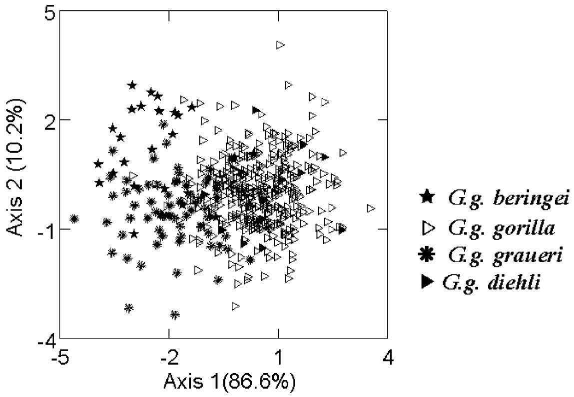

Fig. 4. Plot of non size-adjusted CVA on Groves' mandibular data for adult *Gorilla*. The greatest difference is between eastern (*G.g. beringei* and *G.g. graueri*) and western (*G.g. gorilla* and *G.g. diehli*) gorillas, comparable to results obtained using craniometric data. Note that *G.g. gorilla* and *G.g. diehli* overlap completely for mandibular dimensions, which runs contrary to results obtained using craniometric data. Accuracy of group classification and intergroup distances are presented in Tables 12a-b.

Previously, Taylor (2002, 2003) has argued that scaling patterns of the deciduous and permanent mandibular corpus may be linked to eruption of the dentition in the African apes. The deciduous molars erupt well before one year of age in both chimpanzees and gorillas; the mean age of eruption of the first permanent molars is 3.2 years for *P. troglodytes* and 3.5 years for *G. gorilla* (Smith et al., 1994). The "drop" in relative rate of growth for mandibular corpus width coincides with the timing of eruption of M_1 (Taylor 2002). There is a similar, though less marked decrease in the positive allometry of mandibular corpus height (Taylor, 2002). Cole (1992) also attributed the relatively thicker mandibular corpora in younger as compared to older *Cebus* to the developing molars, and Daegling (1996) argued that the higher slopes in females as compared to males for his measure of corpus height reflected an accelerated pattern of growth in females and the concomitant need to accommodate the permanent dentition at a relatively faster rate than males. As previously suggested (Dean and Beynon, 1991), these data collectively support the hypothesis that tooth development and eruption play an important role in driving the patterning of mandibular corpus growth in the African apes. Space as such does not

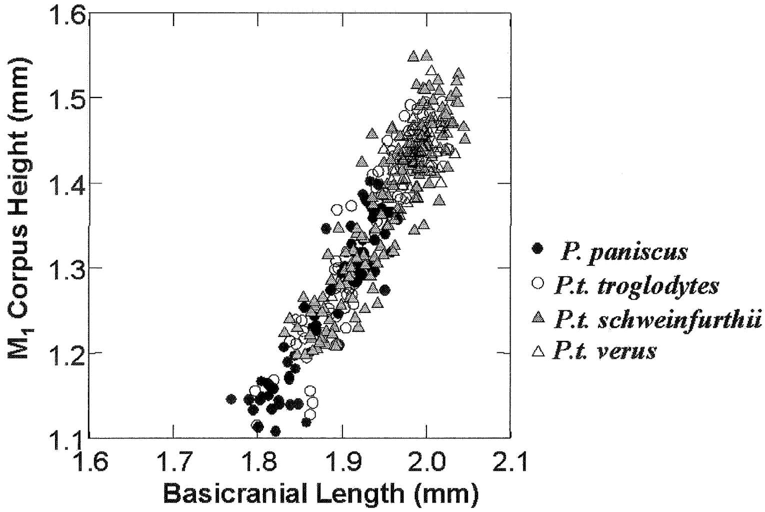

Fig. 5. Bivariate plot of M_1 corpus height vs. basicranial length. The trajectory for *P.t. verus* shows substantial overlap with bonobos and other chimpanzee subspecies. The null hypothesis that *P.t. verus* and other chimpanzees share similar patterns of relative growth of the mandible cannot be ruled out.

appear to markedly constrain dental development in the apes; Dean and Beynon (1991) note that in apes, molar development occurs with their occlusal surfaces oriented perpendicular to the occlusal plane until sufficient space is available for the teeth to reorient properly. Rather, these data suggest that mandibular corpus growth is impelled by dental development: the tooth germs develop and position themselves in whatever space is available and mandibular growth is accelerated to accommodate the dentition.

Finally, we do not see evidence of substantial ontogenetic differentiation on the basis of mandibular morphology, or large-scale differences in the degree to which mandibular vs. other skull morphologies differentiate between and among sexes and taxa. The overall similarity in patterns of cranial and mandibular growth allometry suggests that, at least in the African apes, mandibular morphology is no more or less phenotypically plastic than cranial base, neurocranial, or facial morphologies (cf. Wood and Lieberman, 2001).

The impact of size adjustment on morphological differentiation

Pan

It comes as no surprise that the degree of mandibular differentiation is greatest between *P. paniscus* and *P. troglodytes*. Our results simply confirm that the marked differences in mandibular size between *Pan* species (Cramer, 1977) are substantiated in comparisons amongst bonobos and all chimpanzee subspecies, and parallel the well-established pattern of multivariate craniometric differentiation (e.g., Shea and Coolidge, 1988; Shea et al., 1993). Size adjustment substantially diminishes the degree of distinction between *Pan* species. We see this in both the bivariate and multivariate analyses, as the frequency and magnitude of differences observed in the univariate data diminish with ontogenetic size correction. Bonobos, however, remain clearly differentiated from common chimpanzees, and more distinct than any of the chimpanzee subspecies from each other.

Size adjustment also alters the relative alignment of *P. paniscus* to the three chimpanzee subspecies. Thus, prior to allometric size correction, bonobos are most distinct from *P.t. troglodytes*, whereas after size adjustment, bonobos are most distinct from *verus*. Collectively, our results substantiate Shea et al.'s (1993) size corrected findings for the cranium, and we concur with their conclusion; namely, that a good portion of the observed differentiation between *Pan* species is allometric. We also observe that *schweinfurthii* is most closely aligned with *paniscus* after (as well as before) allometric size correction, which is concordant with size adjusted findings for the cranium as well (Shea et al., 1993).

Within *P. troglodytes*, there is decidedly more overlap amongst chimpanzee subspecies than between *Pan* species (or amongst gorilla subspecies). Despite this overlap. *P.t. verus* appears relatively the most distinctive amongst chimpanzee subspecies, as evidenced primarily by the CVAs. Our findings also suggest the possibility that *schweinfurthii* and *troglodytes* show greater overlap in craniometric as compared to mandibular morphology (cf. Shea and Coolidge, 1988; Shea et al., 1993). We draw this conclusion from comparison of our 90% probability ellipsoids for both the unadjusted and size corrected data (*P. paniscus* included), with those of Shea et al. (1993: Figs. 1 and 3) for the cranium. The relatively greater degree of distinction of *verus* from the other two subspecies is possibly more evident in our study because we observe the greatest overlap between *troglodytes* and *schweinfurthii* (Figs. 1a and 2a), whereas Shea et al.'s (1993) findings show greatest overlap between *troglodytes* and *verus*. We do not, however, find a degree of distinction between *verus* and the other *Pan* groups akin to that observed by Uchida (1996) in her multivariate analyses of upper and molar cusp areas.

Prior to size correction, the greatest intergroup distance between chimpanzee subspecies is between *P.t. troglodytes* and *verus*, whereas after size adjustment, *schweinfurthii* is most distinct from *verus*. These results are also concordant with the geographic separation of *verus* from *schweinfurthii*, as *verus* are distributed west of the Niger River, whilst *schweinfurthii* are located east of the Niger and furthest from *verus* (Groves, 2001). We do not mean to suggest that intergroup distances derived from mandibular morphology (or any other regional system) should be strictly interpreted as a precise mapping of phylogenetic proximity; these are phenotypic distances that are presumed to accord to some degree with phylogenetic distance (Albrecht and Miller, 1993), but reflect other influences as well such as drift and ecophenotypic plasticity. We do note that the centroid distances between *P.t. verus* and the other two subspecies—even the size-adjusted ones—are notably larger than those derived from craniometric measures (cf. Shea et al., 1998), suggesting that divergence between *verus* and the other two subspecies may be driven to a greater extent by mandibular, as opposed to cranial, variation. The predominance of mandibular effects has been observed in some earlier comparisons among the African apes (Daegling, 1996; Taylor, 2002) and within *Gorilla* (Vogel, 1961; Groves, 1967; Taylor, 2003), and suggests that the mandible and cranium are not necessarily subject to the same constraints.

Gorilla

Amongst the three traditionally recognized gorilla subspecies, the greatest distinction is between eastern and western gorillas, both before and after allometric size correction. The relative distinctiveness of these groups is supported by the bivariate analyses as well as the raw and size adjusted multivariate analyses; but the method of size correction influences both the accuracy of group classification and the intergroup distances. Size correction using basicranial length decreases the accuracy of group classification for two of the three groups, whereas the use of palatal length, as would be expected, substantially improves the percentage correctly classified for all three groups. In addition, with palatal length, the intergroup centroid distances increase between *G.g. gorilla* and the other two gorilla groups such that the centroids of all three groups are positioned approximately equidistant from each other. We note that the frequency of departures from ontogenetic scaling is greatest in comparisons between *G.g. graueri* and *G.g. gorilla*, whereas the degree of multivariate differentiation (i.e., intergroup distance) is greatest between *G.g. beringei* and *G.g. gorilla*. The difference in patterning between these two sets of analyses attest to the fact that *more* differences do not necessarily signify *greater magnitude* of difference. Analyses of dental variation (Uchida, 1996, 1998) have variously shown *G.g. graueri* to be more distinct in some features, *G.g. beringei* in others.

Mandibular variation and taxonomy

Chimpanzees

Establishing the pattern and degree of mandibular variation in chimpanzees and gorillas, and evaluating species-level distinctions against well established patterns of within-group variation in *P. paniscus* and *P. troglodytes*, may shed insight into current issues surrounding African ape taxonomy. Amongst the three widely recognized subspecies of *P. troglodytes*, *P.t. verus* is relatively the most distinctive in mandibular morphology, somewhat more, perhaps, than in metric cranial morphology (but see Braga (1995a,b) on non-metric variation). Nevertheless, there is considerable overlap between *P.t. verus* and the other two chimpanzee subspecies and the degree of overlap increases with size adjustment, indicating that much of the variation amongst chimpanzee subspecies is allometric. Clearly, mandibular (and cranial: Shea et al., 1993) differentiation between *P. paniscus* and *P. troglodytes* is still markedly greater even after size adjustment, in comparison to the degree of distinction amongst common chimpanzee subspecies without any size correction. This pattern of within- vs. between- group variation provides further compelling evidence of species distinctions between bonobos and chimpanzees.

Species-level status for bonobos and chimpanzees was formally recognized based on Coolidge's (1933) documentation of a single bonobo skeleton. We point out, however, that the validity of bonobos as a separate species has been recognized only after a lengthy period of investigation and debate (Frechkop, 1935; Schultz, 1954; Hill, 1969; Horn, 1979; Groves, 1986), and is based on a composite of data, including blood groups (Moor-Jankowski et al., 1972, 1975; Socha, 1984), molecular genetics (Burrows and Ryder, 1997; Altheide and Hammer, 1999, 2000; Jensen-Seaman et al., 2003), body build (Zihlman and Cramer, 1978; Zihlman, 1984), and social behavior (Kuroda, 1979, 1980), in addition to skeletal and dental variation.

Appreciably less is known about *P.t. verus*. Results of our multivariate analyses, along with those of others investigators (Shea and Coolidge, 1988; Shea et al., 1993; Braga, 1995a,b), suggest that while *verus* is morphologically the most distinctive amongst the three chimpanzee subspecies, the degree of difference is relatively small; certainly smaller than between *Pan* species, or even between eastern and western gorillas. Our bivariate analyses further provide little evidence of divergent growth allometries that would be suggestive of selection for altered proportions. Amongst the local populations of *verus* chimpanzees, those of the Taï Forest remain the best studied to date in terms of social structure (Boesch and Boesch, 1989; Boesch, 1994, 1996). Doran (Doran and Hunt, 1994; Doran, 1996) has suggested a greater degree of sex differences in locomotor and positional behavior between male and female *verus*, and between *verus* males and other chimpanzees. These differences, however, have not been accompanied by postcranial morphological distinctions (Inouye and Taylor, 2000; Taylor and Inouye, in preparation). We also note that preliminary molecular data are suggestive of a greater distinction in mitochondrial DNA between *P.t. verus* and the eastern and central chimpanzees (Morin et al., 1994; Arnanson et al., 1996; Gagneux et al., 1999; Kaessmann et al., 1999), but differentiation based on additional loci, nuclear DNA and other genetic markers has not yet been explored.

Further investigation into the patterning and degree of craniomandibular variation, including larger samples of local populations, and more comprehensive study of postcranial, genetic, and behavioral variation, are needed to determine just how different *P.t. verus* is, and whether such differences warrant further taxonomic division. Given the degree of overlap amongst all three chimpanzee subspecies in mandibular, cranial, and postcranial morphology, we currently find little evidence either to separate *verus* as a full species or, conversely, to support the collapse of eastern and central chimpanzees into a single, highly variable subclade (Gagneux et al., 1999). Elsewhere we have noted (Groves, 2003; Taylor and Goldsmith, 2003) that morphological differences (at least those that are not ecophenotypic) have a genetic basis, and failure to find reciprocally monophyletic mtDNA clades says little about the existence or otherwise of genetic differentiation as a whole. Groves (in preparation) finds that, on morphological grounds, some further division may even be warranted within what is now referred to as *P.t. schweinfurthii*.

Gorillas

Analysis of the Nigerian gorillas does not corroborate findings of morphological distinctiveness that have been suggested for the cranium (cf. Sarmiento and Oates, 2000; Stumpf et al., 2003). Mandibular variation alone does not support the recognition of Nigerian gorillas as a distinct subspecies. The intergroup distance between *G.g. gorilla* and the Nigerian gorillas is conspicuously small, smaller than any other observed intergroup distances between chimpanzees or gorillas, and all specimens belonging to *G.g. diehli* are misclassified as *G.g. gorilla* (Table 12b). In contrast to some visually appreciable separation of the Nigerian from other western lowland gorillas (Stumpf et al., 2003), our results show extensive overlapping with no discernable separation (Fig. 4). It is of interest, therefore, that differences in the nuchal region were particularly important in effecting the separation of the Nigerian from other western lowland gorillas, since these results suggest a very localized distinction; the face appears to be notably less distinctive (Stumpf et al., 2003), and the mandible not at all. Thus, whatever local environmental factors may be driving some of the mandibular variation amongst the western and eastern gorillas, such factors do not appear to have induced a similar pattern of divergence between local populations of western lowland gorillas, despite differences in altitudinal range and preliminary evidence of accompanying seasonal variation in diet (Oates et al., 2003).

We note that, in the analysis by Stumpf et al. (2003), size adjustment had only a marginal impact on the degree of craniometric differentiation between Nigerian and other western lowland gorillas, as one might expect given that differences in skull and body size amongst western gorillas are relatively minor. Thus, while Nigerian gorillas exhibited a greater degree of separation from other western lowland gorillas compared to any other western lowland gorilla deme, with and without size adjustment (Stumpf et al., 2003), the degree of differentiation remained relatively unchanged. These results suggest that, contrary to ontogenetically size corrected findings for both *Pan* and the three conventionally recognized gorilla groups, little if any of the observed craniometric distinctions between Nigerian and other western lowland gorillas “are size-related or ‘allometric’ in a general sense” (Stumpf et al., 2003).

Finally, the mandibular data presented here and elsewhere (Vogel, 1961; Groves, 1970a,b; Taylor, 2002, 2003) are equivocal with regard to the recent separation of gorillas into two species (Groves, 2001, 2003). Based on Groves’ data, the unadjusted intergroup centroid distances show the greatest differentiation between eastern and western gorillas, while closely aligning the two eastern groups (Table 12b). Taylor’s unadjusted data identify *G.g. beringei* as being the most distinctive, while closely aligning *G.g. gorilla* and *G.g. graueri* (Table 11b); Groves (1967, 1986) previously found a pattern of craniometric differentiation similar to Taylor’s, though the values of the intergroup distances were substantially greater. This may be a function of Groves’ larger sample sizes and/or of his partitioning of lowland and highland gorillas into local demes, but it may also be that gorillas are characterized by a relatively greater degree of craniometric, as opposed to mandibular, divergence. At times Grauer’s gorillas have appeared more similar to the Virunga mountain gorillas, and at others more akin to western lowland gorillas, according to which anatomical region is studied (Coolidge, 1933; Vogel, 1961; Groves, 1967, 1970a,b; Uchida, 1996, 1998; Taylor, 2003).

Size adjustment alters the relative distances between groups, but so does the manner of size correction. Thus, adjusting for basicranial length decreases the distance between *G.g. beringei* and the two gorilla groups, while slightly increasing the distance between *G.g. gorilla* and *G.g. graueri*, but similarly adjusting for palatal length approximates the more equally “three-way” relationship reflected in the lower molars (Uchida, 1998). Groves (2001), in his decision to separate eastern and western gorillas into distinct species, took these differences into account and tried to gauge the degrees of overlap amongst the three taxa: if a pair of taxa do not overlap, then they are best ranked as distinct species, whereas if they do overlap, then subspecific status is appropriate. Indeed, this was an important consideration in our assessment of *P.t. verus*; while *verus* emerges as the most metrically distinct in cranial and mandibular morphology based on intergroup distances, the degree of overlap with other chimpanzees is sufficiently great to support subspecific status. The regional and local differences noted above in comparisons between the Nigerian and other western lowland gorillas, coupled with the contrast in findings based on our two independent datasets, speak to the relative ease with which systematic alliances can alter depending upon which variables are incorporated and how the data are manipulated. These results advise in general a cautious approach to taxonomic decisions in the absence of adequate samples and appropriate size adjustment (cf. Sarmiento et al., 1996), although non-overlapping differences, where they do occur, cannot be ignored and the indications are that in many features eastern and western gorillas do not overlap.

In comparison to chimpanzees, gorillas exhibit a greater degree of mandibular (and cranial: compare Groves' (1967, 1970a) Mahalanobis' D^2's for gorilla demes with Shea and Coolidge's Mahalanobis' D^2's for chimpanzee subspecies) differentiation, though not as great as that between bonobos and chimpanzees. This is reflected empirically in the degree of multivariate separation. Estimates of divergence based on mitochondrial DNA also show a substantial degree of separation between eastern and western gorillas (Ruvolo et al., 1994; Garner and Ryder, 1996), though much smaller divergence estimates have been obtained from nuclear DNA (Jensen-Seaman et al., 2003). Furthermore, molecular data (Gagneux et al., 1999) confirm that chimpanzees have a more recent evolutionary history than gorillas, and their timing of divergence is estimated to have been considerably later. The gorilla lineage separated from the human/chimpanzee clade some 7.7 mya, while the chimpanzee lineage separated from the human line around 4.7 mya, so gorillas have had a longer time in which to diversify; and the divergence between *Pan troglodytes* and *Pan paniscus* occurred about 2.5 mya, whereas that between eastern and western gorillas, while not absolutely clear, is certainly more than this (Gagneux et al., 1999).

Degree of divergence may, of course, be accounted for by many factors, including relative timing of divergence, degree of geographic isolation, and concomitant changes in gene flow. In contrast to the geographic isolation of gorilla groups from each other (Groves and Meder, 2001), the relatively continuous distribution of chimpanzees may be associated with higher levels of gene flow, which Shea and Coolidge (1988) have suggested may partially explain the comparatively low levels of phenotypic differentiation. Ecological differences may also factor in the relatively lower levels of morphological distinctiveness among chimpanzee subspecies, as chimpanzees are more widely distributed and their range and habitat do not correspond to specialized ecological niches in the same way as do those of gorillas' (Shea and Coolidge, 1988), even in spite of the purported dietary flexibility of the latter (Tutin, 2003). Thus, adaptive and phenotypic responses to ecologically specific niches may also account for some of the observed morphological differentiation in gorillas.

Nevertheless, we emphasize that the patterning and degree of mandibular variation largely parallels that of cranial variation, both in species and subspecies comparisons. Indeed, the preponderance of ontogenetic scaling of mandibular proportions in *Pan* and *Gorilla*, and the degree of differentiation as reflected in both bivariate and multivariate analyses of mandibular variation, is considerably less than might be expected if, as has been suggested (Lieberman, 1997; Wood and Lieberman, 2001), the mandible is more strongly influenced by epigenetic factors (i.e., is more phenotypically plastic) than the skull. If this were the case, dietary specialization would predict a greater degree of mandibular differentiation between gorilla subspecies than between species of *Pan*, which we did not observe. The absence of any multivariate differentiation between *G.g. diehli* and other western lowland gorillas based on the mandible is particularly noteworthy in this regard, since the skull (Stumpf et al., 2003), and not the mandible, appears to be largely responsible for this separation. Thus, our results provide little evidence to suggest that mandibular morphology is less taxonomically valent (Wood and Lieberman, 2001) than other features of the cranium and dentition.

Conclusions

In *Pan* and *Gorilla*, within- and between-group phenotypic differentiation based on mandibular morphology is generally comparable to differentiation based on cranial morphology, with the exception of the newly recognized (Sarmiento and Oates, 2000) *G.g. diehli*. Thus, patterns and degrees of mandibular variation support previous conclusions of species-level distinctions between bonobos and chimpanzees, and substantiate a greater degree of differentiation amongst gorilla subspecies as compared to chimpanzee subspecies. However, it is apparent that the patterning and degree of morphological differentiation in *Pan* and *Gorilla* varies, not only vis-à-vis cranial, dental and mandibular morphology, but with regard to the application and manner of size adjustment.

Beyond that, the picture is more clouded. Minimal support is provided for the potential distinctiveness of the West African chimpanzee, *P.t. verus*, which is somewhat more distinctive in mandibular and dental metrics (and nonmetric cranial morphology: Braga 1995a,b) than are other subspecies from each other, whereas in craniometrics, the three conventionally recognized subspecies show greater overlap. Size correction further alters the relative positioning of *verus* with respect to other members of *Pan*.

Within gorillas, the three widely recognized subspecies are clearly distinct; more distinct than any subspecies of *P. troglodytes*. Relative alignment of taxa, however, is quite fluid; depending on the variables used, and whether (and how) size standardization is undertaken, different patterns of phenotypic interrelationships are found. Nigerian gorillas, distinct in their nuchal region, show no divergence along an axis of mandibular variation, which runs contrary to the general patterning of cranial, dental and mandibular divergence that characterizes the three traditionally recognized gorilla subspecies. The greatest degree of separation based on mandibular morphology is between eastern and western gorillas, similar to previous studies of gorilla craniodental variation.

Finally, degree of overlap in mandibular morphology does not accord well with the craniometric distinctiveness of the eastern and western gorillas; mandibular variation alone would not seem to corroborate other sources of evidence in supporting a two-species classification of gorillas. We can note that size adjustment using palatal length generates a greater degree of separation than basicranial length, and results in a more equal three-way relationship among taxa. We emphasize that results presented here for the mandible (or, for that matter, any morphological complex) should not be used alone to argue for or against taxonomic decisions. At a minimum, lack of concordance amongst patterns and degrees of variation requires explanation, and advises a judicious approach to taxonomic decisions until the underlying bases for such patterns are more fully understood.

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Appendix

Descriptive statistics for craniomandibular dimensions for *Pan* separately by taxon and sex

	P. paniscus						*P.t. troglodytes*						*P.t. schweinfurthii*						*P.t. verus*					
	Male			Female			Male			Female			Male			Female			Male			Female		
Variable (mm)	mean	sd	n	mean	sd	n	mean	sd	n	mean	sd	n	mean	sd	n	mean	sd	n	mean	sd	n	mean	sd	n
Basicranial length	87.4	2.2	17	85.1	3.8	15	102.6	6.3	27	97.2	4.7	50	98.1	4.8	14	96.0	5.1	13	100.4	4.3	28	96.5	3.4	25
Palatal length	57.4	1.9	17	54.7	3.7	15	72.9	5.7	28	68.9	4.8	50	75.2	4.8	14	69.8	4.6	13	71.1	4.4	29	67.1	3.9	26
M_1 corpus height	21.6	3.3	17	22.7	1.7	15	29.1	3.2	27	28.0	3.0	47	28.7	2.0	14	27.3	1.7	13	27.6	1.9	30	27.2	1.6	26
M_2 corpus height	21.7	1.2	17	21.8	1.8	15	27.4	3.0	27	25.9	2.8	46	27.2	2.5	14	25.5	1.8	13	26.3	1.8	30	25.9	1.6	26
M_1 corpus width	10.0	0.7	17	10.3	0.6	13	14.3	1.1	27	13.4	1.2	47	13.9	1.4	14	13.2	1.3	13	14.2	1.0	30	13.4	0.7	26
M_2 corpus width	10.7	1.0	17	11.3	0.9	15	15.1	1.0	26	14.1	1.1	46	14.4	1.2	14	67.7	7.2	14	15.0	0.9	30	14.4	1.0	26
Symphyseal height	32.5	1.3	17	33.3	1.8	14	44.0	3.8	27	41.8	3.6	48	46.0	3.3	14	42.9	3.0	13	45.3	2.9	30	42.1	2.3	26
Symphyseal width	12.4	0.8	17	13.4	1.6	14	16.9	1.7	27	15.7	1.5	48	16.2	1.3	14	14.6	1.6	13	18.0	1.1	30	17.0	1.1	26
Bicondylar breadth	95.2	5.8	17	95.1	4.1	15	107.5	6.9	27	103.0	4.9	45	108.5	5.0	13	103.2	6.5	12	108.7	4.1	29	104.1	3.6	25
Condylar length	10.1	1.2	17	9.6	1.3	15	10.9	1.9	27	10.2	1.4	46	10.4	1.7	14	9.6	1.5	13	10.3	1.5	30	9.5	1.4	25
Condylar width	19.9	1.9	17	19.1	1.4	15	23.2	2.1	27	22.2	2.2	46	24.1	2.1	14	22.5	3.0	13	23.0	1.9	30	22.0	1.3	25
Condyle-incision	112.9	1.6	16	111.0	3.6	15	140.5	8.4	27	133.6	7.3	46	139.3	7.3	13	133.9	6.4	13	136.6	5.2	30	130.9	4.9	26
Gonion-incision	96.9	4.2	16	93.6	3.6	14	120.0	7.6	27	113.9	7.8	43	120.4	7.8	14	113.6	5.6	13	117.1	5.4	29	111.1	4.0	26
Condyle-coronoid	32.1	4.0	17	31.5	2.9	14	40.9	4.6	27	38.8	4.3	45	37.6	4.1	14	35.5	3.7	13	37.7	3.3	30	37.6	3.0	26
Ramal width	37.7	2.1	17	36.3	1.7	15	48.0	4.8	27	43.8	4.0	46	47.8	4.5	14	43.0	3.4	13	44.9	2.7	30	41.7	2.2	26
Anterior ramal height	55.5	3.0	17	52.8	2.6	15	68.0	4.7	27	64.8	5.3	45	67.7	7.2	14	63.3	5.7	13	64.8	3.7	30	62.2	3.7	26
Posterior ramal height	61.7	3.4	17	57.8	2.8	15	78.0	6.8	27	73.0	5.6	44	77.0	6.3	14	70.9	4.9	13	71.9	3.5	24	69.4	3.7	23
Condylar height	40.1	2.3	17	35.2	3.1	15	48.9	5.6	27	45.0	5.0	44	48.3	5.6	14	43.6	4.6	13	44.2	3.7	24	42.3	3.2	23
Incisor cord length	22.9	0.9	16	22.5	1.1	12	29.1	2.3	25	27.9	1.5	42	26.7	1.8	13	26.7	1.5	13	28.7	1.6	21	28.1	0.9	17

Descriptive statistics for mandibular proportions for *Pan* separately by taxon and sex

	P. paniscus						*P.t. troglodytes*						*P.t. schweinfurthii*						*P.t. verus*					
	Male			Female			Male			Female			Male			Female			Male			Female		
vs. Basicranial length	mean	sd	n	mean	sd	n	mean	sd	n	mean	sd	n	mean	sd	n	mean	sd	n	mean	sd	n	mean	sd	n
M_1 corpus height	24.7	2.0	17	26.6	2.1	15	28.4	2.6	26	28.7	2.7	47	29.3	2.2	14	28.5	1.8	13	27.5	1.9	28	28.3	1.5	25
M_2 corpus height	24.8	1.4	17	25.7	2.1	15	26.7	2.6	26	26.6	2.6	46	27.8	2.4	14	26.6	1.2	13	26.2	1.8	28	27.0	1.6	25
M_1 corpus width	11.5	0.9	17	12.2	0.9	13	14.0	1.1	26	13.8	1.4	47	14.2	1.6	14	13.7	1.4	13	14.2	1.1	28	13.9	0.8	25
M_2 corpus width	12.3	1.3	17	13.3	1.0	15	14.8	1.3	25	14.5	1.4	46	14.7	1.4	14	14.8	1.4	13	14.9	0.93	28	14.9	1.1	25
Symphyseal height	37.1	1.1	17	39.2	1.9	14	43.1	2.9	26	42.9	3.4	48	47.0	3.6	14	44.8	3.1	13	45.1	2.6	28	43.6	2.3	25
Symphyseal width	14.2	0.8	17	15.8	1.7	14	16.5	1.6	26	16.2	1.4	48	16.6	1.4	14	15.2	1.5	13	17.9	1.0	28	17.6	1.3	25

	P. paniscus						*P.t. troglodytes*						*P.t. schweinfurthii*						*P.t. verus*					
	Male			Female			Male			Female			Male			Female			Male			Female		
vs. Basicranial length	mean	sd	n	mean	sd	n	mean	sd	n	mean	sd	n	mean	sd	n	mean	sd	n	mean	sd	n	mean	sd	n
Bicondylar breadth	109.0	6.8	17	111.8	4.6	15	105.1	7.0	26	106.0	5.3	45	111.2	4.4	13	107.8	4.3	12	108.5	5.4	28	107.8	3.9	24
Condylar length	11.6	1.5	17	11.2	1.4	15	10.5	1.7	26	10.5	1.4	46	10.6	1.6	14	10.0	1.2	13	10.3	1.4	28	9.9	1.6	24
Condylar width	22.8	2.4	17	22.5	1.8	15	22.6	2.0	26	22.8	2.2	46	24.5	1.6	14	23.3	2.5	13	23.1	1.6	28	22.7	1.6	24
Gonion-incision	110.9	4.6	16	110.1	6.9	14	116.8	6.0	26	116.9	6.6	43	122.8	7.1	14	118.4	5.4	13	116.6	4.2	27	115.2	5.0	25
Condyle-incision	129.1	2.6	16	130.5	6.3	15	136.9	6.2	26	137.2	6.9	46	142.3	6.3	13	139.5	4.9	13	136.4	5.5	28	135.5	6.5	25
Condyle-coronoid	36.6	4.0	17	37.2	3.2	14	39.7	3.6	26	39.9	3.9	45	38.4	4.3	14	37.0	3.0	13	37.7	3.2	28	39.1	3.4	25
Ramal width	43.2	2.6	17	42.7	2.4	15	46.7	3.5	26	44.9	3.3	46	48.7	3.9	14	44.7	2.5	13	44.7	2.3	28	43.2	2.8	25
Anterior ramal height	63.5	4.4	17	62.1	3.6	15	66.5	4.6	26	66.6	5.1	45	69.0	6.5	14	65.9	5.3	13	64.4	4.0	28	64.6	4.8	25
Posterior ramal height	70.6	3.6	17	68.0	4.1	15	76.0	6.4	26	75.1	5.2	44	78.5	4.9	14	73.9	3.8	13	71.9	3.9	22	72.1	4.3	22
Condylar height	45.9	2.4	17	41.3	4.0	15	47.6	5.8	26	46.3	5.0	44	49.2	4.6	14	45.4	3.9	13	44.2	3.9	22	43.7	3.7	22
Incisor cord length	26.2	1.1	16	26.5	1.9	12	28.6	2.4	24	28.6	1.7	42	27.2	1.7	13	27.9	2.4	13	28.6	2.0	20	29.1	1.4	17

Descriptive statistics for craniomandibular dimensions for *Gorilla* separately by taxon and sex

	G.g. gorilla						*G.g. graueri*						*G.g. beringei*					
	Male			Female			Male			Female			Male			Female		
Variable (mm)	mean	sd	n	mean	sd	n	mean	sd	n	mean	sd	n	mean	sd	n	mean	sd	n
Basicranial length	130.5	8.4	29	113.2	4.4	23	135.9	5.9	19	113.2	3.4	15	135.9	9.5	14	115.7	3.1	9
Palatal length	103.0	9.8	32	83.8	5.2	25	119.8	6.6	20	97.8	7.6	5	120.9	9.7	16	95.8	6.1	9
M_1 corpus height	40.4	4.3	33	34.2	2.8	23	44.7	3.0	20	35.5	2.9	15	44.8	3.9	15	37.8	3.2	10
M_2 corpus height	37.6	4.1	33	32.2	2.9	23	41.4	3.3	20	33.5	2.5	15	42.3	3.9	15	36.0	2.6	10
M_1 corpus width	19.1	1.6	33	17.8	1.2	23	20.3	1.3	20	18.8	1.1	15	21.7	1.7	15	20.4	1.2	10
M_2 corpus width	20.8	1.8	33	19.6	1.6	23	21.6	1.1	19	20.6	0.9	15	22.8	2.0	15	22.1	1.8	10
Symphyseal height	64.2	6.7	33	52.2	3.5	23	71.6	3.2	20	57.4	3.1	15	71.2	5.1	15	55.0	2.9	10
Symphyseal width	27.0	2.0	33	22.4	1.7	23	27.8	2.2	20	23.3	1.7	15	30.7	2.7	15	26.7	1.8	10
Bicondylar breadth	138.3	10.6	29	121.7	4.4	23	142.9	5.2	20	125.3	6.3	15	148.5	7.9	15	129.6	7.8	9
Condylar length	14.8	3.5	32	10.8	2.6	23	16.8	2.9	20	12.6	1.9	15	15.8	2.4	15	12.9	2.5	10
Condylar width	32.9	7.0	32	29.8	1.8	23	35.4	2.8	20	29.6	2.2	15	38.8	4.1	15	34.6	1.8	10
Condyle-incision	186.1	10.7	32	156.4	5.4	23	201.5	8.8	20	165.5	7.2	15	204.3	10.5	15	164.2	7.2	9
Gonion-incision	161.3	11.2	31	135.8	5.8	23	179.4	7.5	20	147.7	6.7	14	178.3	9.1	14	143.3	5.2	7
Condyle-coronoid	45.0	5.4	31	36.0	4.0	22	45.8	5.3	20	38.5	4.2	14	45.3	6.1	15	39.5	4.0	10
Ramal width	69.7	6.1	33	55.8	3.5	22	74.0	4.5	20	58.5	4.0	15	75.9	6.7	14	60.5	2.8	10
Anterior ramal height	115.3	9.8	31	96.2	6.1	22	121.1	7.9	20	98.2	4.2	15	124.4	12.8	15	108.2	6.0	10
Posterior ramal height	117.6	8.4	31	102.9	4.7	23	127.4	5.9	19	106.9	4.7	15	138.6	9.1	15	120.8	4.6	10
Condylar height	77.7	5.3	27	68.7	5.7	23	82.6	4.2	19	71.4	4.3	15	92.8	7.8	14	83.0	4.8	10
Incisor cord length	26.7	5.5	29	26.4	1.2	22	30.2	2.0	20	28.1	1.2	15	30.2	2.0	13	27.5	1.8	8

Descriptive statistics for mandibular proportions for *Gorilla* separately by taxon and sex

	G.g. gorilla						*G.g. graueri*						*G.g. beringei*					
	Male			Female			Male			Female			Male			Female		
vs. Basicranial length	mean	sd	n	mean	sd	n	mean	sd	n	mean	sd	n	mean	sd	n	mean	sd	n
M_1 corpus height	31.0	3.1	28	30.3	2.9	22	33.0	2.3	19	31.3	2.4	15	32.6	2.6	13	31.9	2.0	8
M_2 corpus height	28.8	3.0	28	28.5	2.8	22	30.5	2.5	19	29.7	2.1	15	30.7	2.7	13	30.7	1.9	8
M_1 corpus width	14.6	1.1	28	15.7	1.1	22	15.0	1.3	19	16.6	0.8	15	15.9	1.6	13	17.8	1.2	8
M_2 corpus width	16.0	1.4	28	17.4	1.3	22	15.9	0.9	18	18.2	0.9	15	16.9	1.6	13	19.2	1.7	8
Symphyseal height	48.8	4.2	28	46.2	3.0	22	52.7	2.7	19	50.7	2.3	15	51.8	3.7	13	47.8	2.3	8
Symphyseal width	20.7	1.6	28	19.9	1.4	22	20.5	1.8	19	20.6	1.3	15	22.7	2.0	13	22.8	1.3	8
Bicondylar breadth	105.5	5.3	24	107.9	4.1	22	105.2	6.9	19	110.7	3.9	15	107.9	6.1	13	112.6	8.4	7
Condylar length	11.3	2.7	27	9.4	2.2	22	12.2	2.0	19	11.2	1.7	15	11.6	1.5	13	11.3	2.2	8
Condylar width	25.6	1.8	26	26.3	1.6	22	25.9	1.9	19	26.2	1.8	15	28.3	2.5	13	30.2	2.0	8
Gonion-incision	123.1	5.8	26	120.1	5.9	22	132.1	4.1	19	130.5	5.8	14	129.1	7.9	12	126.2	5.2	6
Condyle-incision	142.1	6.3	27	138.3	5.6	22	148.0	4.2	19	146.3	6.2	15	148.6	8.0	13	143.6	7.4	7
Condyle-coronoid	34.6	4.0	26	31.7	3.3	21	34.1	4.0	19	33.9	3.2	14	32.8	4.1	13	34.5	4.3	8
Ramal width	53.2	3.2	28	49.3	2.8	21	54.3	3.1	19	51.7	3.2	15	55.2	4.6	12	52.7	2.9	8
Anterior ramal height	87.9	6.0	26	85.0	4.9	21	89.2	5.7	19	86.8	4.7	15	90.7	11.1	13	93.4	5.8	8
Posterior ramal height	90.5	7.1	26	91.2	4.4	22	93.9	4.7	19	94.4	3.2	15	100.9	8.8	13	105.2	5.9	8
Condylar height	60.4	3.8	22	60.8	4.9	22	60.9	3.4	19	63.1	3.3	15	67.7	8.1	12	73.3	5.1	8
Incisor cord length	21.1	1.5	23	23.3	1.1	21	22.2	1.5	19	24.8	1.3	15	21.9	1.6	11	23.4	1.5	6

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