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Title

Sagittal crest formation in great apes and gibbons

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Short running page heading

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Abstract

The frequency of sagittal crest expression and patterns of sagittal crest growth and development have been documented in hominoids, including some extinct hominin taxa, and the more frequent expression of the sagittal crest in males has been traditionally linked with the need for larger-bodied individuals to have enough attachment area for the temporalis muscle. In the present study, we investigate sagittal cresting in a dentally mature sample of four hominoid taxa (*Pan troglodytes schweinfurthii, Gorilla gorilla gorilla*, *Pongo pygmaeus pygmaeus* and *Hylobates lar*). We investigate whether sagittal crest size increases with age beyond dental maturity in males and females of *G. g. gorilla* and *Po. pyg. pygmaeus*, and whether these taxa show sex differences in the timing of sagittal crest development. We evaluate the hypothesis that the larger sagittal crest of males may not be solely due to the requirement for a larger surface area than the un-crested cranial vault can provide for the attachment of the temporalis muscle, and present data on sex differences in temporalis muscle attachment area and sagittal crest size relative to cranial size. *Gorilla g. gorilla* and *Po. pyg. pygmaeus* males show significant relationships between tooth wear rank and sagittal crest size, and they show sagittal crest size differences between age groups that are not found in females. The sagittal crest emerges in early adulthood in the majority of *G. g. gorilla* males, whereas the percentage of *G. g. gorilla* females possessing a sagittal crest increases more gradually. *Pongo pyg. pygmaeus* males experience a three-fold increase in the number of specimens exhibiting a sagittal crest in mid-adulthood, consistent with a secondary growth spurt. *Gorilla g. gorilla* and *Po. pyg. pygmaeus* show significant sex differences in the size of the temporalis muscle attachment area, relative to cranial size, with males of both taxa showing positive allometry not shown in females. *Gorilla g. gorilla* males also show positive allometry for sagittal crest size relative to cranial size. Our results suggest that although patterns of sagittal crest expression have limited utility for taxonomy and phylogeny reconstruction, they could be useful for reconstructing aspects of social behaviour in some extinct hominin taxa. In particular, our results in *G. g. gorilla* and *Po. pyg. pygmaeus,* which suggest that the size of sagittal crests in males cannot be solely explained by the surface area required for attachment of the temporalis muscle, offer partial support for the hypothesis that large sagittal crests form in response to sexual selection, and may play a role in social signalling.

Keywords

Cranium; ectocranial cresting; sexual dimorphism; sexual selection; hominoid

Introduction

Although most of the external surface of the cranium of living hominoids is smooth, in some regions the outer table of the cranial vault is raised up into crest-like structures. Some, including those on the external surface of the basicranium, are relatively modest in size. Others can be much larger, especially those at, or close to, the midline between the attachments of the temporal muscles, or those that occur either uni- or bi-laterally between the attachments of the temporal and nuchal muscles known, respectively, as sagittal and nuchal crests (Owen, 1835). Sagittal crests (i.e., ectocranial crests that occur at, or close to, the midline), if they appear at all in living hominoids, are more likely to occur in male than female individuals and they develop relatively late in ontogeny (i.e., their development tends to coincide with, or follow, the eruption of the permanent dentition). Ashton & Zuckerman (1956) found that while the process of sagittal crest formation among hominoid taxa is similar, the age at which sagittal crests develop varies interspecifically, and sagittal crest size varies both intra- and interspecifically. Other research suggests that in extant great apes, sagittal crests are associated with older individuals (Prat & Thackeray, 2001), and a study investigating age-related changes in the temporalis muscle of *Po. pygmaeus* indicates that absolute muscle attachment area is also larger in older individuals (Winkler, 1991).

The inconsistent occurrence of sagittal crests across primate taxa, both extant and extinct (Neuville, 1916; Ashton & Zuckerman, 1956), suggests that sagittal crests have evolved independently in a number of lineages, because their occurrence cannot be predicted from the branching pattern supported by molecular and other morphological evidence. For example, the strong sagittal cresting seen in gorillas and orangutans is not found in chimpanzees, or in most hominins, and in some cases sagittal crests occur in a single taxon within a broader taxonomic group, (e.g., *Sapajus* among New World monkeys (Alfaro, 2012)).

Sagittal cresting in primates has been traditionally linked with the need for larger-bodied individuals to have sufficient attachment area for the temporalis muscle (Ashton & Zuckerman, 1956; Robinson, 1958; Holloway, 1962; Hofer, 1974). The reasoning is that because increases in the size of the brain case do not keep pace with increases in body size, there would not be enough space for the temporalis muscle in larger-bodied individuals without the additional surface area provided by sagittal crests (Robinson, 1958; Hofer, 1974). In extant primates, prominent sagittal crests are found primarily in male gorillas and orangutans, the two largest living primate species, which is consistent with the notion that sagittal crests serve the purpose of providing a more extensive muscle attachment area in large-bodied individuals. However, sagittal crests are also seen in smaller extant primates such as extant cercopithecoids and cebids, as well as in extinct adapids, and in the males of the early anthropoid *Aegyptopithecus* for which a pronounced level of sexual size dimorphism has been inferred (Ashton & Zuckerman, 1956; Fleagle et al. 1980; Simons, 1987; Alfaro et al. 2012). The presence of a prominent sagittal crest in these species has been linked with unusually large masticatory muscles, particularly in males (Simons, 1987; Alfaro et al. 2012).

Although sagittal crests are only moderately expressed in chimpanzees (Ashton & Zuckerman, 1956), and they are not seen in modern humans, they are expressed in several fossil hominin species such as *Paranthropus robustus* (Robinson, 1958), *Paranthropus boisei* (Tobias, 1967; Wood, 1991), *Paranthropus aethiopicus* (Walker et al. 1986) and *Australopithecus afarensis* (Kimbel et al. 2004). Initial interpretations about their occurrence in fossil hominins were controversial. Zuckerman and his colleagues argued that any differences between the sagittal crests seen in *P. robustus* and those seen in extant apes and monkeys “are differences of degree, not of kind” (Ashton & Zuckerman, 1956, p. 606), and thus provided yet more evidence that what were then called “australopithecines” or “prehominines” could not be distinguished from extant Old World primates. Robinson, on the other hand, argued that “the crests in the australopithecines … differ from those in the pongids” because, among other reasons, “the sagittal crest … does not extend back to the superior nuchal line” (Robinson, 1958, p. 427). Both sides of the controversy seemed to agree, implicitly or explicitly, that sagittal crests in what were then called pongids (chimpanzees, gorillas and orangutans), and early hominids, are an emergent property in the sense that they are “a response to the need for additional area of attachment for muscles in a situation where space is restricted” (Robinson, 1958, p. 399). Hofer (1974) suggests that factors other than mastication may influence sagittal cresting in *Pan*, though he offers no suggestions about what these other factors might be. Hofer (1974) also identified three different cresting patterns within *Pan*. In the first, the crest reaches its apex at the highest point of the cranial vault. In the second, termed the “gorilla” pattern, the crest increases slowly from bregma, attaining its highest point just anterior to the occipital protuberance. In the third, which he termed the “australopithecine” pattern, the crest is only found at the highest point of the cranium.

With respect to the ontogeny of sagittal crests, in *Gorilla gorilla* males, the superior temporal lines converge and the sagittal crest begins to form around the time of eruption of the permanent canine and third molar. All dentally mature *G. gorilla* adult males develop a sagittal crest, with young *G. gorilla* adult males having less developed sagittal crests compared to older adult males (Ashton & Zuckerman, 1956; *cf*. Neuville, 1916). This contrasts with *G. gorilla* females, where the temporal lines meet at a later stage of development compared to males, and not all females develop a sagittal crest, with only 37% of a sample of 51 *G. gorilla* females having a sagittal crest (Ashton & Zuckerman, 1956). In *Pongo pygmaeus* males, as with gorilla males, sagittal crest growth continues beyond dental maturity, though a sagittal crest is only present in 36% of a sample of 14 *Po. pygmaeus* males. In *Po. pygmaeus* females, even among older individuals, the temporal lines remain far apart (Ashton & Zuckerman, 1956). In the *Pan troglodytes* sample investigated by Ashton & Zuckerman (1956), sagittal cresting is nowhere near as prevalent as in gorillas and orangutans. For example, although the temporal lines met at the mid-sagittal plane in 16% of 25 *P. troglodytes* males, in only one individual was there a projecting crest, and among 73 *P. troglodytes* females the superior temporal lines met at the mid-line in only one individual (Ashton & Zuckerman, 1956). No specimens of Ashton & Zuckerman's (1956) *Hylobates lar* sample showed sagittal cresting, and although in one *H. lar* individual the temporal lines met at the midline *c.*1 cm anterior to bregma, they diverged posteriorly. Schultz (1944) reported an incidence of sagittal crests of 3% in a sample of 184 specimens of *H. lar* and Holloway (1962) found that 4% of a sample of *H. lar* specimens exhibited sagittal crests, with roughly equal numbers of males and females having crests.

The presence of a sagittal crest increases the height of both the frontal and lateral profile of the head, and recent behavioural research suggests that the sagittal crest in *G. g. gorilla* males is associated with male reproductive success. Caillaud et al. (2008) found a positive relationship in breeding silverbacks between male sagittal crest size (measured as size of the adipose hump, using photographs of head profiles) and the number of females associated with that male. Similarly, Breuer et al. (2012) examined the relationship between male *G. g. gorilla* size variables, including the sagittal crest, and various measures of reproductive success, namely a) the average number of adult females associated with each male throughout adulthood, b) the number of offspring that survived beyond weaning age and c) the rate of offspring survival to weaning age. Males with larger sagittal crests and gluteal muscles had higher siring rates, independent of the number of females they were associated with, and offspring sired by males with large sagittal crests had higher rates of survival. Contrastingly, males with longer bodies were associated with a significantly higher number of females, though this did not translate to higher reproductive success as measured through siring rate and offspring survival. Breuer et al. (2012) proposed that the size of the sagittal crest and gluteal musculature may be proxies for the ability to protect females against attempted infanticide by other males.

Overall, interspecific variation in sagittal crest morphology, the presence of sagittal crests in primates ranging in size from less than 10kg to over 100kg, and data from behavioural studies, suggest that factors other than mastication may affect sagittal crest size. In this paper, we evaluate what we refer to as the ‘muscle attachment’ and the ‘sexual selection’ hypotheses to assess whether the prominent sagittal crests seen in the males of some extant non-human apes are solely the result of the need for a larger muscle attachment area than the surface area of the uncrested neurocranium can provide. If that is not the case then we consider whether part of the variation in male sagittal crest size can be explained by sagittal crest size being a social signal. Specifically, the ‘muscle attachment’ hypothesis suggests that sagittal crests develop because the surface area required for the attachment of the temporalis muscle is greater than the area available on the uncrested neurocranium. The ‘sexual selection’ hypothesis suggests that sagittal crests develop, in part, as a result of social signalling (i.e. sexual selection plays a role in driving sagittal crest development). These two hypotheses are not mutually exclusive.

To better understand the significance of sagittal crest formation in the early hominin taxa listed above, we examined sagittal crest formation in samples of *Gorilla gorilla gorilla*, *Hylobates lar*, *Pan troglodytes schweinfurthii*, and *Pongo pygmaeus pygmaeus*. We expanded on Ashton & Zuckerman’s (1956) study by including larger sample sizes and by applying relevant statistical methods (no statistical tests were performed by Ashton and Zuckerman, whose analyses mainly consisted of qualitative descriptions). We examined sagittal crest growth and development, but given the low cresting frequency in *Pan* and *Hylobates*, this part of the study was confined to *Gorilla* and *Pongo.* We investigated size changes in, and the timing of, sagittal crest development separately in the males and females of these taxa. If sagittal crest development occurs in response to sexual selection in males, we would expect the timing of sagittal crest emergence to coincide with the time at which males normally become socially dominant. Finally, we evaluated the strength of support for the 'muscle attachment' and the 'sexual selection' hypotheses by asking whether the sagittal crest develops because there is a mismatch between cranial surface area and the area needed for the attachment of the temporalis muscle. We investigated this question by testing for intraspecific sex differences in the regression slope between temporalis muscle attachment area (TMAA) and sagittal crest size (SCS), respectively, and cranial size. If the sagittal crest develops in response to sexual selection, we expect a steeper slope between SCS and cranial size in males, compared to females, and we would expect corresponding sex differences in the scaling relationship between TMAA and cranial size. If the sagittal crest develops solely in response to mastication, we would not expect sex differences in these allometric slopes.

Materials and methods

Sample

The sample consists of 357 crania of wild-shot individuals of *G. g. gorilla, H. lar*, *P. t. schweinfurthii*, and *Po. pyg. pygmaeus* (Table 1). Modern humans were excluded because they do not have a sagittal crest. All specimens had upper and lower M3s in full occlusion, and for the few great apes for which sex was not clear from museum records we based the sex assignment on the relative size of the canine crown, following well established findings about sexual dimorphism in the canine size of these taxa (Leutenegger & Kelley, 1977; Harvey et al. 1978; Plavcan & van Schaik, 1992).

Data collection

Sagittal crest size (SCS), temporalis muscle attachment area (TMAA), and linear measurements were taken directly from 3D surface scans. We used a NextEngine 2020i 3D Desktop laser scanner to obtain surface scans for all specimens except for *P. t. schweinfurthii*, for which 3D surface scans were obtained using a Breuckmann optical white light scanner or from CT scan data. All three scanners scan to a high enough accuracy to adequately quantify temporalis muscle attachment area and sagittal crest size, and differences in scanning methods are not likely to have introduced error in the subsequent measurements taken from the scans. We used the geometric mean of superior facial breadth (left frontomalare temporal to right frontomalare temporal), glabellar height (glabella to prosthion), and cranial length (glabella to inion) as a proxy for cranial size. All three linear measurements were taken from 3D surface scans using Landmark, v 3.0.

We measured SCS and TMAA as surface area measurements of the ectocranial surface, taken directly from 3D surface models. We measured SCS by calculating the area between the superior border of the sagittal crest and its base, as seen in lateral view. The posterior border of the sagittal crest was taken as the point of inflexion between the sagittal and nuchal crests (Fig. 1). We measured TMAA following anatomical descriptions of temporalis muscle attachment in great ape taxa (Boyer, 1939; Raven & Gregory, 1950; Miller, 1952; Swindler & Wood, 1973; Winkler, 1991). In specimens with no sagittal or nuchal crest, we used the superior temporal line as the superior boundary, and for specimens with a sagittal crest we used its superior border. The anterior boundary of the TMAA for all specimens begins at the upper lateral margin of the postorbital plate, and extends inferiorly, via the greater wing of the sphenoid, to the most inferior point of the temporal fossa. The inferior boundary for all specimens is the contour along the most inferior edge of the vault, including the supramastoid crest and the superior portion of the root of the zygomatic process

(Fig. 2). Surface area measurements were taken using the corresponding functions in Geomagic Studio v. 12 or Geomagic Design X v. 5. These surface area measurements are calculated through the summation of the surface areas of all triangles (formed by linking the points of the point cloud) within the selected boundaries as described above. Measurements were from the left side unless the cranium was damaged, in which case we measured the right side.

Age categorisation method

To assess age beyond dental maturity, we assigned specimens to adult age quartiles (AAQs) using the relative age estimation procedure devised by Balolia et al. (2013). Photographs of the upper and lower dentition were placed in ranked order based on the relative amounts of occlusal wear on the upper and lower molars. We took premolar and incisor wear into account in cases where there was little to separate specimens based on molar wear. Males and females were seriated separately. Based on the ranked tooth wear, we assigned approximate ages to the nearest 0.5 year to each specimen using a version of the Miles (1962) method of aging, and published molar eruption ages in hominoids (see Balolia et al. 2013 for molar eruption ages and sources). First, we noted the amount of M1 wear at the point where M3 had reached full occlusion (Fig. 3a). Second, we aged specimens where M2 wear has reached the same extent of M1 wear at M3 occlusion by adding the species-specific difference in years between M1 eruption and M3 eruption to the age at M3 occlusion. Third, after assigning an age to a specimen based on M2 wear having reached the same stage of wear as M1 at the stage of M3 occlusion, we again noted the amount of M1 wear (Fig. 3b). A specimen in the series with M2 wear similar to that stage of M1 wear was found and, again, the species-specific age difference between M1 and M2 eruption was added to infer specimen age. We continued this process (Fig. 3c), until all specimens in each ranked series were aged. Finally, the tooth wear photos were reviewed, where we assigned similar ages to teeth at similar tooth wear stages and giving the appropriate relative age assignment to specimens that fell in the intervals between assigned ages (Miles, 1962). Based on the observed range of estimated ages (Table 2), following Balolia et al. (2013), specimens were categorised into one of four AAQs. Each AAQ represents a similar stage of adult life history across taxa. Adults categorised as AAQ1 are referred to as young adults, AAQ2 and AAQ3 represent mid-adulthood, and individuals categorised as AAQ4 are old adults (Table 3).

Statistical analysis

We used Fisher's exact test to establish whether dentally mature males show a higher frequency of sagittal crest expression relative to dentally mature females in the same taxon. We used Spearman correlations between surface area measurements and tooth wear rank to detect evidence of sex-specific SCS changes beyond dental maturity, and we used Kruskal-Wallis tests to test for statistically significant differences in SCS among age groups. Rank-based (non-parametric) tests were judged to be more suitable than ANOVA because of the large number of individuals without a sagittal crest in some samples. To test whether the relationships between TMAA and cranial size, and SCS and cranial size, depart from isometry, and to test for sex differences in regression slopes, we ran ordinary least-squares (OLS) regression on logarithmically-transformed measurements. Our research question examines inter- and intraspecific differences in muscle attachment area and sagittal crest size (TMAA and SCS) at a given cranial size, so because the identification of X and Y variables is non-arbitrary, we followed Smith (2009) and used OLS rather than reduced major axis (RMA) regression. We used analysis of variance (ANOVA) to test whether the models were significant. Because the proxy for cranial size (on the x axis) is based on linear variables, and SCS or TMAA (on the y axis) is derived from a surface area measurement, a slope of 2 indicates isometry, < 2 indicates negative allometry and > 2 indicates positive allometry. We used analysis of covariance (ANCOVA) to test for significant sex differences in regression slopes. For analyses where multiple comparisons were conducted within the same taxon, we corrected statistical results for multiple comparisons; significant comparisons are highlighted in bold. We performed all statistical analyses using SPSS version 21.0 or 22.0.

Results

Sagittal crest frequency in hominoids

Among hominoids, *G. g. gorilla* show the highest frequency of sagittal cresting, with 76% of the sample having a sagittal crest. When each sex is examined separately, 93% of *G. g. gorilla* males and 58% of *G. g. gorilla* females have a sagittal crest. Among the *Po. pyg. pygmaeus* sample, 17% of individuals, representing 39% of the male sample, show sagittal cresting. No *Po. pyg. pygmaeus* females have sagittal crests. Among the *P. t. schweinfurthii* specimens 15% have a sagittal crest, where 24% of males and 7% of females have a sagittal crest. Among the *H. lar* sample, 3% of individuals have a sagittal crest, where 4% of the male sample show sagittal cresting. No *H. lar* females have sagittal crests. Males of *P. t. schweinfurthii*, *G. g. gorilla* and *Po. pyg. pygmaeus* show a significantly higher frequency of sagittal cresting compared to females for each taxon; no such sex difference is shown for *H. lar* (Table 4).

Sagittal crest size changes beyond dental maturity in gorillas and orangutans

Gorilla g. gorilla and *Po. pyg. pygmaeus* males show significant correlations between tooth wear rank and sagittal crest size, and males of both taxa show significant size differences among age groups (Table 5). Female *G. g. gorilla* show no significant correlations between tooth wear rank and sagittal crest size, nor do they show any significant size differences between age groups (Table 5). As no *Po. pyg. pygmaeus* females in the sample have a sagittal crest, no statistical tests were conducted.

The timing of sagittal crest development in gorillas and orangutans

Sagittal crests appear relatively early in *G. g. gorilla* males, where *c.*80% of AAQ1 specimens have a sagittal crest, and by AAQ2 all *G. g. gorilla* males in the sample have a sagittal crest (Fig. 4). In contrast, in *G. g. gorilla* females the percentage of individuals with a sagittal crest increases for each age group until AAQ3. *Pongo pyg. pygmaeus* males show an additional percentage of individuals with a sagittal crest for each successive age group until AAQ4. Contrary to what is observed in gorillas, the percentage of *Po. pyg. pygmaeus* males possessing a sagittal crest increases abruptly between AAQ2 and AAQ3. No females of *Po. pyg. pygmaeus* in any age group have a sagittal crest (Fig. 4).

Scaling relationships among TMAA and SCS, and cranial size

Male *G. g. gorilla* and *Po. pyg. pygmaeus* show a positive allometric relationship between TMAA and cranial size, whereas in *P. t. schweinfurthii* and *H. lar* males, the relationship does not significantly depart from isometry (Fig. 5, Table 6). With respect to females, only *Po. pyg. pygmaeus,* where the relationship is negatively allometric, departs from isometry (Fig. 5, Table 6). There are significant sex differences in allometric slope between TMAA and cranial size for *G. g. gorilla* (ANCOVA: $F_{(1,96)} = 5.078$, $P = 0.027$) and *Po. pyg. pygmaeus* ($F_{(1,89)} = 15.928$, $P < 0.001$). No such sex differences were found for *P. t. schweinfurthii* ($F_{(1,68)} = 0.018$, $P = 0.894$) and *H. lar* ($F_{(1,71)} = 0.008$, $P = 0.930$). Of the four single-sex groups for which enough individuals have a sagittal crest to calculate bivariate regression slopes between SCS and cranial size, only *G. g. gorilla* males depart from isometry in the direction of strong, positive allometry (Fig. 6, Table 6). As the slope between SCS and cranial size for *G. g. gorilla* females is not significant, sex difference in bivariate slope could not be tested statistically.

Discussion

The results of our study provide support for the ‘sexual selection’ hypothesis for sagittal cresting in gorilla and orangutan males. In *G. g. gorilla* and *Po. pyg. pygmaeus*, the timing of sagittal crest emergence in males and sex differences in temporalis muscle attachment area allometry suggest that sagittal crests do not solely develop to accommodate a large temporalis muscle, and both are consistent with the hypothesis that sexual selection contributes to sagittal cresting in males of these taxa. In contrast, in *P. t. schweinfurthii* and in *H. lar*, the frequency of sagittal cresting is low, and there is no evidence of scaling differences between the sexes, nor is there evidence in either sex that the relationship between TMAA and cranial size departs from isometry. Therefore, in these two taxa, patterns of allometric scaling provide no support for the sexual selection hypothesis. Our results show that sagittal crest size increases beyond dental maturity in *G. g. gorilla* and *Po. pyg. pygmaeus* males, and that sagittal crests in *G. g. gorilla* males emerge in young adults (*c.*80% of AAQ1 males possessing a sagittal crest). This contrasts with the situation in *Po. pyg. pygmaeus* males where there is an abrupt increase in mid-adulthood of the percentage of male individuals possessing a sagittal crest (*c.* 30% of AAQ2 males and *c.*80% of AAQ3 males possess a sagittal crest). These findings suggest that the timing of sagittal crest emergence in *G. g. gorilla* and *Po. pyg. pygmaeus* males may be a response to taxon-specific selective pressures, perhaps related to differences in their habitat and social structure, discussed in further detail below. Our findings of positive allometry in SCS and TMAA in *G. g. gorilla* males, but not in females, and sex differences in scaling relationships between TMAA and cranial size, provide further support for the ‘sexual selection’ hypothesis in gorillas. The positive allometry of TMAA in *Po. pyg. pygmaeus* males, and the sex differences in scaling relationships between TMAA and cranial size, are also consistent with the hypothesis that sexual selection contributes to sagittal cresting in male orangutans.

By contrast to what is found in *G. g. gorilla* and *Po. pyg. pygmaeus*, the emergence of sagittal crests in *P. t. schweinfurthii* or *H. lar* is best explained by the ‘muscle attachment’ hypothesis based on the low frequency of sagittal cresting in males of these two taxa and the finding that scaling relationships between TMAA and cranial size do not depart from isometry in either sex, and that there are no sex differences in allometric slope. Given that our findings indicate that mastication contributes to sagittal cresting in *P. t. schweinfurthii* and *H. lar*, it is also likely that some of the variation in sagittal crest size in *G. g. gorilla* and *Po. pyg. pygmaeus* is also a result of mastication. Further research is required to investigate how much of the variation in sagittal crest size is explained by mastication and sexual selection respectively.

The results of the present study mirror Ashton & Zuckerman’s (1956) findings that among dentally mature male hominoids, gorillas show the highest incidence of sagittal cresting, followed by orangutans, chimpanzees and gibbons. Also similar to Ashton & Zuckerman’s (1956) findings, over half of our dentally mature female gorilla sample have a sagittal crest, with fewer female chimpanzees showing evidence of sagittal cresting. Among the taxa investigated in this study, males show a higher frequency of sagittal cresting than do females. It is also consistent with patterns of cranial growth beyond dental maturity and with spheno-occipital fusion being delayed in both taxa (Randall, 1943; Leutenegger & Masterson, 1989a, 1989b; Masterson & Leutenegger, 1990, 1992; Röhrer-Ertl, 1988; Uchida, 1996; Hens, 2003, 2005; Balolia et al. 2013; Gordon et al. 2013; Balolia, 2015).

The finding that in the majority of *G. g. gorilla* males a sagittal crest develops in early adulthood, and that all males develop a sagittal crest by the second quarter of adult life, can be considered in the context of their social behaviour and male intrasexual dominance relationships. Breeding groups of *G. g. gorilla* are almost exclusively uni-male/multi-female (Robbins et al. 2004; Gatti et al. 2004). Males who reach sexual maturity early in adulthood are more likely to establish and defend a breeding group and thus enhance their reproductive success, and such a strategy is likely aided by early development of a large sagittal crest (Breuer et al. 2012). The timing of sagittal crest emergence in *G. g. gorilla* males differs from that in *Po. pyg. pygmaeus,* where the onset of sagittal crest development is delayed such that between the second and third adult age quartiles there is a threefold increase in the number of male specimens exhibiting a sagittal crest. The relatively late sagittal crest development in *Po. pyg. pygmaeus* males coincides with a secondary growth spurt (Utami & van Hooff, 2004). Other evidence of a secondary growth spurt in *Po. pygmaeus* comes from the facial skeleton and the cranium (Leutenegger & Masterson, 1989a, 1989b; Masterson & Leutenegger, 1990, 1992; Röhrer-Ertl, 1988; Uchida, 1996; Hens, 2003, 2005; Balolia et al. 2013).

The pattern of sagittal cresting in *G. g. gorilla* and *Po. pyg. pygmaeus* males is consistent with the nature of male intrasexual relationships in these taxa, where males of both taxa are mostly intolerant of one another and show a high intensity of intrasexual male aggression (Watts, 1996; Knott et al. 2010). Furthermore, there is evidence that females of these taxa prefer to mate with dominant males (Stokes et al. 2003; Knott et al. 2010; Breuer et al. 2012). With respect to contextualising these findings in terms of orangutan behaviour, *Po. pygmaeus* males employ two alternative reproductive strategies (Utami et al. 2002). In the first, dominant, flanged males control a territory and are intolerant of other dominant males with whom females prefer to mate (Knott et al. 2010). In the second, subordinate unflanged males attain reproductive success through forced copulation with females (Fox, 2002). Subordinate males, who can remain unflanged for up to 20 years beyond sexual maturity (Utami et al. 2002), use this strategy to avoid inter-male aggression from dominant males. Therefore, the late and abrupt onset of sagittal crest development in the *Po. pyg. pygmaeus* males examined in this study is consistent with the suggestion that sagittal crest development in *Pongo* males may be a secondary sexual characteristic that helps to determine dominance ranking. This explanation is consistent with interpretations by Ashton & Zuckerman (1956) who, based on the relatively late timing of sagittal crest emergence and sagittal crest development beyond dental maturity in males of some taxa, suggested that sagittal crests are "secondary sexual characters, induced at least partly as a result of hormonal action" (p. 604). Under this scenario, the sagittal crest may serve as a visual signal of dominance in males in that the presence of a large sagittal crest increases the height of the head in frontal and lateral profile (Caillaud et al. 2008; Breuer et al. 2012). Our findings of positive allometry for TMAA in *G. g. gorilla* and *Po. pyg. pygmaeus*, and for SCS in *G. g. gorilla*, are consistent with the proposal that if sagittal crest size varies in response to sexual selection, it will be most prominent in the males of taxa that show high levels of male intrasexual aggression. In this regard, sagittal crest size and associated musculature may be an honest indicator to females of mate quality and the ability to protect against infanticide, as well as an honest indicator of the ability to fight and to dominate other males.

One aim for this study was to better understand the significance of sagittal crest formation in early hominin taxa, particularly in taxa that show a relatively high frequency of sagittal cresting compared to other hominins. These taxa include *Paranthropus boisei* and *Paranthropus robustus* (Tobias 1967, 1991), *Paranthropus aethiopicus* (Walker et al. 1986), and *Australopithecus afarensis* (Kimbel et al. 2004). Our results confirm previous findings that chimpanzees, one of the two great ape taxa most closely related to the early hominins, show little or no sagittal cresting, whereas some gorilla and orangutan specimens, taxa that are more distantly related to hominins, show large sagittal crests and vary in their frequency of sagittal cresting. These findings are consistent with the suggestion put forward in the introduction that strong sagittal cresting in some primate taxa evolved independently (i.e.

may be a result of homoplasy) and imply that among hominin taxa sagittal crest expression is likely to be an autapomorphic trait. What is clear is that differences in sagittal crest expression among hominids demonstrates its evolutionary plasticity, and that sagittal crest expression should be considered to have limited utility for generating phylogenetic hypotheses (*cf.* Lockwood & Fleagle, 1999, p. 208), though further work is required to test this hypothesis in other parts of the primate clade. Furthermore, because the sagittal crest is a sex-specific trait, yet it is not expressed in all dentally mature males and it is manifest only late in ontogeny, it also has limited utility for alpha taxonomy.

The results of the present research could alternatively be explained by sex differences in amount of food consumed, or other dietary differences between males and females. However, among Western lowland gorillas, no sex differences in diet composition have been found (Doran et al. 2002) and despite the large difference in overall body size, silverback mountain gorillas eat only *c.*25% more food per day than do adult females (Rothman et al. 2008). There is evidence of sex differences in the amount of time feeding and in diet composition among orangutans (Fox et al. 2004; Wich et al. 2006). Adult female orangutans spend longer periods of time feeding than do males, and this additional time is spent eating insects, rather than fruit (Fox et al. 2004). During periods of high fruit availability, reproductive females eat more fruit (excluding figs) and insects, and unflanged males rely more heavily on more flowers during periods of low fruit abundance (Wich et al. 2006). Given that these food types, with the possible exception of insects, are relatively soft it is unlikely that sex differences in their consumption strongly impacts temporalis muscle development. There is no research of which we are aware documenting sex differences in food consumption (time spent feeding or type of food consumed) in other great ape taxa. Positive allometry has also been associated with biomechanical factors (Tseng & Rowe, 1999; Bonduriansky, 2007). We argue that the positive allometry for sagittal crest size in *G. g. gorilla* males (slope = 12.00) substantially exceeds the scaling relationships between TMAA and cranial size, so dietary or biomechanical explanations are unlikely to account for the sex differences in TMAA allometric slopes observed in *G. g. gorilla* and *Po. pyg. pygmaeus*. However, further research is required to understand the influence of diet and biomechanical factors on sex differences in sagittal cresting for taxa that show a high degree of body size dimorphism.

A further confounding factor in understanding the relationship between the area of the neurocranium required to accommodate the temporalis muscle and sagittal crest emergence is the extent to which temporalis muscle size is associated with TMAA. There are limited data in hominoids investigating this relationship, though the data that do exist suggest that the relationship between skeletal data, measured using mandibular size measurements, and temporalis muscle physiological cross-sectional area (PCSA) is not clear cut (Taylor & Vinyard, 2013). Taylor & Vinyard (2013) also show interspecific variation in temporalis fibre length among hominoid taxa, though there is no evidence to suggest a trade-off between PCSA and fibre length. Combined, these results suggest that further research into the relationship between actual temporalis muscle size, muscle architecture, and our measure of TMAA in hominoids is warranted. It is possible that sex differences in scaling relationships between TMAA and cranial size in gorillas and orangutans could be the result of differences in muscle architecture, with force potential being increased through increased pennation instead of through increased attachment area on the skull. Sex differences in temporalis muscle weight, fibre lengths and temporalis muscle PCSA, but not pennation angle, have been found in macaques (*Macaca fascicularis*) and these differences are suggested to be a result of sex differences in maximum gape, associated with large male canine size and associated display behaviours (Terhune et al. 2015). These results mean that factors other than mastication may influence sex differences in temporalis muscle architecture, which may in turn affect the amount of space on the ectocranial surface required for attachment of the temporalis muscle. Specifically, reduced pennation, or increased relative fibre length combined with larger overall muscle size, to allow for a wider gape associated with larger canines in males would create a need for larger TMAA, and possibly drive the development of sagittal crests as a consequence of sexual selection for increased canine size. Further research investigating the association between TMAA and muscle size and architecture among hominoids, and how sex differences in maximum gape affects temporalis muscle architecture is required.

Finally, an understanding of the biological basis of sagittal crest development related to the timing of other indicators of maturity (e.g. Shea, 1986, 1988; Leutenegger & Masterson, 1989a, 1989b; Masterson & Leutenegger, 1990, 1992; Röhrer-Ertl, 1988; Uchida, 1996; Hens, 2003, 2005; Gordon et al. 2013; Balolia et al. 2013; Balolia, 2015), in conjunction with the need to increase muscle attachment area, have important applications for reconstructing the social behaviour of extinct primate taxa. In particular, if the timing of sagittal crest development in males is associated with a male reproductive strategy characterised by intense intrasexual competition across primates, examination of sagittal crest emergence and associated scaling relationships in fossil assemblages may allow us to begin to reconstruct the nature of intrasexual male competition in those extinct hominin taxa that display evidence of a sagittal crest. These findings raise the possibility that sagittal cresting in fossil hominin taxa such as *Paranthropus boisei* may have been driven by both diet-related factors and sexual selection.

It is important to note that hypotheses about sagittal crest emergence may be pluralistic in that sagittal crests may serve more than one function and be subject to both sexual and other aspects of natural selection (e.g. Darwin, 1871; Tomkins et al. 2010; Padian & Horner, 2011a, 2011b; Knell & Sampson, 2011). For example, the results of the present study indicate that sagittal crests in *G. g. gorilla* males provide support for both the ‘muscle attachment’ and the ‘sexual selection’ hypotheses. To further evaluate that possibility, studies investigating the relationships between temporalis muscle attachment area, muscle architecture, sagittal crest size and aspects of primate social systems in a broader range of taxa are needed. For example, evidence that sagittal crests only occur in males of robust capuchin monkeys (Alfaro et al. 2012) suggests that sex-specific patterns of sagittal crest emergence may not be restricted to hominoids. The finding that sagittal crest development coincides with the timing of sexual maturity and territorial displays in male California seals (*Zalophus californianus*), where seasonal fat deposition exaggerates the size of the sagittal crest during the reproductive season (Schusterman & Gentry, 1971) provides further evidence that sagittal crests may emerge in response to sexual selection in a diverse range of mammalian taxa.

Although sagittal crest expression can be considered to have limited utility for generating phylogenetic hypotheses, our results indicate that patterns of sagittal crest development may provide some insight into sociality in the extinct hominin taxa in which they do occur. For example, further investigations could test the hypothesis that the sagittal crest in the males of some extant taxa emerges around the time individuals begin to exercise social dominance, and thus provide support for Ashton & Zuckerman's (1956) hypothesis that the sagittal crest in males is a secondary sexual characteristic, subject to sexual selection. Similar suggestions have been made with respect to the emergence of silverback hair in fully mature gorillas, and facial flanges and a developed throat sac in mature male orangutans (Watts et al. 1991; Utami et al. 2002). But while it makes sense to investigate whether sagittal crest emergence coincides with the time at which males of some taxa attain dominance status, it is also necessary to evaluate the potential for sexual selection of crest expression against the background requirement of increasing muscle attachment area with increasing body size (Robinson, 1958). It is possible that in *P. boisei*, which has unusually small and sexually monomorphic canines (Wood & Constantino, 2007), the sagittal crest may have replaced canine size as a signalling mechanism.

In conclusion, the scaling patterns reported here, and the timing of sagittal crest emergence in gorilla and orangutan males provide support for the hypothesis that sexual selection contributes to the formation of sagittal crests in hominoid primates. To what extent sagittal crests may serve a direct function in social signalling, and to what extent they are a consequence of biomechanical constraints imposed on males to accommodate wider gapes and, hence, a correlate of canine size, remains unresolved without further data on temporalis muscle architecture, and on fitness consequences and behavioural correlates of sagittal crest size in hominoids.

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Table 1 Taxa, sample sizes and sources of specimens

Taxon	Male	Female	Repository/collection
Pan troglodytes schweinfurthii	37	41	Royal Museum of Central Africa, Tervuren
Gorilla gorilla gorilla	56	50	Powell Cotton Museum, Kent
Pongo pygmaeus pygmaeus	41	54	State Anthropological Collection, Munich
Hylobates lar	46	32	Natural History Museum, London; Anthropological Institute and Museum, University of Zürich; American Museum of Natural History, New York

Table 2 Approximate ranges of AAQs for *Gorilla* and *Pongo* (in years). Balolia et al. (2013).

Adult age group	*Gorilla gorilla*	*Pongo pygmaeus*
AAQ1	11.8-16.8	12.9-19.1
AAQ2	16.8-21.8	19.1-25.3
AAQ3	21.8-26.8	25.3-31.5
AAQ4	26.8-32.0	31.5-38.0

AAQ = Adult age quartile

Table 3 *Gorilla* and *Pongo* sample for each sex and age group.

Taxon	AAQ1	AAQ2	AAQ3	AAQ4
G. g. gorilla (Male)	21	12	14	9
G. g. gorilla (Female)	21	9	9	11
Po. pyg. pygmaeus (Male)	19	11	5	6
Po. pyg. pygmaeus (Female)	17	14	12	11

AAQ = Adult age quartile

Table 4 Frequency of sagittal cresting in dentally mature great apes and gibbons. Numbers in parentheses represent the total number of individuals in the sample.

Taxon	Male frequency	Female frequency	Fisher's exact test results
P. t. schweinfurthii	9 (37)	3 (41)	**P = 0.038**
G. g. gorilla	52 (56)	29 (50)	**P < 0.001**
Po. pyg. pygmaeus	16 (41)	0 (54)	**P < 0.001**
H. lar	2 (46)	0 (32)	P = 0.345

Statistically significant results are highlighted in bold.

Table 5 Sagittal crest size (SCS) growth following dental maturity in *Gorilla* and *Pongo*: Spearman's rank correlations between SCS and tooth wear rank; Kruskal-Wallis tests for differences in SCS among AAQs (Adult Age Quartiles).

Sagittal crest size

Taxon	Sex	N	Correlation	Kruskal-Wallis test
G. g. gorilla	Male	56	**r = 0.401, P = 0.002**	**$H_{(3)}$ = 11.285, P = 0.010**
	Female	50	r = 0.304, P = 0.032	$H_{(3)}$ = 6.429, P = 0.093
Po. pyg. pygmaeus	Male	41	**r = 0.508, P = 0.001**	**$H_{(3)}$ = 11.012, P = 0.012**
	Female	54	n/a	n/a

r = Spearman's rank correlation coefficient; significant results following correction for multiple comparisons are highlighted in bold.

Table 6 Ordinary least squares regression results between log cranial size and log temporal muscle attachment area (TMAA) and log cranial size and log sagittal crest size (SCS) in dentally mature great apes and gibbons.

Temporalis muscle attachment area

	Males						
					95% CI for B		
Taxon	***r***	**N**	**Slope (B)**	**ANOVA**	**Lower Bound**	**Upper Bound**	**Allometric relationship**
P. t. schweinfurthii	**0.392**	**34**	**1.332**	**$F_{(1,32)}$=5.827, P=0.022**	**0.208**	**2.456**	No divergence from isometry
G. g. gorilla	**0.897**	**54**	**2.57**	**$F_{(1,52)}$=214.544, P<0.001**	**2.218**	**2.922**	Positive allometry
Po. pyg. pygmaeus	**0.866**	**41**	**3.279**	**$F_{(1,39)}$=116.55, P<0.001**	**2.664**	**3.893**	Positive allometry
H. lar	**0.475**	**45**	**1.608**	**$F_{(1,43)}$=12.545, P=0.001**	**0.693**	**2.524**	No divergence from isometry

	Females						
					95% CI for B		
Taxon	***r***	**N**	**Slope (B)**	**ANOVA**	**Lower Bound**	**Upper Bound**	**Allometric relationship**
P. t. schweinfurthii	**0.367**	**38**	**1.442**	**$F_{(1,36)}$=5.614, P=0.023**	**0.208**	**2.677**	No divergence from isometry
G. g. gorilla	**0.67**	**46**	**1.74**	**$F_{(1,44)}$=35.910, P<0.001**	**1.155**	**2.325**	No divergence from isometry
Po. pyg. pygmaeus	**0.329**	**52**	**1.082**	**$F_{(1,50)}$=6.064, P=0.017**	**0.199**	**1.965**	Negative allometry
H. lar	**0.504**	**30**	**1.548**	**$F_{(1,28)}$=9.536, P=0.005**	**0.521**	**2.574**	No divergence from isometry

Sagittal crest size

	Males						
					95% CI for B		
Taxon	***r***	**N**	**Slope (B)**	**ANOVA**	**Lower Bound**	**Upper Bound**	**Allometric relationship**
P. t. schweinfurthii	0.339	9	-2.79	$F_{(1,7)}$=0.909, P=0.372	-9.71	4.129	Model not significant
G. g. gorilla	**0.79**	**52**	**12.004**	**$F_{(1,50)}$=82.739, P<0.001**	**9.354**	**14.655**	Positive allometry
Po. pyg. pygmaeus	0.041	16	-0.576	$F_{(1,14)}$=0.023, P=0.881	-8.697	7.544	Model not significant

	Females						
					95% CI for B		
Taxon	***r***	**N**	**Slope (B)**	**ANOVA**	**Lower Bound**	**Upper Bound**	**Allometric relationship**
P. t. schweinfurthii	n/a	n/a	n/a	n/a	n/a	n/a	n/a
G. g. gorilla	0.215	27	-3.646	$F_{(1,24)}$=1.213, P=0.281	-10.464	3.172	Model not significant
Po. pyg. pygmaeus	n/a	n/a	n/a	n/a	n/a	n/a	n/a

r = Pearson's correlation coefficient; CI = Confidence Interval; Significant slopes are highlighted in bold.

FIGURES

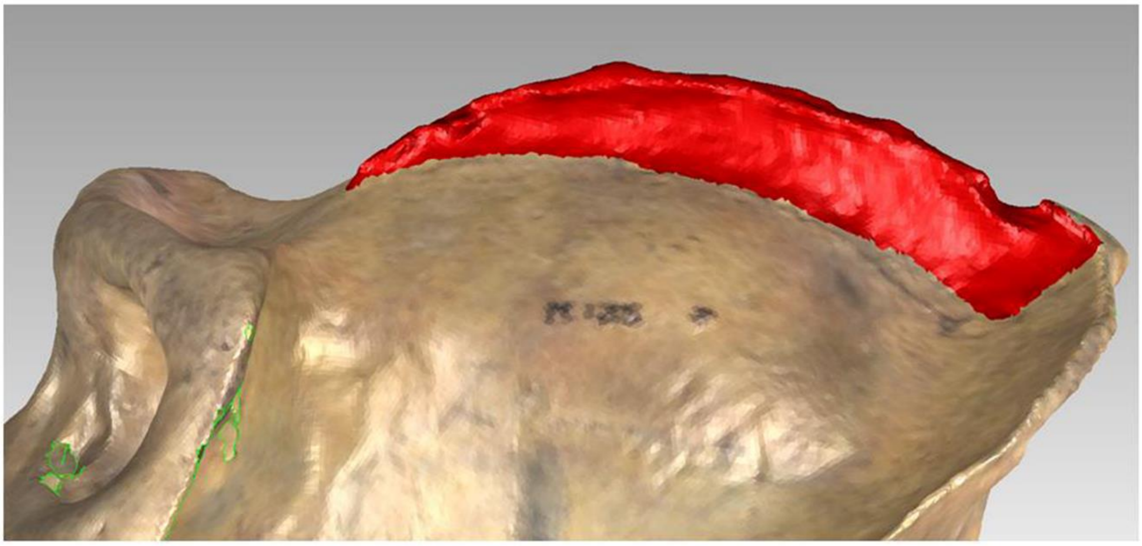

Fig. 1 Sagittal crest size (SCS) measurement (red area) in the cranium of a male *G. g. gorilla* specimen. This measurement represents the area of sagittal crest when seen in profile.

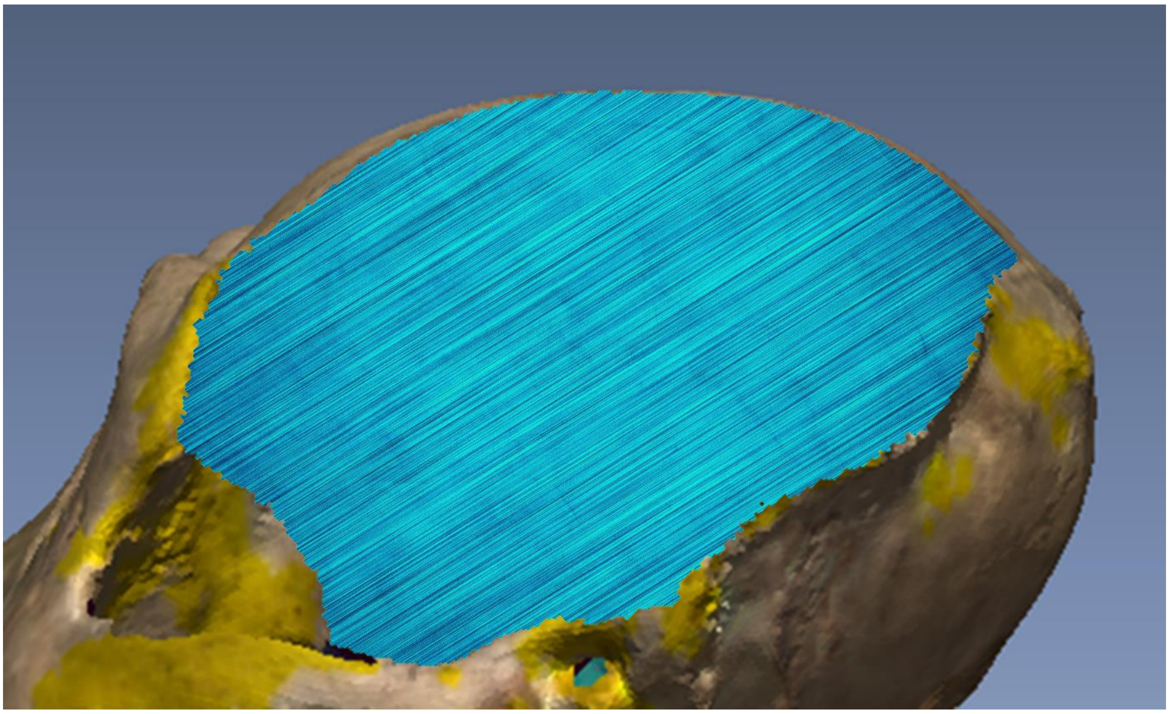

Fig. 2 Temporalis muscle attachment area (TMAA) measurement (light blue area) shown on the cranium of a male *Po. pyg. pygmaeus* specimen.

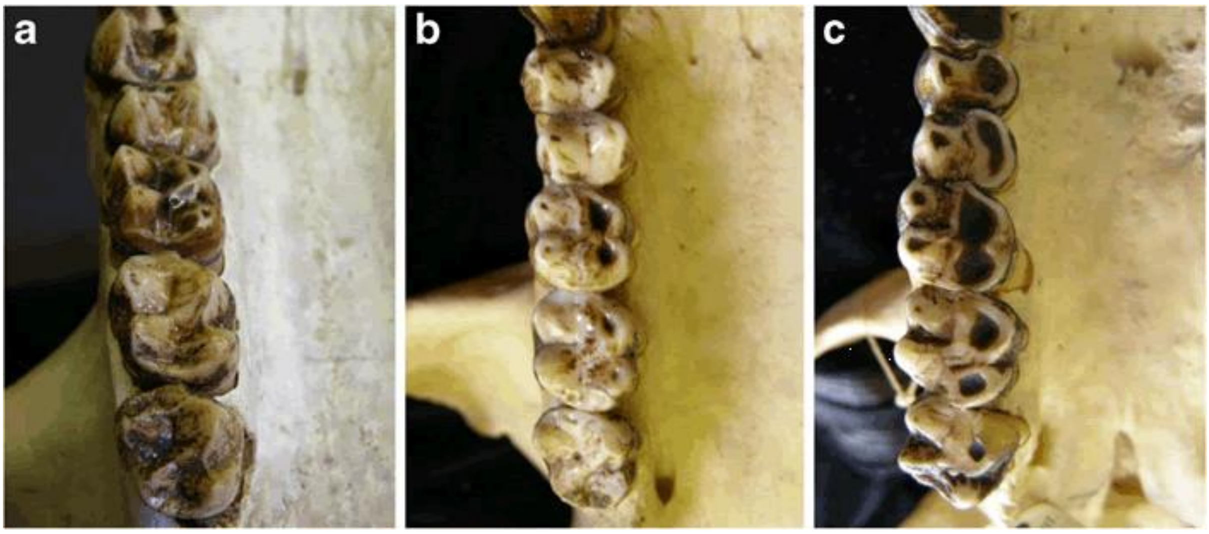

Fig. 3 Depiction of the approximate aging procedure. a) Female gorilla specimen in which the upper M3 has reached full occlusion. b) Female gorilla specimen in which M2 wear equals M1 wear when M3 is at full occlusion. c) Female gorilla specimen in which the M2 is showing a further ca. 3.5 years of wear. Reproduced from Balolia et al. (2013).

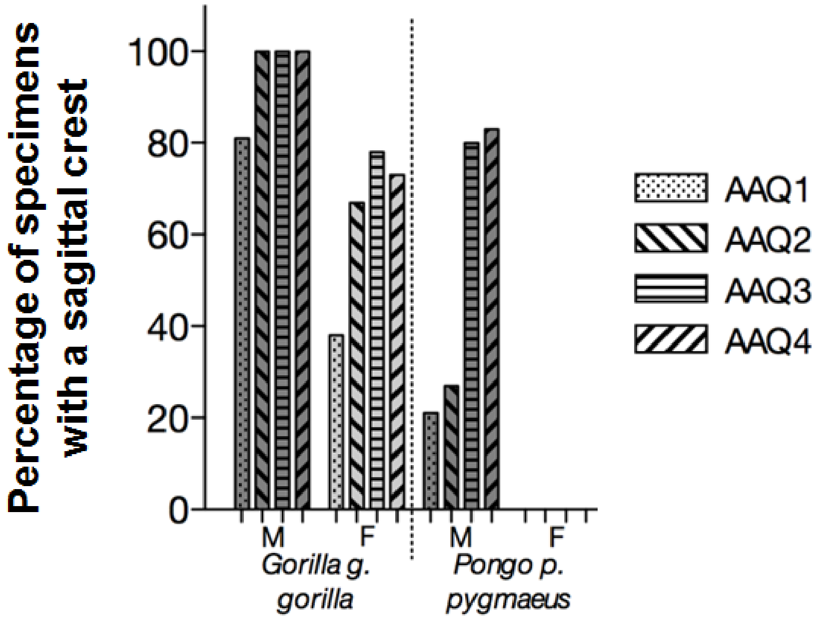

Fig. 4 Percentage of *G. g. gorilla* and *Po. pyg. pygmaeus* male and female specimens exhibiting a sagittal crest for each age group. Dark grey bars = males; light grey bars = females. AAQ = Adult age quartile.

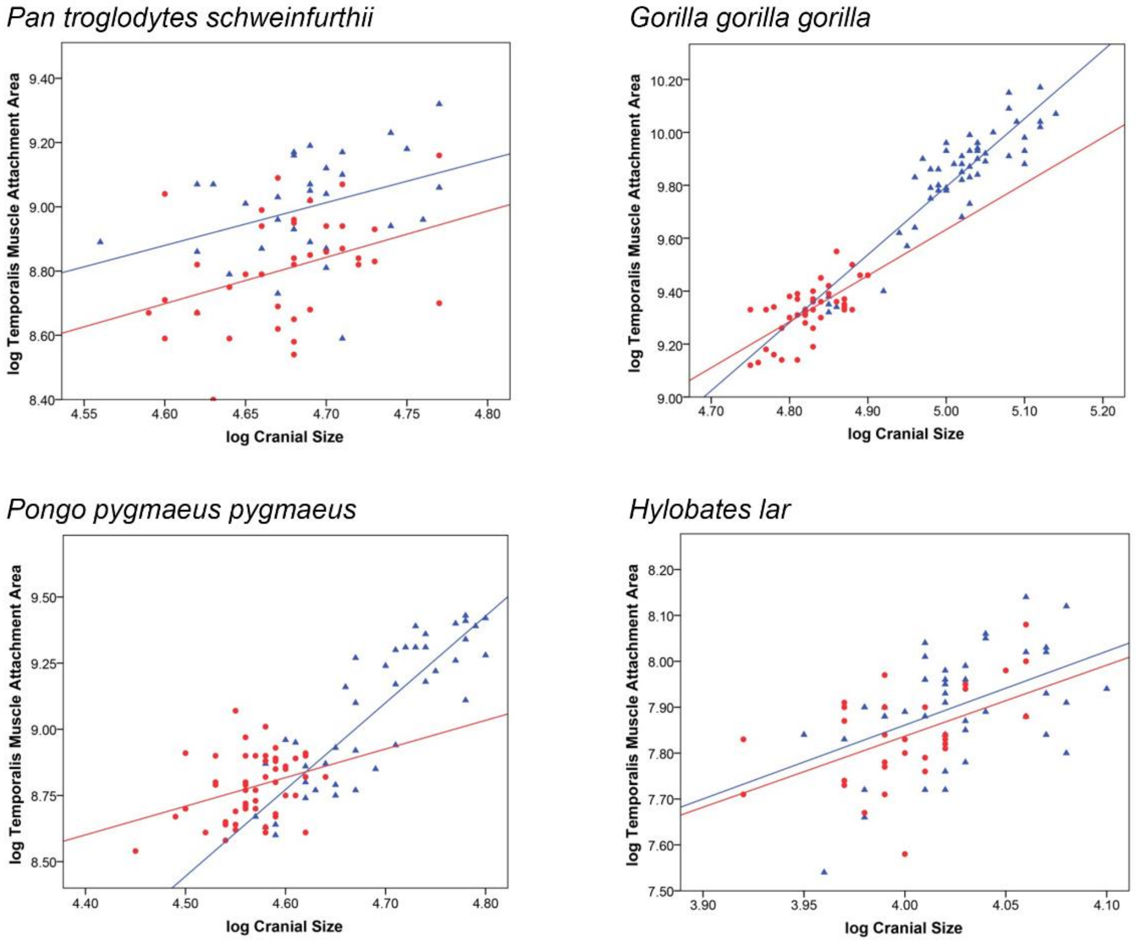

Fig. 5 Log cranial size (x axis) vs log temporalis muscle attachment area (TMAA) (y axis) for great apes and gibbons. Blue triangle = males; red circles = females. Males of *G. g. gorilla* and *Po. pyg. pygmaeus* show positive allometry, and females of *Po. pyg. pygmaeus* show negative allometry. Sex differences in allometric slopes are found in *G. g. gorilla* and *Po. pyg. pygmaeus*. 95% confidence intervals and the significance of each model are provided in Table 6.

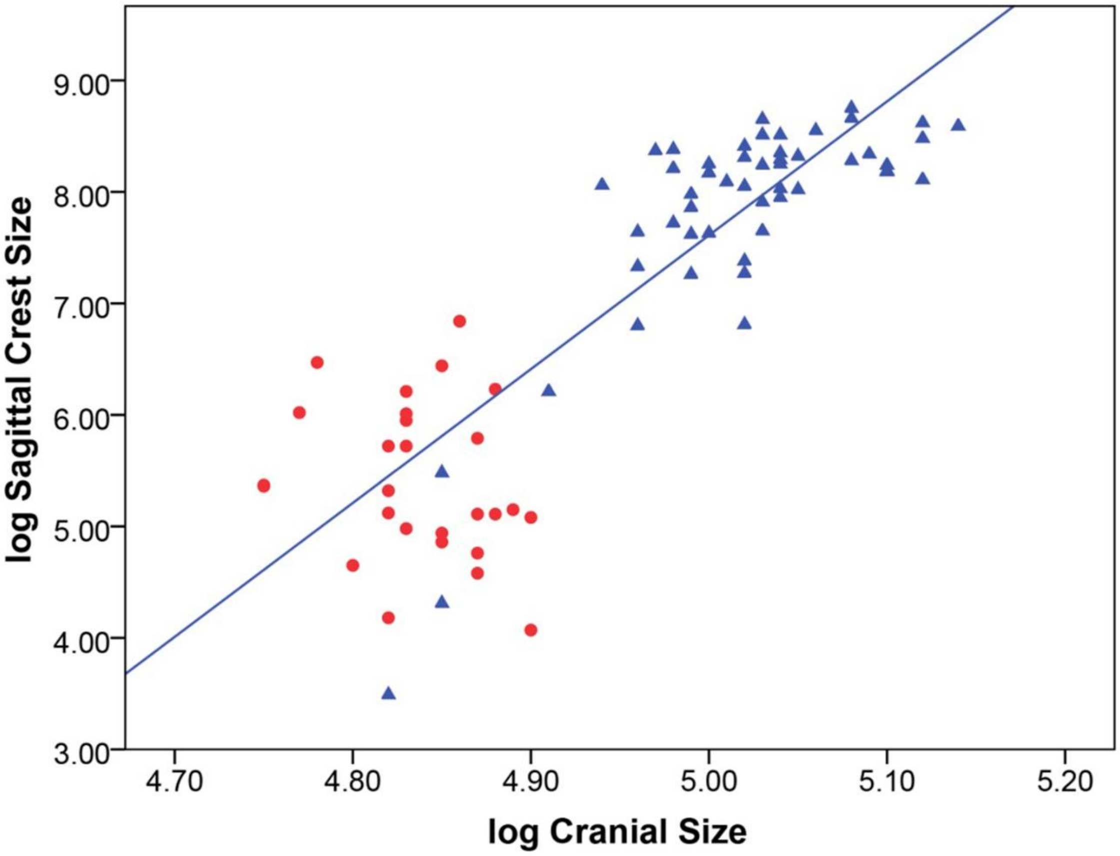

Fig. 6 Log cranial size (x axis) vs log sagittal crest size (SCS) (y axis) for *G. g. gorilla*. Blue triangle = males; red circles = females. Males of *G. g. gorilla* show strong positive allometry. There is no statistically significant relationship in females, so no female slope is shown. 95% confidence intervals and the significance of each model are provided in Table 6.