Ectocranial Suture Closure in *Pan troglodytes* and *Gorilla gorilla*: Pattern and Phylogeny

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ABSTRACT The order in which ectocranial sutures undergo fusion displays species-specific variation among primates. However, the precise relationship between suture closure and phylogenetic affinities is poorly understood. In this study, we used Guttman Scaling to determine if the modal progression of suture closure differs among *Homo sapiens*, *Pan troglodytes*, and *Gorilla gorilla*. Because DNA sequence homologies strongly suggest that *P. troglodytes* and *Homo sapiens* share a more recent common ancestor than either does with *G. gorilla*, we hypothesized that this phylogenetic relationship would be reflected in the suture closure patterns of these three taxa. Results indicated that while all three species do share a similar lateral-anterior closure pattern, *G. gorilla* exhibits a unique vault pattern, which, unlike humans and *P. troglodytes*, follows a strong posterior-to-anterior gradient. *P. troglodytes* is therefore more like *Homo sapiens* in suture synostosis. Am J Phys Anthropol 136:394–399, 2008. ©2008 Wiley-Liss, Inc.

The biological basis of suture synostosis is currently poorly understood, but appears to be influenced by a combination of vascular, hormonal, genetic, mechanical, and local factors (see review in Cohen, 1993). A primary goal of suture biology research is to investigate what causes craniosynostosis. This has shed some light on the processes of normal sutural fusion and the roles of transforming growth factors (TGFβ) and fibroblast growth factors (FGF). Cohen and others have argued (Cohen and MacLean, 2000; Law et al., 2005) that a suite of growth factors interact to regulate suture morphogenesis, patency, and eventual fusion, and recent studies of pathological craniosynostosis have consistently demonstrated that premature fusion can result from failure of either up-regulation or down-regulation of genetic signaling (Morriss-Kay and Wilkie, 2005). Suture closure is seen to proceed largely by genetic mechanisms, especially those involving the expression of FGFs and their receptors (FGFRs) as well as TGFβ. The TGFβs (1, 2, and 3) have been shown to regulate suture patency by regulating cell proliferation and apoptosis among those cells within the articulating bone fronts (Opperman and Ogle, 2002).

The FGF signaling pathway is highly conserved in evolution and appears to play a crucial role in development and early patterning of the entire craniofacial region. It is likely important in suture and synchondrosis regulation (Carinci et al., 2002; Nie et al., 2006, Ogle et al., 2004). Patency and growth are believed to be maintained by inductive interaction with the underlying dura mater and its FGFs (Alden et al., 1999, Kim et al. 1998), although this model has been called into question (Mooney et al., 2001). Specifically FGF2, localized to the underlying dura mater, becomes highly expressed in the osteogenic bone fronts of fusing sutures (Opperman and Ogle, 2002). Basic fibroblast growth factor (*bFGF*) expression is increased in the dura just prior to suture fusion, and by increased expression in osteoblasts surrounding the suture during fusion (Alden et al., 1999). Morriss-Kay et al. (2001) found that maintenance of proliferating osteogenic stem cells at the margins of membrane bones forming the coronal suture requires *FGF* levels to be relatively low, while higher levels of *FGF* are associated with osteogenic differentiation. In the normal suture, this mechanism involves differential levels of *FGF*, from high in the differentiated region to low in the suture, and is thought to ensure that sutural stem cell populations are maintained at the periphery of growing bones. However, when receptor activation is increased, either experimentally, or pathologically, *FGFR*2 is prematurely down-regulated and proliferation ceases (Morriss-Kay et al., 2001). Bone morphogenetic proteins (BMP), MSX2, Twist, and RUNX2/Cbfa1, also all appear to be necessary for normal suture morphogenesis and the regulation of suture patency (Kim et al., 1998; Opperman and Ogle, 2002).

There is no current agreement on the functional relationship between strain and suture morphology or its effect on suture morphology. Some have argued that mechanical forces are too small in magnitude to affect suture morphology (Henderson et al., 2004). In support of this conclusion, Sun et al. (2004) observed that mechanical forces generated by chewing in pigs do not correlate with sutural strain magnitude. However, these authors did suggest that fusion of the interfrontal suture in their model was associated with increased strain and ectocranial surface growth. Other investigators have concluded that there is a positive functional relationship

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between masticatory muscle force and sutural complexity, evidenced by sutural interdigitation (Byron et al., 2004, 2006, Fong et al., 2003). Kopher and Mao (2003) suggest that cyclic compressive forces, e.g., chewing activity, increase bone deposition at sutural margins. Wu et al. (2007) suggest that suture complexity is directly influenced by environmental factors, and variation seen in the complexity of human sutures is directly due to that influence, owing to little genomic variation. Age has also been shown to have an impact on suture morphology (Byron et al., 2004). It is possible that sutures respond to increased strain by upregulating activity of extracellular matrix proteins (Opperman and Rawlings, 2005), but this relationship has not been well studied. Most recently, an experimental study associating rat calvarial bone morphology and biomechanical strain showed no influence on the fusion of the interfrontal suture or patency of the sagittal suture with increased biomechanical strain (Shibazaki et al., 2007).

Sutural architecture, growth, and eventual fusion is very likely the result of several complex factors, including gene expression and epigenetic factors including environmental factors such as compressive and tensile forces causing mechanical signaling, activity of local cell populations, and cytokines, as well as hormones (Cohen and Maclean, 2000; Mooney and Richtsmeier, in press). The apparent disassociation in humans and perhaps their closest living relatives (*Pan* and *Gorilla*) between brain growth and suture activity complicates the issue and suggests that mechanical factors, specifically the growing brain, is not solely responsible for the onset of suture architecture, growth, and fusion. The question still remains whether gene responses within the cell are responsible for the final morphology of the suture are mediated by morphogenetic or paracrine signals, or whether they are generated by mechanical stimulation.

The use of suture closure patterns to deduce phylogenetic information

With the exception of some rare genetic disorders of cranial growth, sutural synostosis is very likely largely a genetic trait that should contain substantial phylogenetic information not subject to selection. Linkage analysis has suggested that in nonpathological populations, single nucleotide polymorphisms (SNPs) on the *FGFR1* gene are associated with normal craniofacial variation (Coussens and Daal, 2005). In addition, recent research on suture pattern in rhesus monkeys has demonstrated that variation in patterns show familial aggregation, strongly suggesting that variation is heritable (Wang et al., 2006). While early research on cranial suture synostosis concentrated on the forensic implications of the relationship between suture synostosis and age (Todd and Lyon 1924, 1925a,b,c), later work compared patterns of cranial suture synostosis among nonhuman primates (gorilla, chimpanzee, orangutan, gibbon, baboon, and rhesus monkey). Krogman (1930) noted that the ectocranial closure sequences in *G. gorilla* and *P. troglodytes* shared three primary features: 1) Their vault sutures are the earliest to close; 2) "circum-meatal" sutures close either uniformly or in a posterior to anterior gradient; and 3) the lambdoid suture commences closure earlier in *Gorilla* than in *Pan*, in which the coronal is earliest to close.

In 1985, Meindl and Lovejoy used a series of specific observation sites to assess closure order as part of a forensic ageing study in modern humans. They employed 10 such sites, determined a modal pattern of closure, and noted four primary observations with respect to both initiation and commencement: 1) closure in the lateral-anterior (i.e., "circum-meatal") sutures follows an anterior-to-posterior pattern; 2) final closure of the lateral-anterior sites also follows this pattern; 3) the sagittal suture commences closure before the lambdoid and coronal; and 4) the sagittal suture is first to complete closure along its middle section (at obelion), is followed, in sequence, by closure at bregma and lambda, and finally by closure of the inferior portions of the coronal and lambdoid.

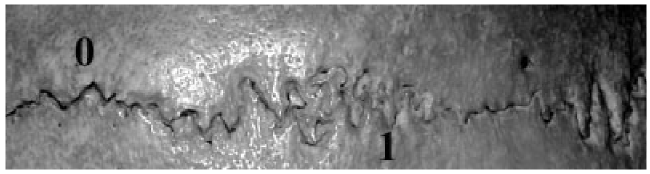

Fig. 1. Suture closure stages. Illustration of a suture site scored as a 0 or no observable closure and a site scored 1 or 1–50% closure. University of Pittsburgh, Department of Anthropology, Comparative Anatomy Collection.

The methods used by Meindl and Lovejoy to determine the modal patterns of closure for humans can be used to determine patterns of other species. Because sutural synostosis should contain phylogenetic information, it would be useful to apply these methods and to revisit Krogman's findings to determine the modal sequence of closure for *G. gorilla* and *P. troglodytes*, and to describe potential differences between these species. Description of this variation is a major goal of the present research. In addition, this may also provide a better understanding of functional and developmental implications of suture biology, including the role of genetics in the species studied here, and the role that functional influences may play in variations of suture morphology.

MATERIALS AND METHODS

Samples comprising 381 *G. gorilla* (56.4% Male, 32.8% Female, 10.8% unknown sex) and 126 *P. troglodytes* (32.8% Male, 47.0% Female, 20.2% unknown sex) crania from the Hamman-Todd Collection, housed at the Cleveland Museum of Natural History, were examined at a total of 10 ectocranial suture sites: midlambdoid, lambda, obelion, anterior sagittal, bregma, midcoronal, sphenofrontal, pterion, inferior sphenotemporal, and superior sphenotemporal (see Meindl and Lovejoy, 1985).

Sites were scored on a scale of 0–3 (0: no closure; 1: 1–50% closure; 2: 51–99% closure; 3: complete closure). Suture sites that exemplify each score can be found in Figures 1–3. Modal patterns of commencement and termination of suture activity, osteoblastic and osteoclastic activity that results in bone formation across the fibrous joint, were investigated for lateral-anterior suture sites (sphenofrontal, inferior sphenotemporal, superior sphenotemporal, pterion, and midcoronal) and vault suture sites (midlambdoid, lambda, obelion, anterior sagittal, bregma, midcoronal, and pterion), defined in Table 1. Commencement is defined as the earliest onset of bone formation activity within the fibrous joint. Termination is the cessation of that activity or synostosis, i.e., the fibrous joint is replaced by bone. Sites are illustrated for *Gorilla gorilla* and *Pan troglodytes* in Figures 4–6. For

Fig. 2. Suture closure stages. Illustration of a suture site scored as 2 or 51–99% closure. University of Pittsburgh, Department of Anthropology, Comparative Anatomy Collection.

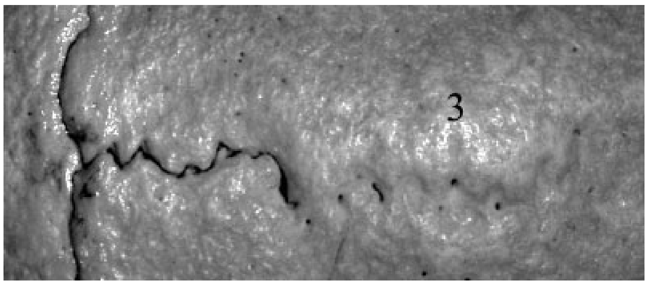

Fig. 3. Suture closure stages. Illustration of a suture site scored as 3 or closure. University of Pittsburgh, Department of Anthropology, Comparative Anatomy Collection.

individual ape crania to be included in the analysis, some activity in at least one ectocranial suture site must have been discernable; otherwise, it was labeled "inactive." Any cranium which exhibited complete termination at all sites also was termed "inactive" and not included in the analysis. All patterns of commencement, i.e., the orderings of initiation of all sutures, as well as the patterns of termination, i.e., the orderings of full closure, were observed. Meindl and Lovejoy (1985) suggest that this system of scoring activity levels (i.e., values 0–3) is highly repeatable and lacks significant interobserver error. In this study, one of us (JC) observed each skull twice, on separate days. Intraobserver reliability was 98.5%.

Guttman scaling was used to determine the most commonly occurring patterns of ectocranial suture synostosis for commencement, for termination, for *G. gorilla* and for *P. troglodytes*. The Guttman approach assesses the likelihood of unidimensionality, a notion best assessed by the summary measure, CR, the coefficient of reproducibility (Pendleton et al., 1982): $CR = 1 - (E/C)S$, where E = number of abmodal sequences; S = number of suture sites; C = number of crania.

This coefficient is reduced by the number of abmodal specimens and measures the strength and validity of a unidimensional cumulative scale. Abmodal patterns are orderings of synostosis that differ in some way from the most commonly occurring pattern. However, scores that approach 1.00 suggest the existence of a single pattern of synostosis and only a small fraction of minor deviations. The coefficient of reproducibility also can be understood in terms of seriation and observer error. The higher the coefficient of reproducibility, the fewer abmodal patterns exist, the greater the preponderance of a single continuum, and the more useful that the crania can be in seriation by the observer to determine relative biological age.

TABLE 1. Ectocranial suture sites for modal pattern analysis, from Meindl and Lovejoy, 1985

Midlambdoid: midpoint of each half of the lambdoid suture (in "pars intermedia" of the lambdoid suture)
Lambda: at lambda (in "pars lambdica" of the sagittal and "pars intermedia" of the lambdoid suture)
Obelion: at obelion (in "pars obelica" of the sagittal suture)
Anterior sagittal: point on the sagittal suture at the juncture of the anterior one-third and posterior two-thirds of its length (usually near the junction of the "pars bregmatica" and "pars verticis" of the sagittal suture)
Bregma: at bregma (in "pars bregmatica" of the coronal and "pars bregmatica" of the coronal suture)
Midcoronal: midpoint of each half of the coronal suture (in "pars complicate" of the coronal suture)
Pterion: at pterion, the region of the upper portion of the greater wing of the sphenoid, usually the point at which the parietosphenoid suture meets the frontal bone
Sphenofrontal: midpoint of the sphenofrontal suture
Inferior sphenotemporal: point of the sphenotemporal suture lying at its intersection with a line connecting both articular tubercles of the temporomendibular joint
Superior sphenotemporal: point on the sphenotemporal suture lying 2 cm below its juncture with the parietal bone

RESULTS

The culling of inactive crania reduced the samples to 162 *G. gorilla* and 91 *P. troglodytes*. Results for *Gorilla* are provided in Table 3 and indicate largely unidimensional scales with the strongest scale being vault suture termination. In other words, there is a strong reproducible pattern, across specimens, of ectocranial suture closure, suggesting a normative pattern of suture site fusion. Those for *Pan* indicate lateral-anterior commencement and anterior-to-posterior termination (Table 4). However, unlike *Gorilla*, the vault coefficients of reproducibility do not suggest any single directional pattern for commencement, although termination appears to consistently begin in the sagittal suture and to terminate in the coronal. The lateral-anterior synostosis pattern is less variable than is that of the vault.

DISCUSSION

G. gorilla and *P. troglodytes* exhibit different modal patterns of ectocranial suture closure for both lateral-anterior and vault sutures. Meindl and Lovejoy (1985) found that the lateral-anterior sutures of humans exhibit an anterior-to-posterior pattern of activity (Table 2). This same pattern appears to also characterize *Pan*. Termination of these sutures in humans also appears to follow an anterior-to-posterior progression. This characterizes both African apes.

Vault commencement in humans is earliest in the sagittal suture and delayed in the coronal. This is unlike the clear pattern of posterior-to-anterior activity in *Gorilla* and more similar to the pattern exhibited by *Pan*. Vault termination in humans appears to begin in the mid-sagittal suture with later activity at its proximal and distal ends (bregma and lambda). Again, this is

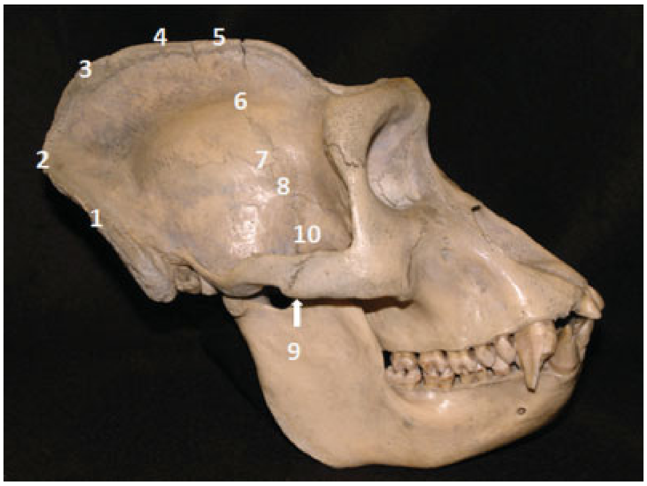

Fig. 4. Suture observation sites: *Gorilla gorilla*. Illustration of anthropometric suture sites used in analysis: midlambdoid (1); lambda (2); obelion (3); anterior sagittal (4); bregma (5); midcoronal (6); pterion (7); sphenofrontal (8) inferior sphenotemporal (9); superior sphenotemporal (10). University of Pittsburgh, Department of Anthropology, Comparative Anatomy Collection. [Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.]

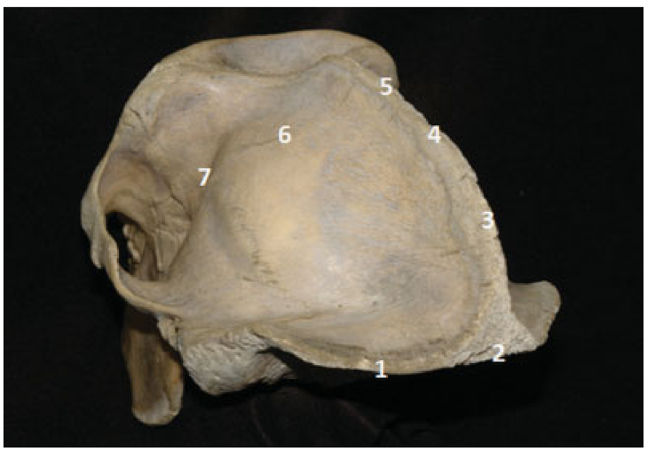

Fig. 5. Suture observation sites posterior view: *Gorilla gorilla*. Illustration of anthropometric suture sites used in analysis: midlambdoid (1); lambda (2); obelion (3); anterior sagittal (4); bregma (5); midcoronal (6); pterion (7). University of Pittsburgh, Department of Anthropology, Comparative Anatomy Collection. [Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.]

unlike *Gorilla's* clear posterior-to-anterior pattern of vault termination, and more like *Pan* which, although variable, begins and ends in a fashion similar to that of humans.

In our sample, *Gorilla* had a very consistent pattern of both commencement and termination, exhibiting a posterior-to-anterior vault closure pattern, and an anterior-to-posterior pattern in the lateral-anterior sites. *Pan* did not exhibit any unidimensional scale as strongly as did *Gorilla*. The *Pan* vault pattern is more similar to that of humans, with early activity along the sagittal suture and progressing to termination in the coronal and lambdoid sutures. *Pan* did have higher lateral-anterior scores, which suggests that these suture sites are less

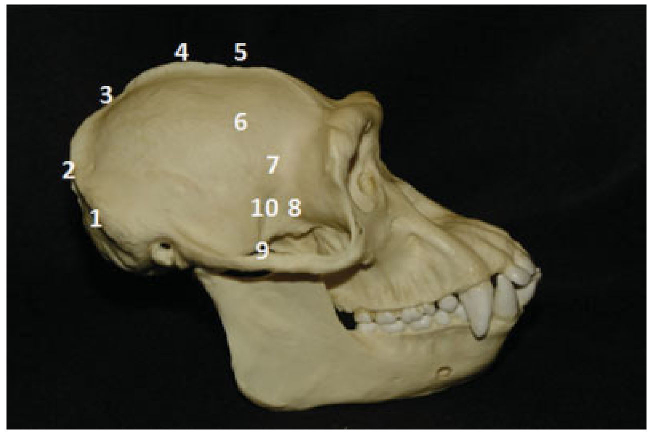

Fig. 6. Suture observation sites: *Pan troglodytes*. Illustration of anthropometric suture sites used in analysis: midlambdoid (1); lambda (2); obelion (3); anterior sagittal (4); bregma (5); midcoronal (6); pterion (7); sphenofrontal (8); inferior sphenotemporal (9); superior sphenotemporal (10). University of Pittsburgh, Department of Anthropology, Comparative Anatomy Collection. [Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.]

variable in their pattern of closure, similar to what was found for humans (Meindl and Lovejoy, 1985). Like humans and *Gorilla*, *Pan* exhibits termination in the lateral-anterior sutures in an anterior-to-posterior sequence. Our results agree with Krogman's (1930) suggestion that there was early commencement of the lambdoid in *Gorilla*. However, the delay in commencement of the lambdoid in *Pan*, as suggested by Krogman, is less apparent. For *Pan* the most parsimonious modal pattern is one in which the first three sites to commence (in order) are the coronal, sagittal, and lambdoid, respectively, and the last three are the sagittal, lambdoid, and coronal sutures.

Meindl and Lovejoy (1985) found high coefficients of reproducibility for the commencement and termination of the lateral-anterior and vault sutures in humans. While our data for *Gorilla* are similar, the coefficients of reproducibility in *Pan* are not as high. This may be an issue of sampling. Overall, there does not appear to be a generalizable pattern of ectocranial suture closure for hominoids, with the exception of the lateral-anterior sutures. These appear to share an anterior to posterior progression of suture activity in all three taxa. *Pan*'s pattern is clearly more like that of humans than is that of *Gorilla*, and appears to reflect the known phylogenetic relationships of these species.

Questions that remain to be addressed are those of biological significance, e.g., what is special about suture behavior at the site of obelion in humans and chimpanzees such that we see earliest activity and earliest cessation of activity for the vault, whereas in gorillas closure seems to be more posterior, at midlambdoid? The variation in closure at suture sites across species, or even within these species could be due to muscle attachment sites, perhaps with those sites with less active muscle attachments closing earliest or those with greater activity remaining patent longer due to function (Herring, 1993; Moss, 1960). Interestingly, those sutures that seem to be most subject to the influence of masticatory musculature in all three species, the lateral-anterior ones, showed the least amount of variation across these

TABLE 2. Modal patterns of ectocranial suture closure for Homo sapiens*, from Meindl and Lovejoy, 1985*

		Coefficient of reproducibility
Commencement		
Lateral-anterior	Pterion-midcoronal-sphenofrontal-inferior sphenotemporal-superior sphenotemporal	0.92
Vault	Obelion-pterion-anterior sagittal-lambda-midlambdoid-midcoronal-bregma	0.90
Termination		
Lateral-anterior	Pterion-sphenofrontal-midcoronal-inferior sphenotemporal-superior sphenotemporal	0.97
Vault	Obelion-pterion-anterior sagittal-lambda-bregma-midlambdoid-midcoronal	0.91

TABLE 3. Modal pattern of ectocranial suture closure for G. gorilla

		Coefficient of reproducibility
Commencement		
Lateral-anterior (n = 156)	Inferior sphenotemporal-pterion-midcoronal-sphenofrontal-superior sphenotemporal	0.95
Vault (n = 130)	Midlambdoid-lambda-obelion-anterior sagittal-pterion-midcoronal-bregma	0.93
Termination		
Lateral-anterior (n = 61)	Midcoronal-pterion-sphenofrontal-superior sphenotemporal-inferior sphenotemporal	0.93
Vault (n = 90)	Midlambdoid-lambda-obelion-anterior sagittal-bregma-midcoronal-pterion	0.98

n = No. of skulls used in the analysis of each pattern respectively.

TABLE 4. Modal pattern of ectocranial suture closure for P. troglodytes

		Coefficient of reproducibility
Commencement		
Lateral-anterior (n = 88)	Midcoronal-sphenofrontal-pterion-inferior sphenotemporal-superior sphenotemporal	0.90
Vault (n = 79)	Midcoronal-obelion-midlambdoid-pterion-anterior sagittal-lambda-bregma	0.87
Termination		
Lateral-anterior (n = 23)	Sphenofrontal-midcoronal-pterion-superior sphenotemporal-inferior sphenotemporal	0.90
Vault (n = 31)	Obelion-anterior sagittal-lambda-midlambdoid-midcoronal-bregma-pterion	0.80

n = No. of skulls used in the analysis of each pattern respectively.

species even though each presumably has very different masticatory habits.

Variation in suture site commencement and synostosis might also be due to regional differences in osteogenic signaling of the dura mater (Levine et al., 1998). Another interesting possible line of inquiry is that of dural tracts and their spatial relation to the timing and pattern of suture synostosis. It seems possible that sutures may respond to the expanding cranial base, brain, or positional changes in anterior posterior, mediolateral skull architecture (Blechschmidt, 1961; Moss, 1958). It is also possible that dural tracts are oriented differently in different species, which could lead to variation in the expression of local factors (FGFs) that are genetically based or as a response to function that may account for differences in suture and suture site synostosis (Alden et al., 1999; Cohen, 1993; Kim et al., 1998; Morriss-Kay et al., 2001, 2005; Opperman, 2000).

CONCLUSIONS

G. gorilla, *P. troglodytes*, and humans display different patterns of cranial suture synostosis. All three species are more alike in activities of their lateral-anterior sutures, *contra* Krogman (1930). The vault sutures in *Gorilla* exhibit a stereotypic activity pattern, progressing posterior to anterior, and support Krogman's finding of early commencement of the lambdoid. The vault sutures in *Pan* did not display as reproducible a pattern of activity, although this may be a sampling issue. The evidence for *Pan*, however, suggests early closure in the sagittal suture, with more delayed changes in coronal and lambdoid. This pattern is more similar to that of humans than to *Gorilla*. The biological implications of these variations should continue to be explored, including further examination of sutural growth patterns in other closely related primates and hypermuscular models for human suture synostosis patterns to deduce that variation inherent to phylogeny from that governed by environmental variables.

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