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Comparing cranial suture interdigitation in humans and non-human primates: unearthing links to osteopathic cranial concept

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Abstract

Context: Since William Garner Sutherland's inception of osteopathic cranial manipulative medicine (OCMM), osteopathic physicians have practiced with the knowledge that cranial sutures exhibit motion. We hypothesize that the complexity of suture interdigitation in humans may provide clues to elucidate the concept of OCMM.
Objectives: We compared the interdigitation of sagittal, coronal (left and right), and lambdoid (left and right) sutures in computed tomography (CT) scans of humans and five nonhuman primate species (*Gorilla gorilla*, *Pongo pygmaeus*, *Pan troglodytes*, *Hylobates lar*, and *Nasalis larvatus*).
Methods: Human ages are evenly distributed between 10 and 65 years of age, with an equal number of males (n=16) and females (n=16) in the sample. Nonhuman primates are all females, and the sample includes juveniles (n=6) and adults (n=34). Sutures were evaluated on a scale ranging from 0 to 3 (0: fused sutures; 1: no interdigitation; 2: low complexity; and 3: representing the highest degree of interdigitation and complexity).
Results: Based on ordinary least squares linear regression, we found no significant relationship between suture interdigitation and age in humans. Chi-square tests were utilized to assess sex differences within humans, species-level differences, and differences between humans and nonhuman primates across all five sutures. Humans exhibited a statistically significant greater degree of suture complexity than all five nonhuman species across all five sutures.
Conclusions: These findings indicate that human suture interdigitation is more complex than their closest living relatives (African apes) and other primates (Asian monkeys and apes). We theorize that this would enable subtle movement and serve to transmit forces at the cranial sutures from dietary or ethological behaviors, similar to the pattern observed in other mammals. While humans have a softer diet compared to other living primates, the uniqueness of human craniofacial growth and extended developmental period could contribute to the necessity for complex cranial sutures. More studies are needed to understand variation in human and nonhuman sutural complexity and its relationship to cranial motion.

Keywords: human anatomy, osteopathic cranial manipulative medicine, osteopathic manipulative medicine, primate anatomy, suture development

Osteopathic physicians have utilized the concept that sutures are made for motion since the inception of osteopathic cranial manipulative medicine (OCMM) [1]. This method posits that the calvaria (top part of the skull) of healthy individuals maintain suture patency and mobility throughout life. OCMM is a concept developed by William Garner Sutherland, DO. Dr. Sutherland first inquired about motion in the human cranium because he observed the beveled articular surfaces of the temporal squamous suture, suggesting the ability for articular motion [1]. Based on Dr. Sutherland's concept, a driving force known as the Primary Respiratory Mechanism (PRM) was proposed. There are five key aspects to PRM: (1) the inherent mobility of the brain and spinal cord; (2) fluctuation of the cerebrospinal fluid (CSF); (3) mobility of the intracranial and intraspinal membranes; (4) articular mobility of the cranial bones; and (5) involuntary mobility of the sacrum between the ilia. The inherent mobility of the brain and spinal cord are thought to drive the rhythmical fluctuations of CSF throughout the ventricles. This inherent motion is due to fluid pressure changes and suggests compliance or restriction of the cranial bones during these fluctuations in pressure. Dr. Sutherland felt

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that areas of increased suture interdigitation were representative of the apex of cranial bone motion [1, 2].

CSF flow is one key driver of the PRM. In a pilot study on OCMM use in aged rats, a technique called Compression of the Fourth Ventricle demonstrated improved mobility of the cranial mechanism, improved spatial memory, and a decrease in the accumulation of neurotoxins in the intervention group. Researchers attributed the improvement to OCMM-induced bone deflections due to the administration of the technique [3].

More recent research demonstrates that the sutures are viscoelastic structures impacted by three types of strain regimes. The first strain regime is a sudden-loading strain such as an object falling on a suture. The second is a cyclic strain such as repeated tensile forces like chewing. The third is a quasi-static compressive strain from pressure or growth from the presence of adjacent tissues. Few studies exist on quasi-static strain patterns, but the best human example is positional lambdoidal plagiocephaly in infancy. In studies performed on this condition, sutures demonstrate increased levels of TGF-β3, a growth factor implicated in preserving suture patency. Quasi-static strain patterns are presumed to affect the suture via mechanotransduction from the dura mater [4].

Mechanical influences on cranial suture development play an influential role in the growth and development of the mammalian skull. To date, studies comparing suture interdigitation across primate and human species are rare. One study has compared suture interdigitation among humans to juvenile apes, monkeys, and ruminant mammals [5]. However, human cranial development is distinct within the Order Primates, and suture interdigitation has not been compared consistently in adults across primate species and humans.

Background on sutures

The location, morphology, and growth of cranial sutures are largely responsible for cranial morphology and development [6, 7]. The same four developmental processes govern mammalian suture morphology: (1) the osteogenic fronts of articulating bone plates; (2) suture mesenchyme; (3) overlying cranial periosteum; and (4) underlying dura mater, although humans have an elongated period of sutural expansion relative to other primates [8, 9]. This is reflected by the frequency with which human sutures remain patent late into adulthood [10–12]. However, cranial sutures do not function exclusively as sites of growth. The presence and morphology of cranial sutures also allow for shock absorption during mechanical loading [13], including during locomotion and mastication [14, 15].

The development and morphology of cranial sutures demonstrate the many functions that they serve over the course of an organism's life. Sutures are typically more linear early in life and become increasingly interdigitated with age in humans and other primates [16], and this process of remodeling is attenuated in large apes through surgical resection of the masseter muscle [17]. Likewise, primates with more fibrous diets have more complex cranial suture interdigitation than closely related species [18]. Mechanical strain, compressive forces, and environmental stress have also been observed to affect the development of sutures [15, 16]. External forces, such as muscular attachments, may have an influence not only on suture complexity but also on suture patency. The most frequently patent suture in the human skull is the lambdoid suture. Researchers have hypothesized that it is the least likely to be obliterated due to the mechanical influence of musculature in the region [19].

The purpose of this study is to compare the complexity of suture interdigitation in human and nonhuman primate specimens along the largest straight sutures of the calvarium: the sagittal, coronal, and lambdoid sutures. Digital computed tomography (CT) images of skeletonized crania from five nonhuman primate species (*Gorilla gorilla*, *Pongo pygmaeus*, *Pan troglodytes*, *Hylobates lar*, and *Nasalis larvatus*) were compared to digital CT images of cadaveric human crania. Specimens were compared and rated for suture interdigitation on a fixed scale based on the degree of complexity. Data were analyzed utilizing chi-square analyses and generalized linear models to nonhuman primates. We hypothesize that human and nonhuman primate suture interdigitation will be similar based on the shared developmental processes governing these structures across taxa. Support for this hypothesis would indicate that suture interdigitation is driven by highly evolutionarily conserved developmental processes. Rejection of this hypothesis would suggest the influence of species- or even population-specific factors in suture development, including genetic and environmental effects such as motion at the cranial sutures.

Methods

Digital images of human cranial sutures were acquired from the New Mexico Decedent Image Database (NMDID), which makes available whole-body CT data collected through the New Mexico Office of the Medical Investigator [20]. Individuals with a history of craniofacial conditions, surgery, or trauma, and individuals with decomposition, were excluded from the sample. The human sample includes 16 females, with an average age of 36.7 years and a range of 11–64 years of age, and 16 males, with an average age of 36.9 years and a range of 10–65 years of age. Data were collected

Table 1: Results of ordinary least squares linear regressions of age on suture interdigitation scores, chi-square tests of sex and suture interdigitation score, and chi-square tests for differences between nonhuman primates (*G. gorilla*, *H. lar*, *N. larvatus*, *P. troglodytes,* and *P. pygmaeus*) and by humans (*Homo sapiens*).

	Ordinary least squares linear regression by age coefficient (p-value)	X^2 by sex	X^2 by group
Sagittal	0.002 (p=0.704)	1.11 (p=0.574)	45.138 (p<0.05)
Right coronal	−0.006 (p=0.262)	1.25 (p=0.264)	52.788 (p<0.05)
Left coronal	−0.010 (p=0.062)	1.25 (p=0.264)	50.617 (p<0.05)
Right lambdoid	−0.003 (p=0.546)	1.49 (p=0.475)	42.432 (p<0.05)
Left lambdoid	−0.004 (p=0.558)	5.94 (p=0.051)	41.990 (p<0.05)

from reconstructions of the head and neck with 670 images of 1 × 0.5 mm bone. The Office of the Medical Investigator (OMI) Adult Protocol, as described in the NMDID materials, was utilized for all individuals [20]. An equal number of males and females of each approximate age were included in the study. Age and sex data were available for all human images. This project utilized only de-identified images and is not human subjects research, as determined by the Western University of Health Sciences Institutional Review Board.

Nonhuman primate images were acquired from Morphosource.org [21]. These specimens are from the Museum of Comparative Zoology (MCZ) in Cambridge, Massachusetts. The nonhuman primate sample is comprised of 39 specimens in total with *G. gorilla* (n=8), *H. lar* (n=10), *N. larvatus* (n=10), *P. troglodytes* (n=9), and *P. pygmaeus* (n=2) individuals (Supplementary Table 1). All nonhuman primate specimens are female [21]. For some individuals, sex was not recorded by the MCZ and was determined by researcher IA by examining highly sexually dimorphic features (e.g., relative canine size and the size of chewing muscle attachment sites) and recorded as "F?" in Table 1. Thirty-three specimens are from adult individuals, whereas six specimens were juveniles. Adult vs. juvenile age assessment was based on tooth eruption stage, also determined per researcher IA. Maxillary teeth were checked for deciduous teeth and the number of permanent teeth. Mandibular dentition was also evaluated if scans of the mandible were available for specimens. Adult individuals had all permanent teeth in occlusion (I^1, I^2, C, P^3, P^4, M^1, M^2, M^3), whereas juveniles had one or more permanent molars missing or partially erupted in the alveolar crypt yet they were not in full occlusion [22].

Investigators scored the sagittal, coronal (left and right), and lambdoid (left and right) sutures on a 4-point scale, in which 0 represents a fused or fully linear suture, 1 represents a suture with little complexity and some linearity, 2 represents a complex suture with a little linearity, and 3 represents a very complex suture with a high degree of interdigitation (Figure 1). First, one investigator (LA) scored a subset of 10 human images in three independent trials, and the other investigator (JP) scored the same subset of 10 individuals once. Likewise, one investigator (JP) scored 10 *N. larvatus* images in three independent trials, and the other investigator (LA) scored the same 10 individuals once. This procedure was intended to familiarize both observers with the range of potential variation in suture interdigitation across species, and the repeated measurements were utilized to assess intra-observer reliability and inter-observer reproducibility. Given the simplicity of the data being collected, this repeated sample of 10 images was deemed adequate to account for error in the data collection process. One observer (LA) then scored the remaining human images, while the other (JP) scored the remaining nonhuman primate images. Image manipulation and scoring was performed utilizing the

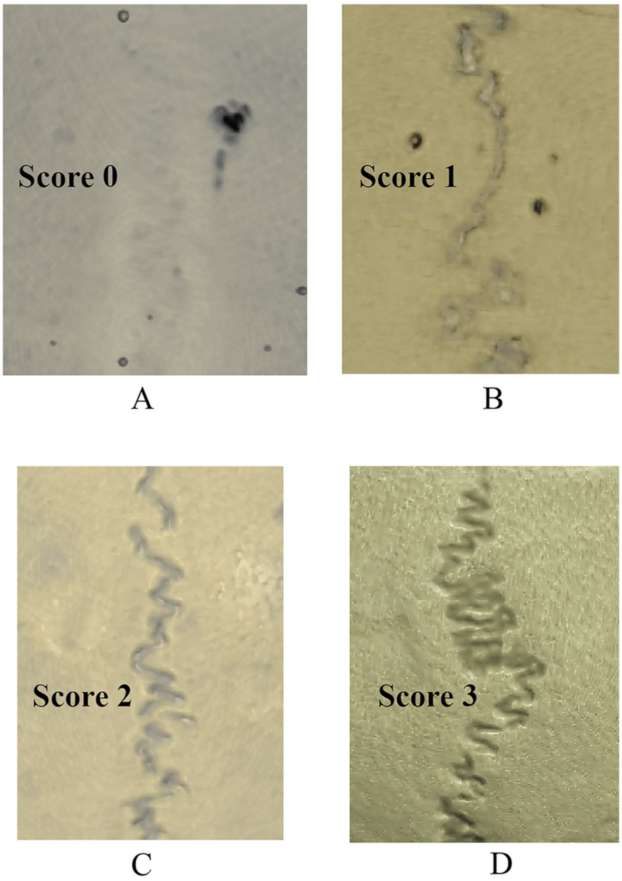

Figure 1: Scores of suture interdigitation (complexity). (A) Display of an externally obliterated suture site where interdigitation is not visible. (B) An open suture with little complexity and some linearity. (C) An open suture with more complexity and clear curvature, peaks, and valleys. (D) Display of an open suture with higher complexity with a more tortuous pattern.

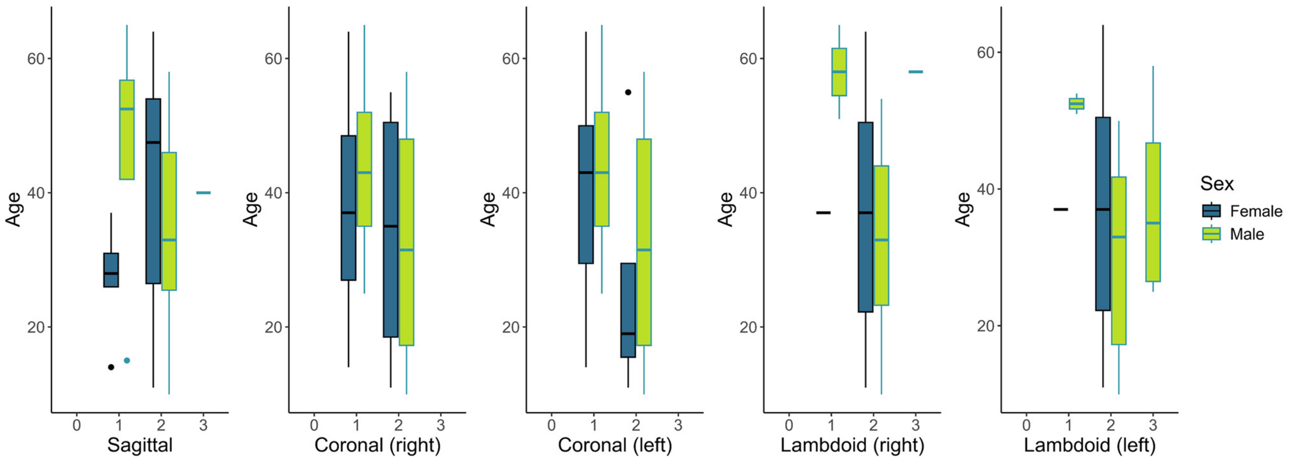

Figure 2: Box plots showing the mean age and age ranges for each score at each suture.

imaging software Dragonfly, Version 2022.2 for Windows [23, 24]. Data were collected over approximately two months (from March 2023 to May 2023) and stored on password-protected computers in a secure research space.

Repeated measures were utilized to assess intra-observer reliability and inter-observer reproducibility. Intra-observer reliability was calculated with Light's Kappa for three trials of repeated observations for 10 human images by a single observer (LA) and for 10 nonhuman primate images by a single observer (JP). Light's Kappa was estimated using the R package software program to train inter-rater reliability (IRR) [25]. Inter-observer reproducibility was assessed through the calculation of polychoric correlation coefficients between the two observers' independent scoring of 10 human and 10 nonhuman primate images. For all additional analyses, one observer (LA) scored all human images, and another observer (JP) scored all nonhuman primate images.

The relationship between suture interdigitation and age in humans was assessed through ordinary least squares linear regression. Chi-square analyses were utilized to assess sex differences within humans, species-level differences, and differences between humans and nonhuman primates across all five sutures. All analyses were performed in the statistical software package R (v.4.2.3) during May to June, 2023 [26].

Results

Intra-observer reliability testing produced statistically significant Light's Kappa estimates for both observers (humans: n=10; K=0.599, p=0.001; nonhuman primates: n=10; K=0.783, p=0.012), meaning that each trial of observations was significantly correlated with the other trials for each observer. The polychoric correlation coefficient for inter-observer reproducibility assessment was 0.959 for a sample of 10 humans and 10 nonhuman primates, demonstrating a high degree of agreement between the two observers.

Linear regressions of age on suture interdigitation indicate no significant relationships between age and the degree of interdigitation (Table 1, Figure 2) at any suture (sagittal: coefficient=0.002, p=0.704; right coronal: coefficient=–0.006, p=0.262; left coronal: coefficient=–0.010, p=0.062; right lambdoid: coefficient=–0.003, p=0.546; left lambdoid: coefficient=–0.004, p=0.558). Average suture scores also did not differ by sex in humans for any of the five sutures (Table 1) (sagittal: X^2=1.11, p=0.574; right coronal: X^2=1.25, p=0.264; left coronal: X^2=1.25, p=0.264; right lambdoid: X^2=1.49, p=0.475; left lambdoid: X^2=5.94, p=0.051). Given the lack of age and sex effects, the human sample contains males and females of all ages in the following analyses.

The median suture interdigitation scores for all nonhuman primate species were 0 across all five sutures (*P. troglodytes*: n=9; *G. gorilla*: n=7–8; *H. lar*: n=9–10; *N. larvatus*: n=9–10), apart from the orangutan (*P. pygmaeus*) coronal sutures, which had a median of 1 (n=2). In contrast, median suture interdigitation scores for humans varied from one to two depending on the suture (Table 2) (n=37–38). Suture interdigitation scores were significantly different (p<0.05) between humans and nonhuman primates at all five sutures (Table 1) (sagittal: χ^2=45.138, p<0.05; right coronal: χ^2=52.788, p<0.05; left coronal: χ^2=50.617, p<0.05; right lambdoid: χ^2=42.432, p<0.05; left lambdoid: χ^2=41.990, p<0.05).

Discussion

General findings

In this study comparing the complexity of suture interdigitation, we found a statistically significant difference in

Table 2: Median suture scores by species and by group for each suture.

	P. troglodytes	*G. gorilla*	*P. pygmaeus*	*H. lar*	*N. larvatus*	*H. sapiens*	Nonhuman primates
Sagittal	0 (n=9)	0 (n=8)	0 (n=2)	0 (n=10)	0 (n=9)	2 (n=30)	0 (n=38)
Right coronal	0 (n=9)	0 (n=8)	1 (n=2)	0 (n=9)	0 (n=9)	1 (n=30)	0 (n=37)
Left coronal	0 (n=9)	0 (n=8)	1 (n=2)	0 (n=10)	0 (n=9)	1 (n=30)	0 (n=38)
Right lambdoid	0 (n=9)	0 (n=8)	0 (n=2)	0 (n=10)	0 (n=9)	2 (n=31)	0 (n=38)
Left lambdoid	0 (n=9)	0 (n=7)	0 (n=2)	0 (n=10)	0 (n=10)	2 (n=30)	0 (n=38)

interdigitation between nonhuman primate skeletal specimens and human cadaveric specimens across five suture sites. More specifically, we found significantly more complex suture interdigitation in humans than in nonhuman primates across a range of ages.

Comparative mammalian studies

In general, comparisons of suture complexity between humans and other primates or mammals are rare. Knowledge of human interdigitation compared to other primates comes from one study by Gibert and Palmqvist [5]. The authors revealed that values of sagittal and lambdoidal suture complexity in a sample of extant and fossil humans (including infants, children, and adults), juvenile great apes, and a mixed sample of juvenile and adult cercopithecoid monkeys overlapped extensively, yet adult modern humans had the highest values of complexity among the primate sample. Results from this study comparing a larger adult human sample to adult ape and cercopithecoid taxa complement findings from the above study and confirm that adult humans have more complex cranial sutures than other adult primates. Further, in the same study by Gibert and Palmqvist [5], adult humans have less complex sutures than equid and ruminant mammals, whose higher levels of suture interdigitation has been linked to shock absorption from head-butting impacts [27]. Broad taxonomic comparisons of suture complexity among mammal species can be useful for interpreting external and internal pressures acting on cranial bones that are associated with increased strain at sutures [7].

Suture development is a complex process that can adapt to and be disrupted by diverse external pressures that impact suture complexity [28–30]. Suture complexity has been shown to be impacted by mechanical stresses and quasi-static stresses acting on the suture, to the extent that mice with greater muscle mass also have increased sagittal suture complexity relative to wild-type mice [28]. Suture complexity has also been linked to different mechanical demands of diet and certain behaviors [27, 29, 31]. Among capuchin monkeys, the more robust species, *Sapajus* (*Cebus*) *apella*, consumes a tougher diet and has higher suture complexity than more gracile capuchin species with softer diets [18]. A similar pattern of higher suture complexity associated with more robust masticatory systems and mechanically demanding diets was also found among interspecific comparisons of caviomorph rodents [29]. Non-masticatory sources of stress may also be linked to higher levels of suture interdigitation. For example, behaviors such as chisel-tooth digging and burrowing in Ctenomyid and Octodontid rodents [29], and head-to-head collisions during inter-male fighting among ruminant species [13, 27], are associated with greater suture complexity. Impact loading experiments in goats (*Capra hircus*) show that sutures act as hinges during functional loading, allowing for cranial bone movement, absorbing more energy than surrounding bone [27]. Moreover, areas of increased interdigitation provided higher bending strength during slow loading and absorbed more energy than less interdigitated sutures [13].

It is clear that cranial sutures serve to transmit forces as well as absorb energy to provide strength and flexibility to the skull during cranial postnatal development and in adulthood. The difference between human and nonhuman primate suture complexity found here cannot be fully explained by dietary or environmental factors, because the diets of modern humans, particularly contemporary Americans, require less masticatory effort than those of the nonhuman primates in our sample. *N. larvatus* and *G. gorilla* have especially tough, folivorous diets, yet had no greater degree of sutural complexity than the other primate groups (Figure 3). The pattern of interdigitation observed here does not support the hypothesis that greater cranial strain associated with masticatory effort is associated with more complex sutural interdigitation, despite support in other studies of nonhuman primates [18] and other mammals [28]. Previous studies of human suture morphology have also found that suture complexity is more closely associated with variation in skull morphology than with variation in age or lifestyle [32]. This study supports the hypothesis that suture interdigitation, and potentially patency, exhibits a distinct pattern in humans relative to a cercopithecoid monkey (*Nasalis*) and nonhuman apes (*Hylobates*, *Pongo*, *Gorilla*, and *Pan*).

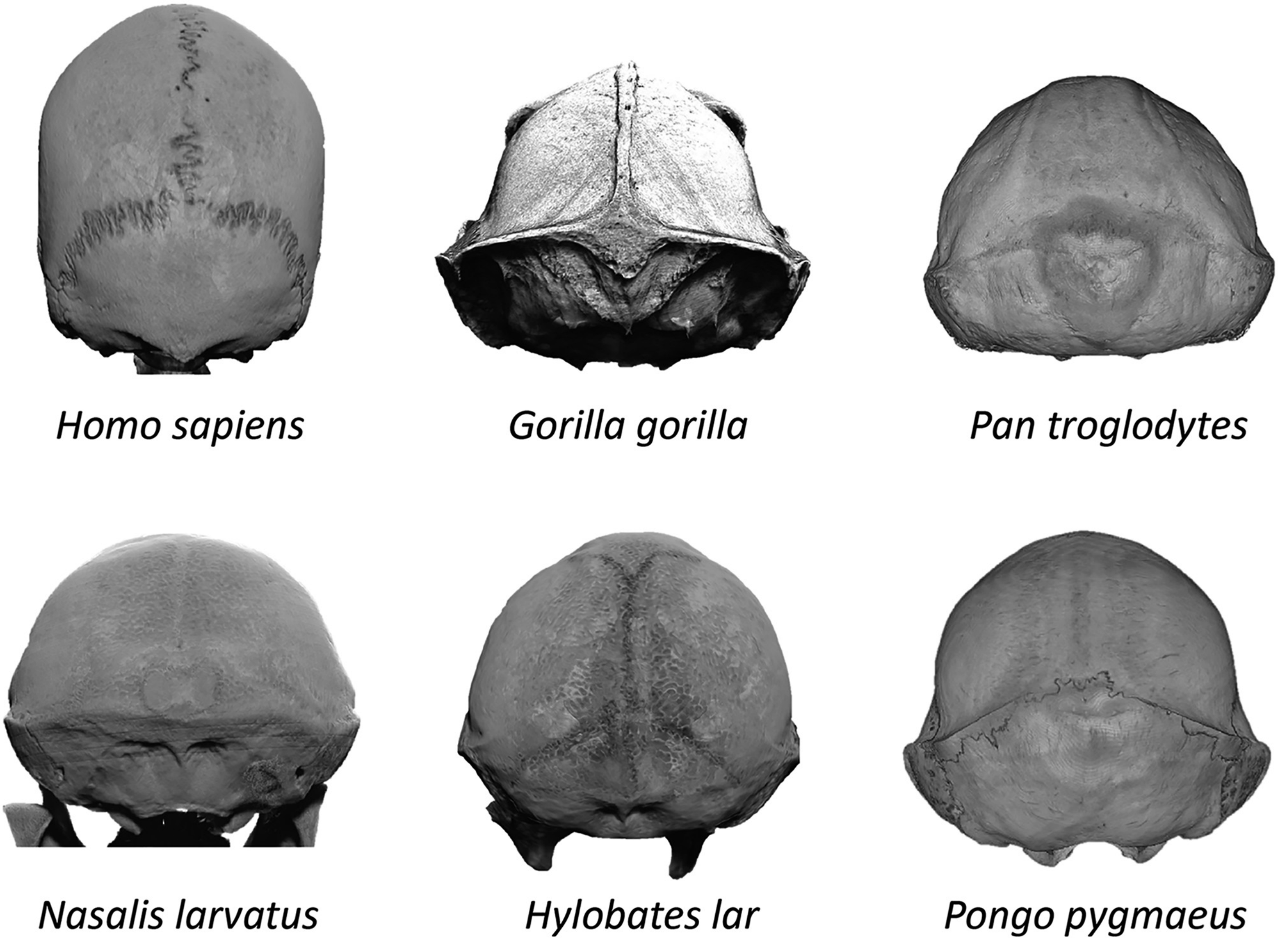

Figure 3: Visual representation of the complexity of sagittal and lambdoid sutures in an adult human (top left), gorilla (top middle), chimpanzee (top right), proboscis monkey (bottom left), gibbon (bottom middle), and orangutan (bottom right) specimens.

Human development

Although many aspects of cranial embryology and genetics are highly conserved across primates, the developmental trajectory of the human skull is quite distinct from that of the nonhuman primates included in our sample. The prenatal growth of the cranial base [33, 34] and rapid postnatal neurocranial expansion [35] distinguish anatomically modern humans from fossil hominins [11, 12, 36] and closely related nonhuman primates. The modern human skull is also typically characterized by neoteny, a tendency to retain more juvenile features throughout the lifetime. Suture patency in adult humans is one marker of this neoteny and has even been found to allow for continued craniofacial growth late in adulthood [37]. Together, these developmental changes are thought to be important for the dramatic evolutionary expansion of the brain in the human lineage [10].

Understanding the interplay between suture patency and suture complexity in cranial development is crucial to the study of cranial motion. Complete sutural closure has been found to occur between 46.9 and 52.7 years of age on average across the suture sites included in this study [38]. Other studies have found the closure of the sagittal suture to be independent of age [39]. On the other hand, suture complexity tends to increase with age in humans and is less exaggerated in individuals under 20 years of age [16]. It is clear that suture patency and complexity change developmentally but do not necessarily follow the same trajectory.

How is this reflected in OCMM?

Sutherland's concept of OCMM stated that the sutures were made for motion, and that bevels and interdigitation supported this concept [40]. When compared to other primates, the complexity of human sutures suggests that OCMM is a byproduct of the unique developmental trajectory of the human skull and its encephalization, and not an adaptive response to intense craniofacial impacts or strain. The complex interdigitation observed in humans by Sutherland and many other practitioners of OCMM is consistent with that of other mammals in which suture interdigitation enables small-scale movements to protect the delicate structures of the brain. We propose that further studies of the development of suture interdigitation across the human lifespan are needed to more fully understand the concept of OCMM developed by Sutherland.

Limitations and future directions

Limitations of this study include intraspecies variability, specifically with respect to differences between males and females. A sexual dimorphic signal has been identified for some mammalian species that exhibit male-male agonistic interactions [31]. However, evaluating the impact of sexual dimorphism on suture complexity among the nonhuman primate sample was not possible due to the Morphosource comparative dataset that consists of primarily female primate specimens [21].

In addition, age and health history were not always available for the primate sample, which is common for wild-caught primate osteological collections such as the one utilized here. In addition, the sample sizes of each nonhuman primate species were not large enough to provide a full picture of interspecific differences.

Finally, the rating of suture interdigitation could vary by observer. The inter-observer reliability and intra-observer reproducibility were both assessed in this study and were high, indicating excellent reliability and reproducibility. Nevertheless, comparing results across studies may be flawed without communication between research teams. We have provided images encompassing the range of variation in suture interdigitation in attempt to aid future researchers in making these determinations.

Conclusions

Our findings indicate more complex suture interdigitation in human specimens than in closely related primate species. This is especially intriguing because prior studies suggest that complex suture interdigitation corresponds to skulls subjected to considerable stress and strain throughout the course of life [13, 14, 18, 41]. We theorize that Sutherland's osteopathic cranial concept provides an explanation for this sutural complexity and for patency of sutures in many adult human specimens. In this framework, loading strains, cyclic strains, and quasi-static strain patterns all influence the development of sutures, and the quasi-static strain pattern in particular would create pressure from surrounding tissues, especially the dura mater. All of these factors may contribute to the development of suture interdigitation in humans and primates, with species-specific interrelationships between strain patterns, developmental timing, and morphology all impacting the patency and complexity of sutures. These findings may provide clues to support the concept of OCMM, and further research is warranted.

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Research ethics: This project was deemed exempt as determined by the Western University of Health Sciences Institutional Review Board (#1988252-1).

Informed consent: Not applicable.

Author contributions: All authors provided substantial contributions to conception and design, acquisition of data, and analysis and interpretation of data; all authors drafted the article or revised it critically for important intellectual content; JB, IA, and AH gave final approval of the version of the article to be published; and all authors agree to be accountable for all aspects of the work in ensuring that questions related to the accuracy or integrity of any part of the work are appropriately investigated and resolved.

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