

Inheritance of Sutural Pattern at the Pterion in Rhesus Monkey Skulls

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ABSTRACT

Five of the bones that characteristically comprise the cranial vault articulate on the lateral aspect of the skull at or near the cephalometric landmark referred to as the pterion. The pattern of articulation in the sutures associated with these bones varies among and within primate species and has been used as a criterion for classification in taxonomic studies, as well as in archeological and forensic studies. Within species, the sutural patterns found within the region of the pterion have remarkable consistency, which lead to the hypothesis that these patterns have a genetic basis. Sutural pattern variations were investigated at the pterion in 422 skulls from 66 rhesus monkey families with known genealogies from the long-standing colony on Cayo Santiago. Four specific types of articulation patterns were recorded. The results demonstrated that the most common suture pattern at the pterion of Cayo Santiago rhesus monkeys (86%; similar to that seen in some other anthropoid species but not humans and some apes) was characterized by an articulation between the temporal bone and parietal bone. Articulation between the sphenoid and parietal bones (type SP) accounted for 14% of the specimens and was concentrated in a dozen families. Mothers with the SP phenotype had a high incidence of offspring with SP phenotypes. Most non-SP mothers having SP offspring had siblings or family members from previous generations with the SP type. This is the first study to examine variation in sutural patterns at the pterion in pedigrees. Variation of sutural patterns shows familial aggregation, suggesting that this variation is heritable. Future work will be focused on defining the inheritance patterns of variation at the pterion, with the ultimate objective of identifying the specific genes involved and their mechanism of action. *Anat Rec Part A*, 288A:1042–1049, 2006. © 2006 Wiley-Liss, Inc.

Key words: primate; cranial sutures; variation; pedigree; genetics

Craniofacial sutures are the boundaries where craniofacial bones meet and are important sites of skull growth (Opperman, 2000). With premature closure of some sutures, the normal growth of skulls will be disturbed, resulting in abnormal skull shape as a consequence of adjusting growth direction (Cohen, 2002). The infratemporal fossa is an interesting area of the skull where elements of the facial skeleton, skull base, and calvaria converge. Viewed in *norma lateralis*, the infratemporal fossa

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Received 22 May 2006; Accepted 26 June 2006

DOI 10.1002/ar.a.20373

Published online 8 September 2006 in Wiley InterScience (www.interscience.wiley.com).

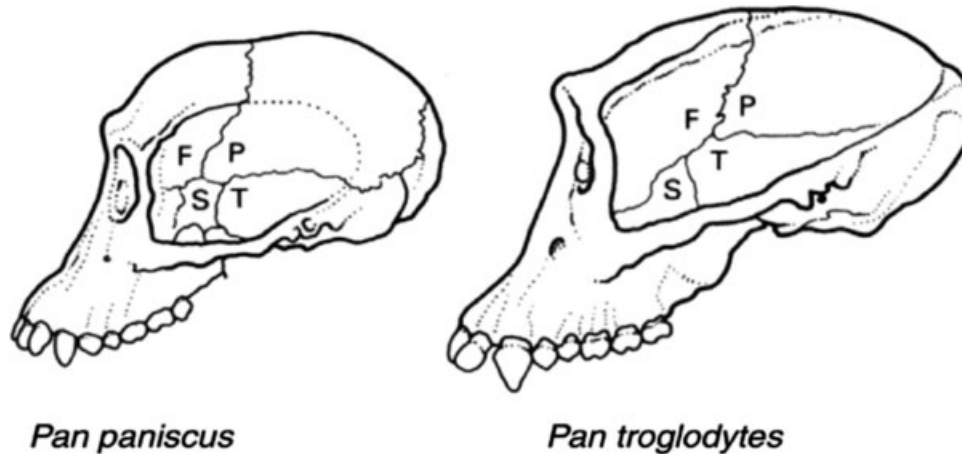


Fig. 1. The pterion area and variation in sutural patterns in two chimpanzee species. Reprinted with permission from Aiello and Dean (1990). F, frontal; P, parietal; T, temporal; S, sphenoid; Z, zygomatic.

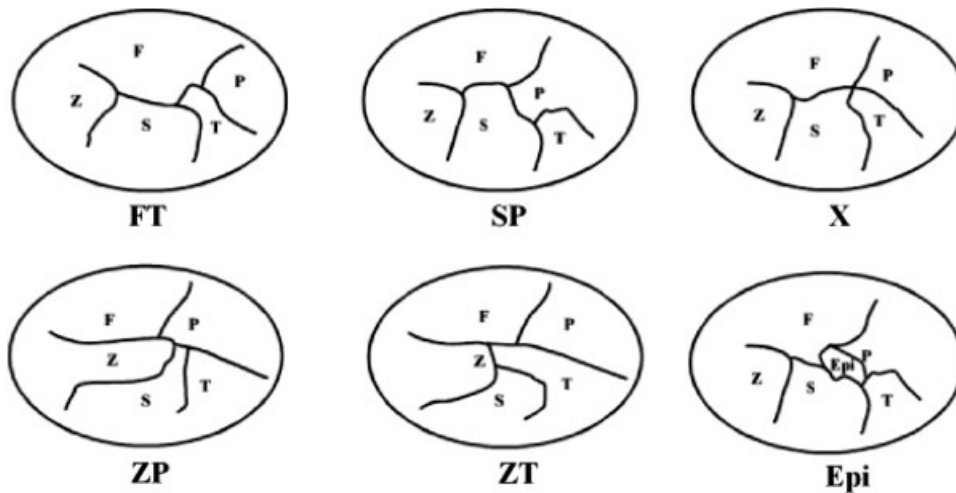


Fig. 2. Diagram of six different sutural patterns in the pterion (view *norma lateralis*). F, frontal; P, parietal; T, temporal; S, sphenoid; Z, zygomatic. Skulls were positioned to face the left as in Figure 1.

of primates is normally characterized by the presence of five distinct bone elements: the greater wing of the sphenoid bone, the frontal bone, the parietal bone, the squamous part of the temporal bone, and the posterior part of the zygomatic bone (Fig. 1). Small but discrete wormian bones may also be present (Fig. 2). All of these bones come together in the region described by the cephalometric landmark, the pterion.

Clinically, the infratemporal fossa is important because it is a site of relatively thin bone that is frequently fractured in traumatic blows to the side of the head. The middle meningeal artery is located deep to this site and may be injured in skull fractures at this location, leading to epidural hematoma. In light of this consideration, Boaz and Ciochon (2004) postulated that *Homo erectus*, the human form in the middle Pleistocene, developed a peculiar branching pattern of the middle meningeal artery in order to divert arteries away from this vulnerable area. Additionally, Broca's motor speech area is found on the left side deep to the region of the pterion. Finally, the pte-

riorion is a primary site for surgical intervention to gain access to the sphenoid ridge and optic canal (Lang, 1984; Oguz et al., 2004). The pterion is the most commonly used neurosurgical landmark and the presence of epipterical bones in the region of the pterion may create a surgical problem. In skulls with an epipterical bone variation, the landmark pterion can mistakenly be assessed to be at the most anterior junction of bones where placement of a burr hole may cause inadvertent penetration into the orbit (Ersoy et al., 2003).

In past anthropological and clinical studies, sutural patterns or bone articulations within the region of the pterion have been generalized into many different types (e.g., Ashley-Montagu, 1933; Hershkovitz, 1977). The six principal types are the frontotemporal type (FT), in which the frontal and temporal bones are in direct contact, preventing the sphenoid and parietal bones from contacting one another; the sphenoparietal type (SP), in which the sphenoid bone and parietal bone are in direct contact, preventing the frontal and temporal bones from

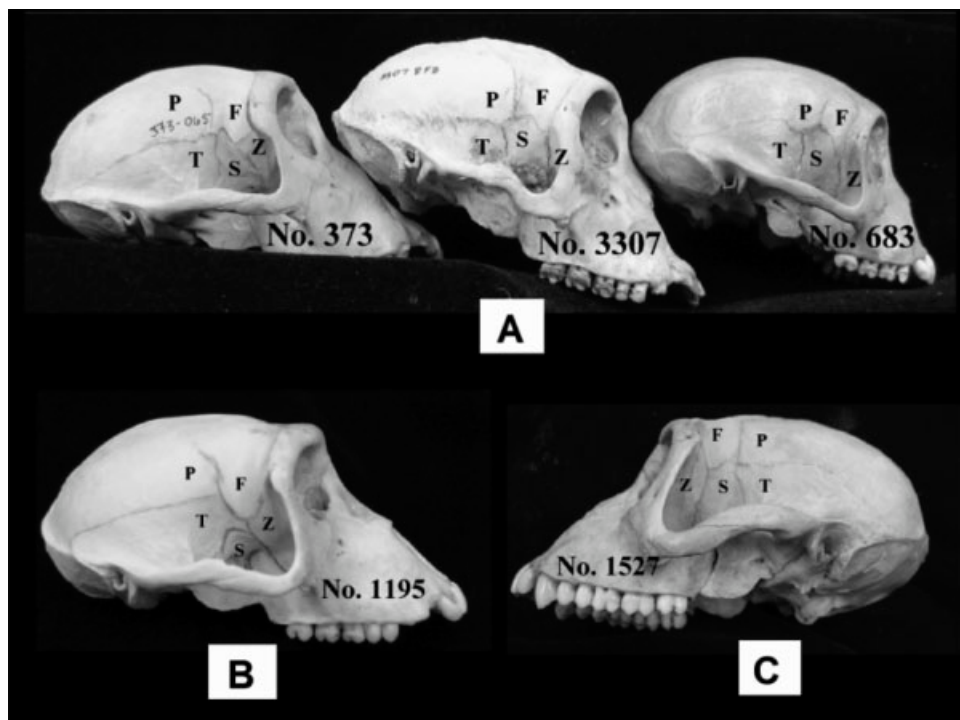


Fig. 3. Skulls with TF, SP, X, and ZP types. Skulls are identified by laboratory catalogue numbers. Skulls were not scaled. **A:** Examples of TF and SP phenotypes. No. 373 exhibits the TF pattern, while both her daughter no. 3307 and grand-daughter no. 683 have the SP pattern. Note there are differences in morphology of the SP type in no.

373 and no. 683; in the former, only half of the superior border of the greater wing of the sphenoid bone contacts with the parietal bone, which raises the question about the threshold of the SP type. **B:** An example of the ZT pattern. **C:** An example of the X pattern. The X type further raises the question about the threshold of the SP type.

contacting one another; the stellate type (X), in which four bones, the frontal, parietal, temporal, and sphenoid, meet each other at one point; the zygomaticoparietal type (ZP), in which the zygomatic bone has a tongue linked to the parietal bone, separating the frontal bone from either the sphenoid or the temporal bone (a variation of SP type); the zygomaticotemporal type (ZT), in which configuration the zygomatic bone has an elongation to meet the temporal bone, separating the sphenoid bone from the frontal and parietal bones, and is considered a subtype of the FT type; and the epipteric type (E), in which a small wormian bone is found between the parietal bone and the greater wing of the sphenoid bone (Figs. 2 and 3).

It is well known that the exact morphological configuration of the sutural junctions of the bones associated with the pterion varies significantly among primates, including monkeys, apes, and modern humans (Table 1) (Collins, 1925, 1926; Ashley-Montagu, 1933; Fenner, 1939; Oliver, 1960; Iwamoto and Hayama, 1963; Hershkovitz, 1977; Saxena et al., 1988; Matsumura et al., 1991; Manjunath and Thomas, 1993; Asala and Mbajiorgu, 1996; Fleagle, 1999; Urzi et al., 2003; Oguz et al., 2004). More specifically, there is considerable consistency of sutural configuration associated with the pterion within primate species, and striking differences between humans and monkeys. In modern humans, bonobos, orangutans, and gibbons, the SP configuration is most common (Ashley-Montagu, 1933; Aiello and Dean, 1990). However, in common chimpanzees and gorillas, the FT con-

figuration is more common (Ashley-Montagu, 1933; Aiello and Dean, 1990). The common modern human SP configuration occurs consistently in all early fossil hominids (Weidenreich, 1943; Aiello and Dean, 1990).

Previous studies of the configuration of sutural articulation patterns associated with the pterion focused principally on the investigation of variation, including classifications, presence of epipteric bones, and associated cranial measurements and indexes (Urzi et al., 2003). These descriptive statistics reveal interspecific and sex differences suggesting that genetic variation underlies, at least in part, pterion sutural pattern variation. However, considerations of familial inheritance that contribute to this variation have generally not been addressed beyond noting that the observed variation is likely a result of a combination of environmental and genetic factors (Murphy, 1956). Aiello and Dean (1990) concluded that little phylogenetic significance could be attached to variation in the region of the pterion as several sutural patterns occur in all extant hominoids, and Asala and Mbajiorgu (1996) concluded simply that these variations are "epigenetic." However, the ways in which developmental or environmental factors might contribute to observed variation at the pterion have not been investigated.

The study presented here tests the hypothesis that genetic variations underlie variations in sutural patterns at the pterion. One likely reason that this hypothesis has not been previously tested in humans or in other primates is that few collections of human or primate bones have suf-

TABLE 1. Incidence of various sutural patterns at the pterion in human and other primates

Specimen	N	Sex	Side	SP	TF	X	Epi	Source
Macaque	210	–	–	–	88.70%	–	–	Collins, 1925
Japanese monkey	329	Mixed	–	–	82.20%	–	–	Iwamoto and Hayama, 1963
Chimpanzee	385	–	–	–	89.80%	–	–	Ashley-Montagu, 1933
Gorilla	376	–	–	–	98.70%	–	–	Ashley-Montagu, 1933
Yellow and hybrid baboons	391	Mixed	–	0.25%	99.50%	–	0.25%	Wang, unpublished data
Orang-utan	578	–	–	–	29.00%	–	–	Ashley-Montagu, 1933
Gibbon	209	–	–	–	19.40%	–	–	Ashley-Montagu, 1933
Human	506	Mixed	–	93.50%	1.50%	0.50%	4.50%	Urzi et al., 2003
Human Australian native	103	–	–	–	10.60%	–	–	Collins, 1926
Human Australian native	231	–	–	–	10.80%	–	–	Ashley-Montagu, 1933
Human Australian native	766	–	–	–	11.90%	–	–	Fenner, 1939
Human Australian native	388	–	–	85.30%	6.70%	–	8.00%	Murphy, 1956
Human European	26240	–	–	–	1.90%	–	–	Ashley-Montagu, 1933
Human Indian	72	–	–	95.30%	3.50%	1.40%	–	Saxena et al., 1988
Human Indian	182	–	–	93.60%	3.50%	2.90%	17.30%	Manjunath and Thomas, 1993
–172 skulls and 10 half skulls								
Human Japanese	614	–	–	95.80%	3.40%	0.80%	>10%	Matsumura et al., 1991
Human Nigerian	212	–	–	82.10%	?10.3%	1.90%	5.70%	Asala and Mbajiorgu, 1996
Human Nigerian	40	–	–	84.80%	10.10%	5.10%	–	Saxena et al., 1988
Human Turkish	300	–	490	–	–	–	9%	Ersoy et al., 2003
Human Turkish	26	–	–	85.50%	10.50%	–	4.00%	Oguz et al., 2003

The sums in rows are not 100% in some cases, as one pattern, such as the Epi, often coexists with other patterns.

ficient numbers of individuals from the same families with relevant pedigree information. The Caribbean Primate Research Center (CPRC) and the University of Puerto Rico have collected skulls and family relationships for rhesus monkeys living on Cayo Santiago for several decades. Although paternity is not known with certainty, maternal lineage and small family group information is available for many individuals in the skeletal collection. In the present study, these skulls were examined for familial aggregation by suture pattern type to test the hypothesis that pterion configuration is heritable. The objectives of this study were to test whether sutural patterns at pterion are heritable by investigating articulation pattern at the pterion in rhesus monkey skulls of various families and examining the occurrence of sutural pattern types in family groups. The null hypothesis was that variation in the sutural patterns at the pterion occurs randomly among family members, thereby showing no evidence that observed phenotypic variation in articulation pattern types is heritable. One indication that a trait is heritable is that the trait shows low incidence in the population but high incidence in certain families. Based on studies in other cercopithecoids, it was expected that the SP pattern would be rare in the Cayo Santiago macaques (with the FT pattern being the predominant suture pattern) and that the rarer variant SP type clustered in families.

MATERIALS AND METHODS

In 1938, a population of about 400 rhesus monkeys from India was introduced onto Cayo Santiago, a small six hectare island a kilometer off the coast of southeastern Puerto Rico. These animals were the basis for the free-ranging colony that exists today as an essential component of the CPRC (Carpenter, 1972). Monkeys on the island are supplied with monkey chow and, to varying degrees, supplement their diet with island vegetation.

The introduced free-ranging population has been growing steadily and has naturally split into many social groups. To date, there are over 700 skeletons with known age and sex included in the CPRC collection, ranging in age from 6 months to 32 years. This collection is housed in the Laboratory of Primate Morphology and Genetics, University of Puerto Rico Medical Sciences Campus, where this investigation was conducted. Through pedigree reconstruction based on mother-child relationships, 422 animals born between 1950 and 2000 were selected; they came from 66 families, with family size ranging from 2 to 26 members. Number of generations ranged from one (only siblings or half-siblings) to five. No paternity information was available for these animals.

At both left and right sides of each skull, the suture pattern of the pterion was determined based on the morphological variants summarized in Figure 2. The same individual (Q.W.) scored all skulls for variations in sutural patterns. These data were incorporated into pedigree trees, and the inheritance was checked through family lines. The criterion chosen to determine inheritance of a feature was that it had low incidence in the population but showed high incidence in certain families. Chi-square tests for statistically significant differences among family groups were conducted using the Minitab statistics program 14.1 (State College, PA). The critical value for significance was $\alpha \leq 0.05$.

RESULTS

Among 422 animals, four types of sutural configuration at the pterion were recorded: the FT type, the SP type, the X type, and the ZT type (Table 2). Both the X type and the ZT type were rare (Table 2). No skull presented with an epipteric intersutural bone. The FT type (including the ZT type) occurred at a frequency of 86.0% in the sample (86.6% of female and 85.4% of male). There

TABLE 2. Variation of sutural patens in Cayo Santiago rhesus monkey collections

	Suture patten	Total	Female	Male
Suture Pattern	TF/TF	361	193	168
	SP/SP	37	20	17
	TF/SP	18	8	10
	X/X	1	1	0
	X/TF	3	1	2
	ZT/TF	2	1	1
Sum of Sample Size		422	224	198
Percentage ¹	TF	86.0%	86.6%	85.4%
	SP	14.0%	13.4%	14.6%

¹Specimens having SP and X were counted as SP, ZT was counted as TF.

TABLE 3. Ten families with high incidence of Speno-Parietal articulation pattern in Cayo Santiago

	SP incidence ¹	Family member	Generation	First mother no.
Family 10	23.5%	17	4	373
Family 22	15.4%	26	4	Tattoo DZ
Family 28	28.6%	7	2	Tattoo ZM
Family 30	38.1%	21	4	Tattoo 073
Family 35	21.0%	24	5	114
Family 47	83.3%	6	2	Tattoo 633
Family 50	50.0%	4	2	465
Family 55	100%	3	3	3017
Family 65	100%	2	1	Tattoo 454
Family 66	66.7% – 100% ²	4	1	Tattoo WF

¹Specimens having X types were not included.

²one of 4 half-siblings do not have examinable bones

was no significant difference between the sexes in term of sutural pattern incidence (chi-square test: $P = 0.72$). The incidence of the SP phenotype was significantly lower than that of the FT phenotype (FT ~ 86% vs. SP ~ 14%; chi-square test: $P < 0.0001$). The frequency of the SP type was almost 13%. Most occurrences of this articulation pattern were concentrated in family groups, occurring in 26 of the 66 family groups (Table 3). The incidence of the SP type was 33.1% in the 26 families examined, with individual family frequencies ranging from 15.4% to 100% (Figs. 4–8). This difference between the 26 families and the whole population was statistically significant (33.1% vs. 13.0%; chi-square test: $P = 0.0001$; Table 3).

When a mother showed the SP variant, her offspring had greater than 33% chances of also having the SP variant. Among the 30 descendants of 11 mothers with offspring of the SP type, 9 were male and 7 were female, with no significant sex effect on suture pattern variation (male 30.0% vs. female 23.3%; chi-square test: $P = 0.11$).

Four individuals had the X type variation on at least one side. Three of them were closely related family members to individuals with the SP type. For example, in

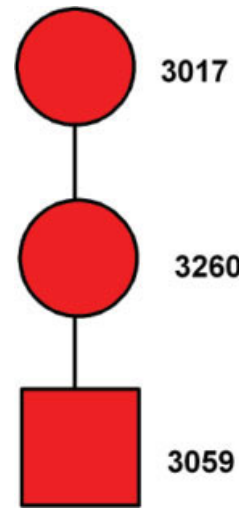


Fig. 4. Matrimonial pedigree of family 55. There are three generations with a single individual in each generation, and all show the SP configuration. Circle, female; square, male; red, SP phenotype.

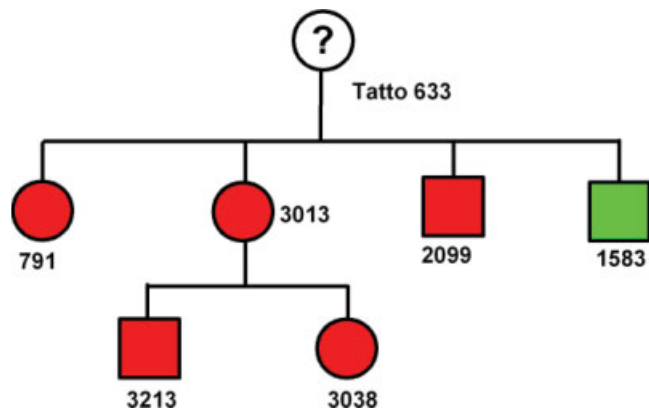


Fig. 5. Matrimonial pedigree of family 47. There are four siblings (two male and two female) in the first generation, three having the SP configuration and one having the X configuration. Among them, no. 3013 with the SP configuration has one son and one daughter, both having the SP configuration. The skull of the first generation is not preserved, so the animal catalogue number (tattoo) is presented. Circle, female; square, male; red, SP phenotype; green, X phenotype.

family 30, no. 3319 had the X type variation with two of four siblings having the SP variation (Fig. 7). The animal no. 2926 in family 10 had the X type variation, with two of five siblings having the SP variation (Fig. 8).

DISCUSSION

It is interesting to see that although the incidence of the SP variation was low in the whole sample, occurrence of this variant was concentrated in two dozen families. Additionally, mothers with the SP phenotype showed a higher incidence of offspring with SP phenotypes than did mothers of the common FT type. Most of the non-SP mothers having SP offspring displayed the X pattern variant, or had siblings or family members of previous generations with the SP type. Variation of sutural patterns showed familial aggregation, suggesting that this variation is her-

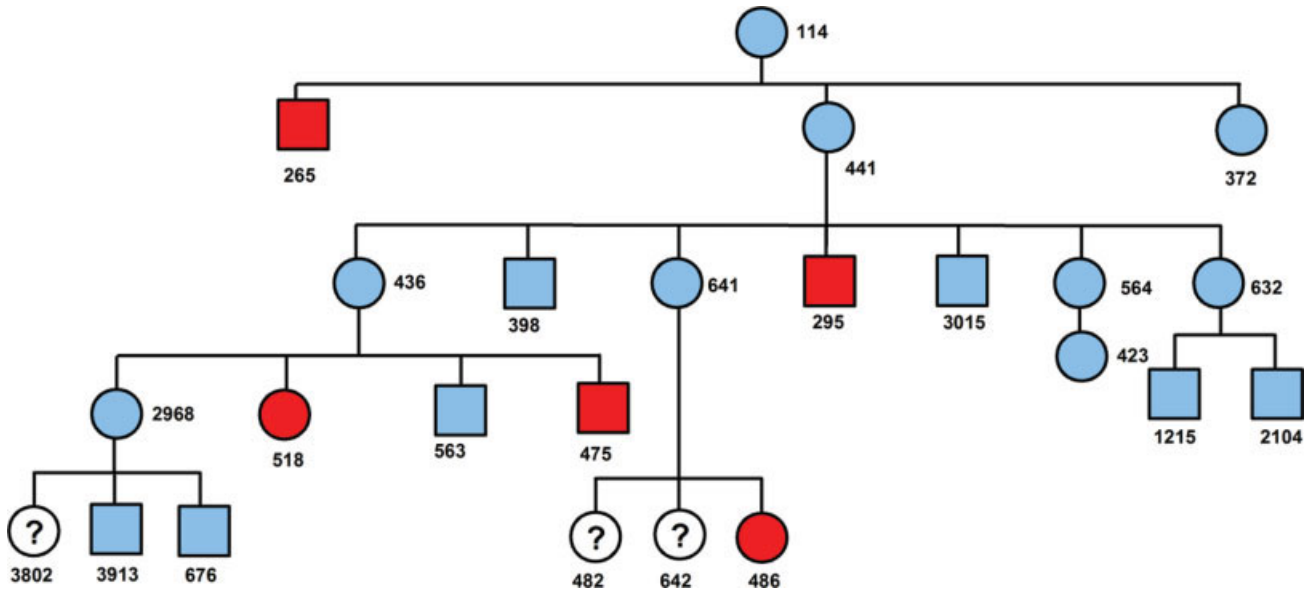


Fig. 6. Matrimonial pedigree of family 35. No. 436 is a non-SP type; two of her four children, one son and one daughter, have the SP configuration. No. 441, the mother of no. 436, is a non-SP type; however, one of no. 441's brothers has the SP configuration. Circle, female; square, male; blue, TF phenotype; red, SP phenotype.

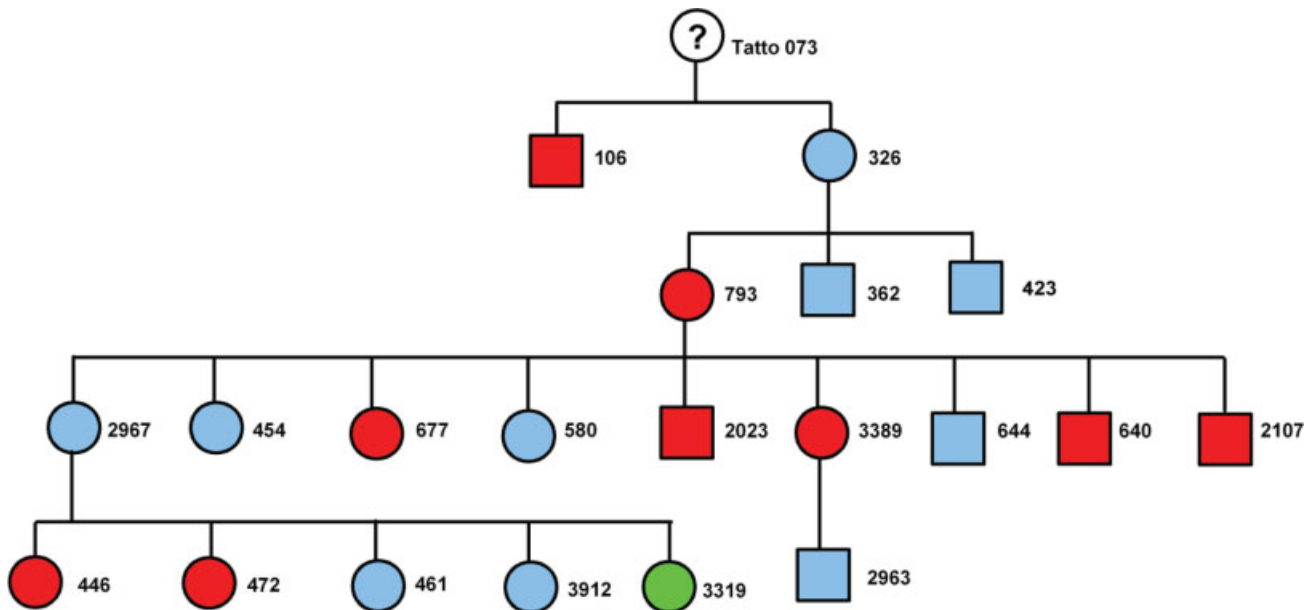


Fig. 7. Matrimonial pedigree of family 30. Five of no. 793's nine children have the SP configuration (three male, two female). No. 793 has the TF configuration; its mother has no SP configuration either. But one of no. 793's siblings is the SP type. One of no. 793's daughters (no. 2967) shows a non-SP phenotype. However, two of No

2967's five daughters have the SP configuration, and one has the X configuration. The skull of the first generation is not preserved, so the animal catalogue number (tattoo) is presented. Circle, female; square, male; blue, TF phenotype; red, SP phenotype; green, X phenotype.

itable. Given that the incidence of the SP phenotype was significantly lower than that of the FT phenotype, it is postulated that a gene (or genes) that influence developmental patterns leading to the SP variant may be recessive and that a gene (or genes) related to the FT variant may

act in a dominant manner. The SP phenotype is not sex-related, as it shows nearly equal occurrence in both male and female offspring, and might be an autosomal recessive variation. It is interesting to note that some individuals have both FT and SP types (Table 2), and that the SP type

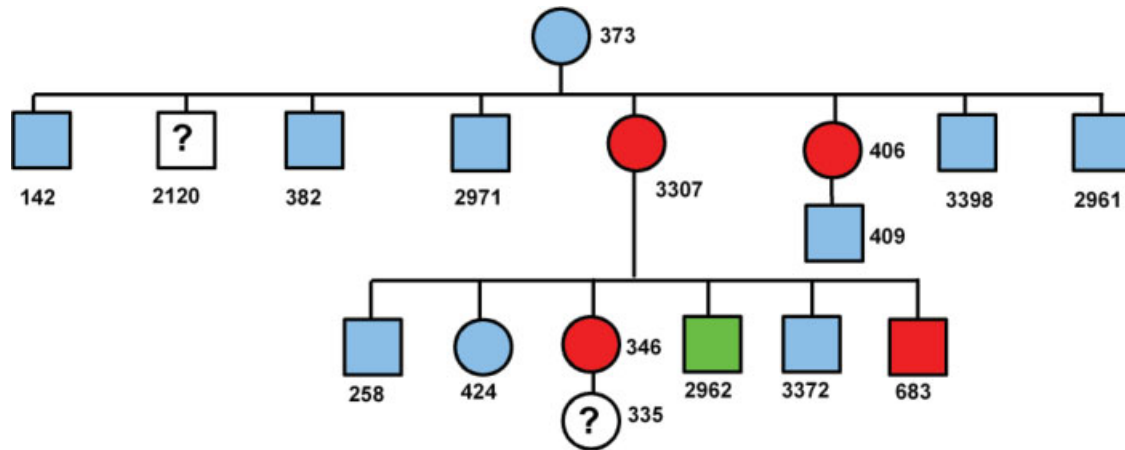


Fig. 8. Matrimonial pedigree of family 10. No. 3307 in the second generation shows the SP phenotype, two of her six children show the SP type, and one shows the X type. Circle, female; square, male; blue, TF phenotype; red, SP phenotype; green, X phenotype.

has different morphology (Fig. 3), suggesting the regulation of multiple genes.

The SP phenotype is the most common sutural pattern in humans, orangutans, and gibbons (Table 1), while the FT phenotype is the predominant pattern in common chimpanzees, baboons, and Japanese and rhesus macaques. The question raised by this observation is whether the phenotype is the result of a mutation or mutations that altered the influence of a gene or genes related to the SP or FT phenotypes. If this were so, it would be interesting to know how these mutations might lead to this change in cranial development.

A limitation of the current study is that only maternal relationships were known for the animals studied. Nonetheless, familial aggregation of the less common variants was observed, suggesting a genetic effect on suture pattern variation at the pterion. Parts of the Cayo Santiago collections have blood samples besides bones, collected during annual physical examinations. Those materials are available for genetic studies. Starting from families of interest, it is possible to begin singling out the genes behind the variation at the pterion.

Sutures are of great importance for craniofacial growth (Opperman, 2000; Cohen, 2002). Genetic knowledge of how contemporary variation in sutural patterns at pterion came to exist in humans, apes, and monkeys will also provide insights into how morphological variation and evolutionary change are patterned in the craniofacial region. The development of calvarial bones is tightly coordinated with the growth of the brain and requires interactions between different tissues within the calvarial sutures (Kim et al., 1998). One might hypothesize that skulls with higher ratios of cranial height over cranial length such as in humans (orthocrany or hypsicrany) are more likely to have experienced neurocranial growth forces causing the sphenoid bone and parietal bone to meet each other, while skulls in monkeys having very low cranial length-height index (chamaecrany) are less likely. This might explain the difference between humans and monkeys, and between the two chimpanzee species (Fig. 1). The cranial length-height index is $\sim 60\%$ in pygmy chimpanzees vs. $\sim 50\%$ in common chimpanzees (these indexes are rough

estimates as no systematic investigation has been conducted). This suggestion raises the question of whether skull shape as influenced by brain growth is the dominant factor determining sutural pattern, or whether sutural patterns are more a result of intrinsic pattern formation in the cell condensations forming the initial anlagen for calvarial bones. In humans, the closure of the sphenoidal fontanelles (*fonticulus sphenoidalis*) and the formation of the pterion sutural configuration are completed about 1 year after the birth, but the sutures stay open for many more years (Wang et al., 2006). However, understanding how the sutural configuration and brain growth and development patterns are linked to each other will require further studies. Investigation of sutural configurations at the pterion in primate and human fossils as well as sutural patterns following experimentally modified growth through transgenic techniques will bring further insights to the causes of variation and the evolution of sutural and skull morphology.

Some genes linked to sutural fusion might play roles in determining sutural configuration patterns, such as *MSX2*. The *MSX2* gene encodes a homeodomain transcription factor that is known to have a role in craniofacial morphogenesis (Rifas et al., 1997; Liu et al., 1999). Mutations in the homeobox genes for *MSX2* as well as FGF receptors cause premature fusion of cranial sutures, known as craniosynostosis, in humans (reviewed in Opperman, 2000), although in dogs, *MSX2* (located at chromosome 4q23) does not contribute to the diversity of face shape (Haworth et al., 2001). It is reasonable to postulate that several genes acting in cranial suture morphogenesis and growth are involved in regulating pterion variability. Therefore, it would be interesting to examine allelic variability in these genes to begin the search for genes responsible for pterion variability and variations in calvarial morphology between species. Further questions to be answered are related to the nature of the threshold characters for the SP phenotype, whether the trait is quasicontinuous or due to a single locus, and why humans and monkeys/apes show such differences in the occurrence of suture pattern at the pterion.

This is the first study to examine variation in the sutural patterns at the pterion in pedigrees. Variation of su-

tural patterns shows familial aggregation, suggesting that this variation is regulated, at least in part, by genes.

ACKNOWLEDGMENTS

The authors thank the Caribbean Primate Research Center, the University of Puerto Rico, Medical Sciences Campus, Laboratory of Primate Morphology and Genetics, and the National Institutes of Health (grant RR03640 to CPRC) for support. Additional support was provided by NSF Physical Anthropology (grant BCS 0240865 to P.C.D.). The authors also thank Drs. Jim Cheverud, Kathy Svoboda, Robert Hinton, Rena D'Souza, John Cant, Don Dunbar, Bob Kensley, Terry Kensley, and Myriam Vinales for their help in various aspects of this study. In particular, Terry Kensley treated Q.W. with great hospitality and permitted extended working hours during his stay, which was crucial for the satisfactory completion of this and related research projects. The editors and reviewers are also thanked for providing valuable comments.

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