

Support for the Spandrel Hypothesis in Artificially Modified Skulls

Jorge Meza Paggi

Abstract

Intentional cranial modification, alike other forms of body modification, has been practiced by many cultures around the globe. Anthropologists have studied the reasons that support such tradition, the methods used for it, and the changes it produces on the cranium among different groups. However, the biological mechanisms that allow for the intentional modification of the skull to take place have not been extensively considered. Using a functional perspective and considering signaling pathways between tissues, four fronto-occipitally modified skulls are analyzed. The change in shape of the cranial vault and the bulging of the sagittal suture caused by the modification are correlated with the spatial redirection of brain growth. The lack of frontal sinuses seen in all individuals is associated with the technique used for the modification. Finally, the potential of a functional approach in the study of human populations and evolution is emphasized.

There has been a lot of debate surrounding the paranasal sinuses of vertebrates. In the center of this debate is their function or evolutionary advantages. Two theoretical avenues have approached this question, one considering possible physiological roles for these cavities and the other structural roles. Researchers that have taken the former approach have related the sinuses to the development of the olfactory complex, to the resonance of emitted sounds, to the conditioning of inhaled air, and other factors (e.g. Braune and Clasen, 1877; Leakey and Walker, 1997; and Gannon et al., 1997). Theories that have related the sinuses to structural functions have suggested that they are linked to the lightening of the skull, to an assistance in facial growth, to the dispersion of masticatory forces, and other structural necessities (e.g. Davis et al., 1996; Moor and Persaud, 1993; and Preuschoft et al., 2002). In recent years, however, with the advancement of non-intrusive imaging techniques (specifically three dimensional computer tomography), a new wave of studies from different disciplines has approached the paranasal sinuses. The new observations have led to the resurfacing of an often overlooked hypothesis that does not assume a specific function for these structures. This hypothesis proposes the paranasal sinuses as biological spandrels, phenotypic characteristics selected as

a product of evolutionary forces acting upon a separate trait, an idea introduced by Gould and Lewontin (1979).

Key to this idea is the allometric development between different cranial components, or functional matrices. The spandrel hypothesis proposes that cranial bones, which are part of different functional matrices, must accommodate this allometric growth, and in this manner allow for pneumatization to occur. This dynamic can be observed well on the frontal bone, since its inner table is part of the cerebral compartment while its outer table responds to the development of the face (Moss and Young, 1960). In the case of humans both tables of the frontal bone advance together until approximately the age of seven. This advancement is directed by the accelerated expansion of the frontal lobe in relation to the nasomaxillary complex. After this period the expansion of the frontal lobe is arrested, however there is still significant facial growth. As a consequence, the outer table of the frontal bone begins to drift forward significantly faster than the inner table (Shapiro and Schorr, 1980). This separation results on a spatial gap in the vertical portion of this bone, which is initially filled with trabecular bone. Just as is the case with long bones, there is here a transition from red to yellow marrow. However, this is then followed

by the opportunistic invasion of this space by the mucous epithelial tissue of the frontal recess, so creating a sinus (Scuderi et al., 1992). Zollikofer et al. (2008) argue that this invasion is possible because the deposition of extracellular bone cannot keep up with the expansion of the outer table of the frontal bone. This causes a thinning of the trabecular mesh that facilitates the invasion and formation of air cells. They note that in the Broken Hill and Forbes' Quarry Neanderthal specimens the frontal sinuses do indeed extend towards areas of less trabecular density.

The sinuses, being a product of an allometric development between different functional matrices, should reflect how these matrices are arranged and sized in relationship to each other. Such arrangements are determined by evolutionary pressures acting on these structures. This notion can clarify multiple observations regarding the sinuses across a variety of taxa. For instance, Vleck (1967) points out that between humans and Neanderthals variations in sinuses follow changes in cranial morphology, and that the size of the Neanderthal sinus is not relatively large. He argues that the frontal sinuses of Neanderthals occupy a great space in the anteroposterior axis only due to more pronounced brow ridges, while they are still confined to the lower portion of the bone due to the slope of the frontal squama. The opposite is true for humans, with a steeper squama.

In a similar manner, Zollikofer et al. (2008) argue the large maxillary sinuses found in Neanderthals are due to the bulging of this bone, absent a canine fossa, and not the opposite. Evidence of this rests on the fossils of infant Neanderthals, which lack a sinus, but already possess more projecting maxillae. They also interpret the invasion of the zygomatic by the maxillary sinus occasionally observed in Neanderthals and great apes as a consequence of the greater zygomatico-maxillary interface present in these groups. All these propositions relate the sinus to structures that are more susceptible to evolutionary requirement.

Shapiro and Schorr (1980), also noticed that the frontal sinuses arise due to “incongruity” between the crania vault and the face. They point out that in wolves, where the eye orbits and nasion are significantly more anterior than the anterior end of the cranial vault, larger frontal sinuses are found than in dwarf dogs, where the eye orbits and nasion are placed immediately below the cranial vault. It is more likely that the sinuses are being suppressed by the domestication complex, rather than lost due to direct selection. They also provide a list of congenital diseases in humans that affect the development of the nasomaxillary complex, and consequently prevent or limit the pneumatization of the frontal bone. Among these are maxillofacial dysplasia, otopalatodigital syndrome, mandibulofacial dysostosis, and Down's syndrome. These observations also associate the sinuses to other cranial components, not only to their evolutionary history, but also to more casual variations.

The maxilla participates in distinct functional matrices as well, mainly the eye orbits and the dentition. Thus, it should be expected that these matrices influence the formation of sinuses in this bone, in a similar fashion as the cranial compartment and face influence the formation of sinuses in the frontal bone. This seems to be the case when comparing these functional matrices in species of new world monkeys with and without maxillary sinuses. Squirrel monkeys (*Saimiri*), which do not have maxillary sinuses, present a high degree of approximation of the orbits to the posterior dentition compared to other new world monkeys that do have sinuses (Hartwig, 1995). This species also possesses a relatively larger posterior dentition, but it is not only the large size of these components that seems to limit the formation of the maxillary sinuses. By comparing the development of *Saimiri* to that of the other two species that present sinuses, Smith et al. (2010) found that the region of trabecular bone in *Saimiri*, where other species would present a sinus, is occupied by the permanent dentition before it emerges. This suggests that, to

understand how pneumatization comes to be, the relative arrangement of functional matrices during the ontogenic process must be considered.

These observations could be used to explain the disappearance and re-appearance of the maxillary sinus among old world monkeys. Since *Macaca* is the only extant cercopithecoid genus that presents sinuses, it was widely accepted that these structures were already lost by an early cercopithecoid common ancestor and that their presence in *Macaca* is due to a reversal. However, the presence of these structures on some extinct fossils belonging to other genera suggests that the structure may simply have been suppressed (Rae, 2007). The spandrel hypothesis allows us to relate this suppression to the pressures acting upon other cranial components in old world monkeys. This approach explains the lack or presence of sinuses on cercopithecoids without the need of arguing for a great amount of homoplasy.

The hypothesis allows us to understand the variation in paranasal cavities as a consequence of evolutionary pressures, environmental factors, diseases, and ontogeny. It should be reflected in any phenomenon that affects the arrangement or development of the functional matrices of the cranium, including cranial deformation. Techniques of intentional cranial modification should have the same effect on the paranasal sinus, specifically the frontal sinus, if they are applied during the time of sinus development. This is because cranial modification practices are correlated with changes in the shape of the cranial vault and of the face. In the case of fronto-occipital deformations, the pressures applied on the frontal and occipital bones lead to a brachycephalic crania vault, and to a wider and shorter face (Anton, 1989; and Cheverud et al., 1992). The flatter and shorter forehead caused by this type of deformation would prevent the pneumatization of the frontal bones.

References

- Anton, S. (1989). Intentional cranial vault deformation and induced changes of the cranial base and face. *Am J Phys Anth*, 79, 253-267.
- Braune, W. and F. Clasen (1877). Die Nebenhöhlen der menschlichen Nase in ihre Bedeutung für den Mechanismus des Rieches. *Zf Anat*, 2, 1-28.
- Cheverud, J. et al. (1992). Effects of fronto-occipital artificial cranial vault modification on the cranial base and face. *Am J Phys Anth*, 88, 323-345.
- Davis et al. (1996). Anatomy of the paranasal sinuses. In Parsosn D. (Ed.). *Otolaryngo Clin North Am*, 29, 57-72.
- Gannon, P. et al. (1997). Maxillary sinus mucosal blood flow during nasal vs tracheal respiration. *Arch Otolaryngo Head Neck Surg*, 123, 1336-1340.
- Hartwig, W. (1995). Effect of life history on squirrel monkey (*Platyrrhini, Saimiri*) cranium. *Am J Phys Anthro*, 97, 435-449.
- Leakey M. and A. Walker (1997). Afropithecus –Function and phylogeny. In Begun, Ward, and Rose (Ed.). *Function, phylogeny, and fossils*. New York: Plenum Press.
- Moore, K. and T. Persaud (1993). “The developing human”. 5th ed. Philadelphia: W. B. Saunders & Co.
- Moss, M. and R. Young (1960). A functional approach to craniology. *Am J Phys Anthropol*, 18, 281-292.
- Preuschoft et al. (2002). Pneumatized spaces, sinuses, and spongy bone in the skulls of primates. *Anth Anz*, 60, 67-79.
- Rae, T. (2007). Paranasal pneumatization in extant and fossil Cercopithecoidea. *J Hum Evo*, 54, 279-286.
- Scuderi, A. et al. (1992). Pneumatization of the Paranasal Sinuses: Normal features of importance to the accurate interpretation of CT scans and MR images. *Am J Radio*, 160, 1101-1104.
- Shapiro, R. and S. Schorr (1980). A consideration of the systematic factors that influence frontal sinus pneumatization. *Investig Radio*, 15, 191-202.
- Smith, T. et al. (2010). The maxillary sinus in the genera of new world monkeys: Factors that constrain secondary pneumatization. *Anat Rec*, 293, 91-107.
- Vleck, E. (1967). Sinus frontales bei europäischen Neandertalern. *Anthro Anz*, 30, 166-189.
- Zollikofer, C. et al. (2008). New insights into the mid-late Pleistocene fossil Hominin paranasal sinus morphology. *Anat Rec*, 291, 1506-1516.