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Three-Dimensional Imaging in Paleoanthropology and Prehistoric Archaeology

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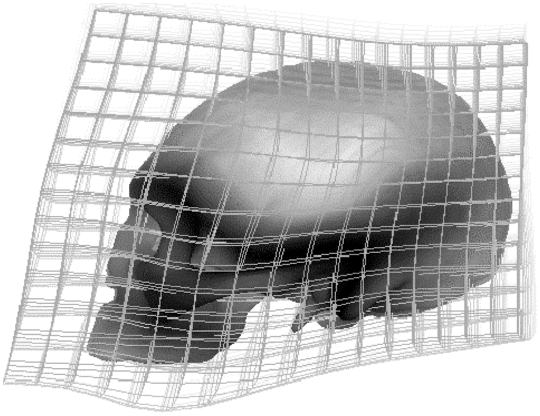

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3D IMAGING AND MEASUREMENT IN STUDIES OF CRANIAL PNEUMATIZATION

Todd C. RAE & Thomas KOPPE

Résumé: Les reconstitutions tridimensionnelles, à partir de coupes scannographiques, sont une source d'informations uniques et un outil aux remarquables potentialités pour étudier les structures internes du crâne. Désormais, il est possible de réaliser des études morphologiques détaillées de régions anatomiques mal connues auparavant, comme les cavités sinusiennes. Ainsi, les hypothèses précédemment émises concernant la croissance et l'évolution des structures internes crâniennes des mammifères peuvent être testées. Nous présentons ici l'étude par imagerie tridimensionnelle de la pneumatisation paranasale, en particulier des sinus maxillaires, chez les primates catarrhiniens. Cette étude a permis une analyse critique des interprétations précédentes de la croissance et de l'évolution des sinus chez les chimpanzés et les singes de l'Ancien Monde qu'il n'aurait pas été possible de réaliser sans l'apport, au plan de la visualisation et de la quantification, de l'imagerie tridimensionnelle à partir de données scannographiques.

Abstract: Three-dimensional reconstructions based on computed tomography (3D-CT) represents a unique and powerful tool for the study of internal structures of the skull. For the first time, detailed analyses of previously understudied features, such as cranial pneumatization, can be used to critically test hypotheses concerning the growth and evolution of aspects of the interior of the mammalian cranium. We report here on studies using 3D-CT to evaluate the expression of paranasal pneumatization, particularly the maxillary sinus, in catarrhine primates. As a whole, the work reported represents a critical re-evaluation of previous interpretations of the growth and evolution of the sinus in apes and Old World monkeys that would not have been possible without the aid of the visualization and quantification that 3D-CT provides.

INTRODUCTION

A persistent problem in cranial morphology is the characterization of internal structures, and particularly hollow spaces, such as sinuses. Increasingly, these morphological characteristics are used for functional and phylogenetic studies of mammals, driven in many cases by the discovery of fragmentary fossil evidence revealing previously unexamined aspects of craniofacial structure (Begun, 1992; Rae, 1999; Ward & Brown, 1986). Although gross differences and some basic measurements are available for these traits via destructive techniques, this is by no means ideal, particularly for rare or delicate specimens. Some non-destructive methods are also available (e.g., seed technique; see Shea, 1977), but in many cases these procedures are not applicable to both extant and extinct taxa, due to matrix infilling of fossil crania and increasingly strict rules on the use of seeds in museums.

Traditional radiography (e.g., Vlček, 1967; Blaney, 1986) circumvents some of the shortcomings of the techniques listed above, but is not without its own limitations. In many cases, fine details of shape are lost in ordinary x-ray visualization, and quantification is often restricted to a maximum dimension in a particular plane (Blaney, 2000). In addition, this technique can be sensitive to matrix infilling, confounding both measurement and interpretation of the internal structures of permineralized tissue.

Advances in medical imaging, however, have solved many of the problems facing those interested in internal cranial morphology. Virtual reconstructions in three dimensions, based on serial computed tomography (CT) scans (Figure 1), are an ideal way to derive shape and size data from structures inside the skull (e.g., Spoor & Zonneveld, 1999). Unlike laser-based methods, which can be used to study external structures only, 3D-CT combines the non-destructive internal visualization of traditional radiography with the ability to discern detailed shape data normally available only from invasive/destructive techniques (Koppe & Nagai, 1995). As a digital technology, 3D-CT also offers an unprecedented method for accurate measuring internal cranial structures, particularly 3D quantities, such as volumes of sinus spaces (Koppe, et al., 1996; Koppe & Nagai, 1999; Uchida, et al., 1998).

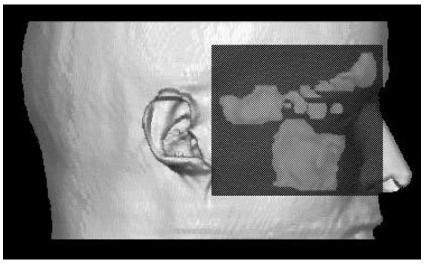

Figure 1 - Lateral view of three-dimensional virtual reconstruction from serial CT scans (3D-CT) of one of us (TCR). A semi-transparent window has been added to show 3D-CT reconstructions of the paranasal pneumatizations.

PRESENCE/ABSENCE OF INTERNAL STRUCTURES

Serial CT analysis, with or without subsequent 3D reconstruction, can be of great use in testing hypotheses of morphology. Even the simple discovery of the presence or absence of a particular pneumatization can alter our ideas about the evolution of characters in mammalian history. An example is taken from our recent work in the evolution of the maxillary sinus in Old World monkeys (Cercopithecoidea, Primates).

It has long been known (Paulli, 1900) that many cercopithecoids lack the maxillary sinus, a distinct pneumatic space in the cheek region of the face. The presence of this cavity in most other primates (Ward & Brown, 1986) and nearly all other eutherians (Moore, 1981) suggests that the sinus was present in the last common ancestor of placental mammals (Novacek, 1993). One Old World monkey, however, has been documented to possess a maxillary sinus; all known species of the genus *Macaca* possess a sinus space indistinguishable from that of other primates (Koppe & Ohkawa, 1999). Most workers have interpreted a small sinus to be the ancestral condition for the group (Harrison, 1987; Rae, 1997), although more recent analyses of extant taxa have suggested that the last common ancestor of the group may have lacked this pneumatic space (Rae, 1999). Nonetheless, this character state distribution among the extant forms makes the reconstruction of the ancestral state for the maxillary sinus in cercopithecoids equivocal.

One way to break the deadlock is to determine the character state in a stem taxon (*sensu* Ax, 1985) of the group. By acting as a closely related outgroup, a stem taxon (usually a fossil) can be instrumental in determining the polarity of a particular character state transformation, and thus provide a robust hypothesis of the ancestral state for the ingroup. In the present case, the only well-known stem cercopithecoid is *Victoriapithecus*, from middle Miocene (ca. 15 Ma) deposits of Kenya; character states of the dentition of this taxon suggest that it precedes the last common ancestor of the extant forms (Benefit, 1993), and this unique phylogenetic position has had a demonstrable impact on interpretations of craniofacial evolution in Catarrhini (Benefit & McCrossin, 1991, 1993). A recently discovered complete cranium of *Victoriapithecus* (Benefit & McCrossin, 1997) provides the perfect test case, as more fragmentary remains can be much more difficult to interpret. CT analysis was crucial in this instance, as the nasal cavity of the specimen was matrix-filled, making any visual inspection of the relevant areas impossible. The presence of heavily permineralized bone and copious matrix also precluded standard radiography.

The results of the CT analysis are unequivocal; *Victoriapithecus* does not possess a maxillary sinus (Rae, et al., in press). The lack of this pneumatization in the Miocene monkey (Fig. 2) strongly supports the interpretation of the absence of the sinus in the last common ancestor of extant cercopithecoids, which in turn implies that the corresponding pneumatization in the maxilla of the genus *Macaca* has evolved convergently (Rae, et al., in press). These results will undoubtedly have profound effects on interpretations of both the function and phylogeny of sinuses in primates. The discovery of the re-emergence of the maxillary sinus in *Macaca* may also help to clarify the (?functional) selection pressures responsible for the initial appearance of cranial pneumatization, which are unclear at present (Witmer, 1997, 1999).

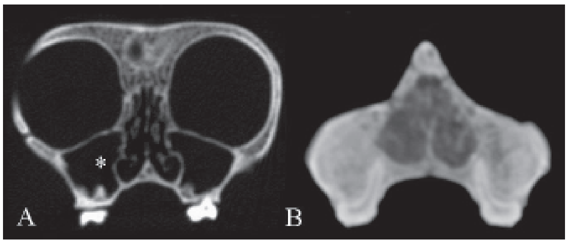

Figure 2 - Coronal CT scans (1mm) through M^2 of A) *Hylobates* (gibbon), and B) *Victoriapithecus*. In the gibbon, the maxillary sinus (*) can clearly be seen lateral of the nasal cavity proper, and separated from the nasal cavity by a wall of bone. In the fossil stem cercopithecoid, no maxillary sinus is present, and the same region consists entirely of spongy bone.

3D RECONSTRUCTION AND QUANTIFICATION

Results for studies of presence/absence characters can be achieved without reconstructing the specimens; visual inspection of the scans alone is necessary. This is not the case, however, if quantification and/or detailed shape information are required. Both the digital nature of CT data and the availability of commercial software packages for reconstruction/measurement have vastly improved the speed and accuracy with which detailed quantitative information can be obtained for characteristics previously unavailable for large scale study. This information can be used to test previous hypotheses based on qualitative assessments of internal cranial features, such as those of sinus volume.

Previous phylogenetic analyses of hominoid primates, or apes (including humans), have included the size of the maxillary sinus as a character supporting various arrangements of the extant and extinct members of the group (Andrews & Martin, 1987; Begun, 1992; Begun, et al., 1997; Harrison, 1987; Rae, 1997). In all, four separate scenarios have been advanced, advocating as few as zero and as many as two character state changes across ape evolution. Thus, a consensus on the pattern of evolution of cranial pneumatization in hominoids has failed to emerge from qualitative analyses, partially due to disagreement over the character state of individual taxa; for example, *Pongo* (the orang-utan) has been interpreted as having a moderately sized maxillary sinus, an expanded sinus, and a greatly expanded sinus (see Rae, 1999). One of the main barriers to such a consensus is that qualitative characters are difficult to interpret when confounding variables such as body size are present; extant hominoid taxa average from 5-125kg (Fleagle, 1999).

Again, new techniques of visualization and quantification can be used to test between competing hypotheses. In the case of ape sinus evolution, 3D reconstructions from CT scans can produce a quantitative evaluation of maxillary sinus volume which, when regressed against a body size indicator, provides an accurate, scaled assessment of the character state for the taxa concerned. The authors (Rae & Koppe, 2000b) performed such a test, using CT analysis of 44 adult dry crania representing all five extant hominoid genera. 3D virtual reconstructions of the crania were obtained using the ALLEGRO graphics workstation (ISG Technologies), and sinus volume was regressed against various measures (2D and 3D) of cranial size.

Contrary to most qualitative evaluations of hominoid maxillary sinus size, the quantitative data support no change across the group (Figure 3). Sinus volume is both highly and significantly correlated with cranial size, and scales isometrically with volumetric measures of the craniofacial skeleton (Rae & Koppe, 2000b).

In this case, 3D reconstruction allows the rejection of hypotheses of morphological change across a topology, and provides a more accurate, scaled character state delineation, both of which suggest that evolutionary trees constructed using maxillary sinus change in hominoids as supporting evidence must be critically re-evaluated. In turn, this may have a significant effect on the placement of fossil taxa, particularly where they have been allocated to clades based in part on the assumed homology of maxillary pneumatization (e.g., Begun, 1992).

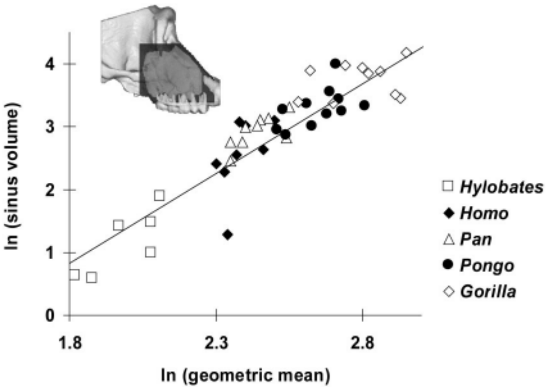

Figure 3 - 3D-CT-derived maxillary sinus volume regressed against size of the craniofacial skeleton ('geometric mean') in Hominoidea (apes, including humans). The 3D-CT reconstruction shown is an adult *Pan* (chimpanzee). Sinus size is significantly correlated with craniofacial size ($r = 0.89$, $p < 0.01$), and the slope of the reduced major axis regression line is not significantly different from isometry. The relationship suggests that no change in sinus volume has occurred in the evolution of extant hominoids. Adapted from Rae & Koppe (2000b).

GROWTH STUDIES

According to the functional matrix hypothesis (Moss & Young, 1960), the skull is thought of as a complex of different components with distinct functions. For each of these functions, such as chewing or respiration, particular functional cranial components have been identified. These components are morphological entities that consist of two parts: (1) the soft tissue that carries out a certain function, and (2) the skeletal unit that support and protect the functional matrix. It is important to consider that each of these skeletal units is characterized by a distinct growth pattern. Because it is held that the differences in the growth velocity of particular parts of the body may produce differences in the morphology of different species (Tanner, 1992), the appreciation of both the individual growth pattern of each of these skeletal units as well as the interaction among the skeletal units is required.

It has been suggested previously (Ward & Brown, 1986) that variation in skull pneumatization among primates, and especially the development of the maxillary sinus, is a function of body size / skull size. In contrast to hominoids and numerous New World monkeys, however, some species of the genus *Macaca* possess pneumatic spaces that are quite small for primates of their body / skull size (Koppe, et al., 1999c). One way to elucidate the differences in the skull pneumatization patterns between macaques and other groups of primates is to test whether the morphology as seen in adults is the result of distinct growth patterns. Therefore, we have used CT data of two cross-sectional series of skulls to compare the relative growth of the maxillary sinus of the Japanese macaque (*Macaca fuscata*) with that of the orang-utan (*Pongo pygmaeus*). Since the maxillary sinus develops via an epithelial recess from the nasal mucus membrane, we also tested whether the relationship between the maxillary sinus and the growing nasal cavity differs between these two species.

Maxillary sinus – The comparison of the two mixed-sex samples of dry crania (*M. fuscata*, $n = 30$; *P. pygmaeus*, $n = 40$) reveals that within a given species both male and female maxillary sinuses tend to grow according to a common growth pattern. Although both species are characterized by a distinct sexual size dimorphism in numerous parts of the skull (Masterson & Leutenegger, 1992; Mouri, 1994), sexual dimorphism in maxillary sinus volume is only observed in the orang-utan.

The comparison of the relative growth of the maxillary sinus of *M. fuscata* with that of *P. pygmaeus*, using basicranial length as a surrogate of skull size, indicates that the maxillary sinus of the orang-utan enlarged postnatally faster and over a longer period than that of the Japanese macaque (Figure 4a). This suggests that differences in the postnatal growth pattern may be responsible in part for the variation in the degree of skull pneumatization among primate species.

Nasal cavity - In primates, the nasal cavity serves mainly as an integrative part of the respiratory tract, and it has been suggested that the growth of the nasal cavity in humans is closely related to the development of the paranasal sinuses. Because little information is available about this association in nonhuman primates, we investigated the implication of the nasal cavity on the growth of the maxillary sinus in catarrhine primates. The CT scans of the skulls of the two cross-sectional series described above served were also used to calculate nasal cavity volume for *M. fuscata* and *P. pygmaeus*. Reduced major axis analysis was applied to describe the growth pattern of the nasal cavity volume and to investigate the relationship between the nasal cavity volume and maxillary sinus volume. In contrast to the differences in the degree of sexual dimorphism in sinus size *between* the species (see above), sexual dimorphism in nasal cavity volume is seen in both the orang-utan and the macaque.

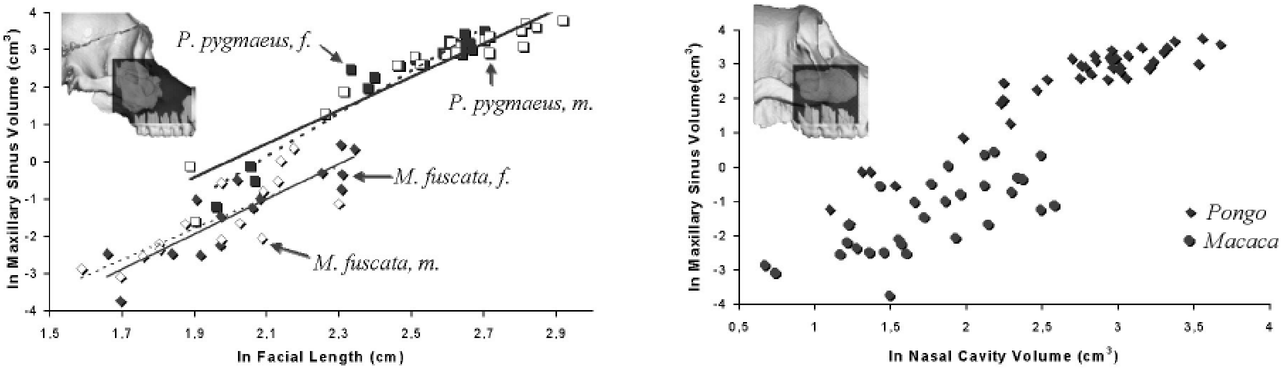

Figure 4 - A) Growth of the maxillary sinus in *Pongo pygmaeus* and *Macaca fuscata*. The trajectories of the growth curves are similar, although the orang-utan sinus grows at a faster rate and for longer than that of the macaque. The 3D-CT reconstruction pictured is an adult *Pongo*.
B) Relationship between growth in the nasal cavity and maxillary sinus in *P. pygmaeus* and *M. fuscata*. The regularity of this relationship, along with the differences seen in the growth of the sinus (A), suggests a common underlying mechanism. The 3D-CT reconstruction pictured is an adult *Macaca*.

In both *P. pygmaeus* and *M. fuscata*, maxillary sinus volume enlarged with a steeper slope than the nasal cavity volume. In contrast to maxillary sinus volume, however, the interspecies comparison (sexes were pooled) revealed no significant differences in the regression slopes of the nasal cavity volume. Although the growth rate of the maxillary sinus volume of *M. fuscata* was significantly less than that of the orang-utan, the two-tailed t-test indicated no significant differences for the relationship between the nasal cavity volume and the maxillary sinus volume (Figure 4b). The similarity in the growth rates of the maxillary sinus in *P. pygmaeus* and *M. fuscata* relative to the growth of the nasal cavity, and the disassociation of the growth of the maxillary sinus volume from that of the nasal cavity, suggests that the underlying mechanism for the development of paranasal pneumatization is similar among anthropoid primates. Notwithstanding that the maxillary sinus is closely associated to the nasal cavity, variation in size and shape of the maxillary sinus among primates is not related exclusively to respiratory function. Studies of different local populations of the Japanese macaque (Koppe, et al., 1999b) as well as studies in humans (Shea, 1977) suggest that epigenetic factors influence the final size and shape of the pneumatic spaces.

DISCUSSION

Because of the difficulties of visualizing and measuring internal structures, pneumatization of the mammalian cranium has remained a relatively unexplored area, despite the fact that sinus spaces were first described three and half centuries ago (Koppe, et al., 1999a). In the past, workers tended to rely on data derived from destructive methods, such as dissection, which limited the size of the data sets that could be obtained. Small sample size compromised even some standard radiographic evaluations of primate sinuses (Lund, 1988), from which misleading terms such as "lateral recess" (Rae & Koppe, 2000a) were derived. Even so, the efforts of Paulli (1900) and later Cave & Haines (1940) were considerable, though still not enough to generate the kind of momentum necessary for a substantial body of research to emerge.

As the studies outlined above make evident, the advent of 3D-CT marks a significant turning point in the study of the mammalian cranium. This has become apparent even in areas other than paranasal pneumatization, such as the study of the bony labyrinth of the ear (Spoor & Zonneveld, 1998). The potential for this method to address long-standing questions, such as the homology of the frontal sinus in anthropoid primates (Ward & Pilbeam, 1983) and the effect of environmental factors on sinus size (Shea, 1977) leaves little doubt that 3D-CT will continue to stimulate new study. Inevitably, our understanding of both the functional (Koppe, et al., 1999c) and phylogenetic (Rae, 1999) aspects of the heretofore hidden internal constitution of the cranium will increase as more researchers (e.g., Márquez, et al., 1997; Rossie, 2000) begin to apply these techniques and procedures.

The degree to which any new method is accepted in science is directly proportional to the number of hypotheses that can be tested and generated from its use. Thus, the application of novel approaches will inevitably result in the critical re-evaluation of previous work, and the development of new avenues of exploration. 3D-CT has already contributed a great deal to the scientific study of the mammalian skull, both analytically and clinically (e.g., Uchida, et al., 1998), and should continue to provide insights towards our understanding of the evolution of cranial pneumatization.

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