# Three-dimensional imaging of the maxillary sinus in anthropoid primates

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## Abstract

The maxillary sinus communicates with the middle meatus of the nasal cavity through a narrow ostium. In this report, I survey the variations in the maxillary sinus anatomy of extant and fossil anthropoids, which has been investigated with computed tomography. A sinus that pneumatizes the entire maxilla is shared by all extant hominoids. In contrast, extant cercopithecoids lack this sinus, with the exception of *Macaca*, which has a small sinus. Cercopithecoids have a maxillary body filled with cancellous bone, except *Papio* and *Theroputhecus*, who lack this cancellous region. Extant platyrrhines have varied forms of the maxillary sinus: a sinus that pneumatizes the entire maxilla occurs in the atelids, *Cebus*, and *Callicebus*; a sinus that pneumatizes the medial part of the maxilla occurs in the callitrichines and *Aotus*; a sinus and expanded inferior meatus that pneumatizes the entire maxilla occurs in *Pithecia*; and the sinus is absent in *Saimiri*, *Cacajao*, and *Chiropotes*. The sinus was lost independently in the *Saimiri* and *Cacajao-Chiropotes* clades, and in a common ancestor of the cercopithecoids. It is argued that a sinus that pneumatizes the entire maxilla is the primitive feature in the anthropoids. This hypothesis is supported by studies of fossil anthropoids. Such studies that are presented in this paper are expected to stimulate future studies of the variations in sinus anatomy in prosimians and other mammals. Such information will potentially facilitate further phylogenetic analyses of unclassified fossil anthropoids.

## Introduction

The paranasal sinuses are cavities within the facial cranium that communicate with the nasal cavity through a narrow ostium. The bony sinuses are lined with respiratory epithelium, extending from the nasal cavity through the ostium. Humans have four sinuses, the maxillary, frontal, sphenoidal, and ethmoidal sinuses, which predominantly pneumatize the bones of the same name. We are usually unaware of their presence, although in extreme cold, we often have a dull pain in the cheeks or head, which is caused by acute paranasal sinusitis –inflammation of the mucosa lining the sinuses. The maxillary sinus is one of the parts affected in chronic sinusitis, so-called maxillary empyema. However, the paranasal sinus
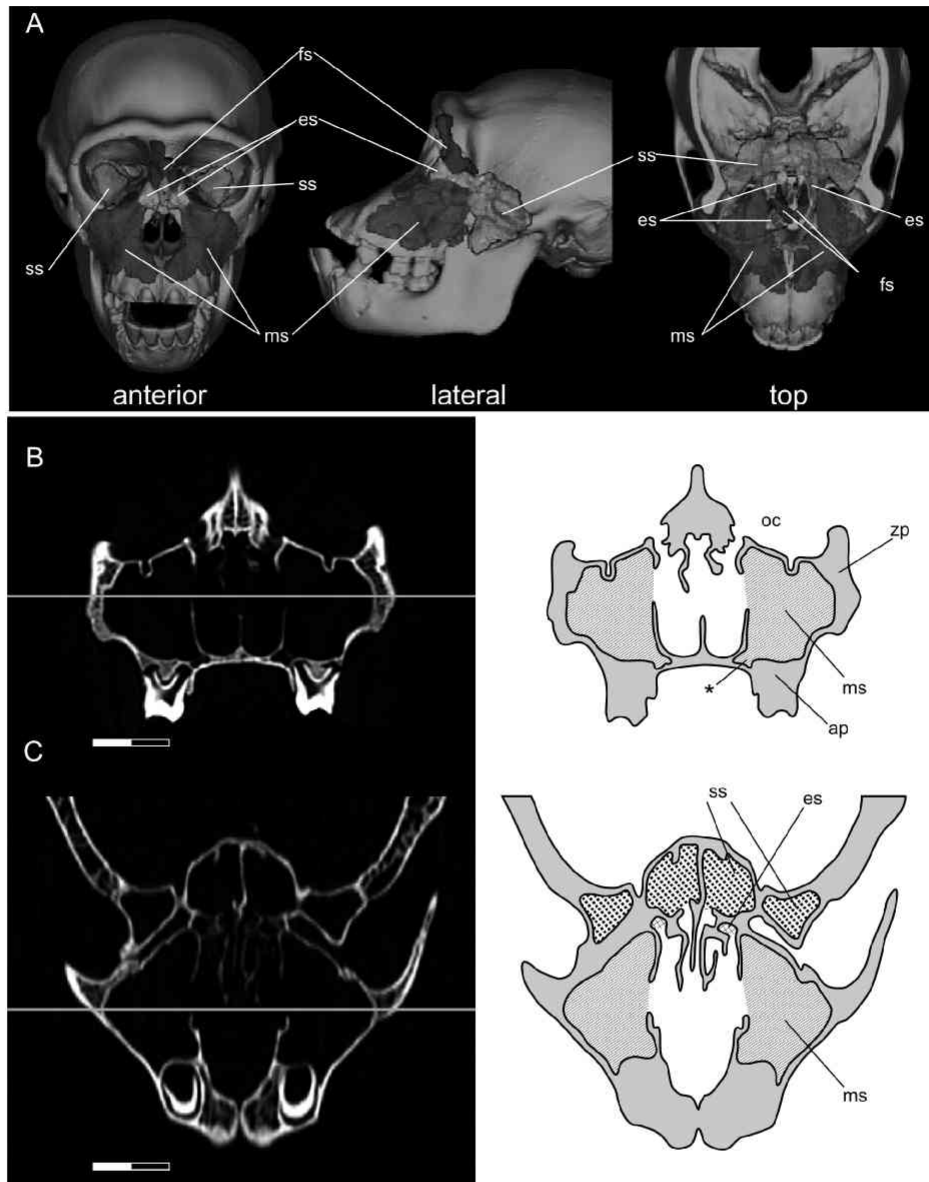
**Figure 1.** Three-dimensional reconstructed images, a coronal computer tomography (CT) image at the level of M[1], and a reformatted axial CT image in *Pan troglodytes*. **A**, the maxillary sinus (ms) pneumatizes the entire maxilla between the orbital floor and alveolar process, and the frontal (fs), ethmoidal (es), and sphenoidal (ss) sinuses pneumatize the bones of the same name, respectively. **B**, **C**, Although this animal shows no confluent sinus, great apes often show such a sinus, which is formed by the resorption of the bony boundary between the maxillary, ethmoidal, sphenoidal and frontal sinuses. The maxillary sinus expanded to the palatine bone (*). Scale in centimeters. Abbreviations: ap, alveolar process; oc, orbital cavity; zp, zygomatic process.

*per se* is well known in scientific fields, and its functions have been debated, for example, in terms of its physiology or the structural mechanics of the facial cranium (Blanton and Biggs, 1969; Witmer, 1997; Rae and Koppe, 2004). Such information facilitates the discussion of the functional adaptations and selective advantages of the various paranasal sinuses. However, sinus functions are highly controversial, and little evidence is available because of the technical limitations involved. On the other hand, improvements in imaging techniques have allowed advances in studies of the variations in the three-dimensional anatomy (including presence or absence) of the paranasal sinuses in primates. These advances have recently
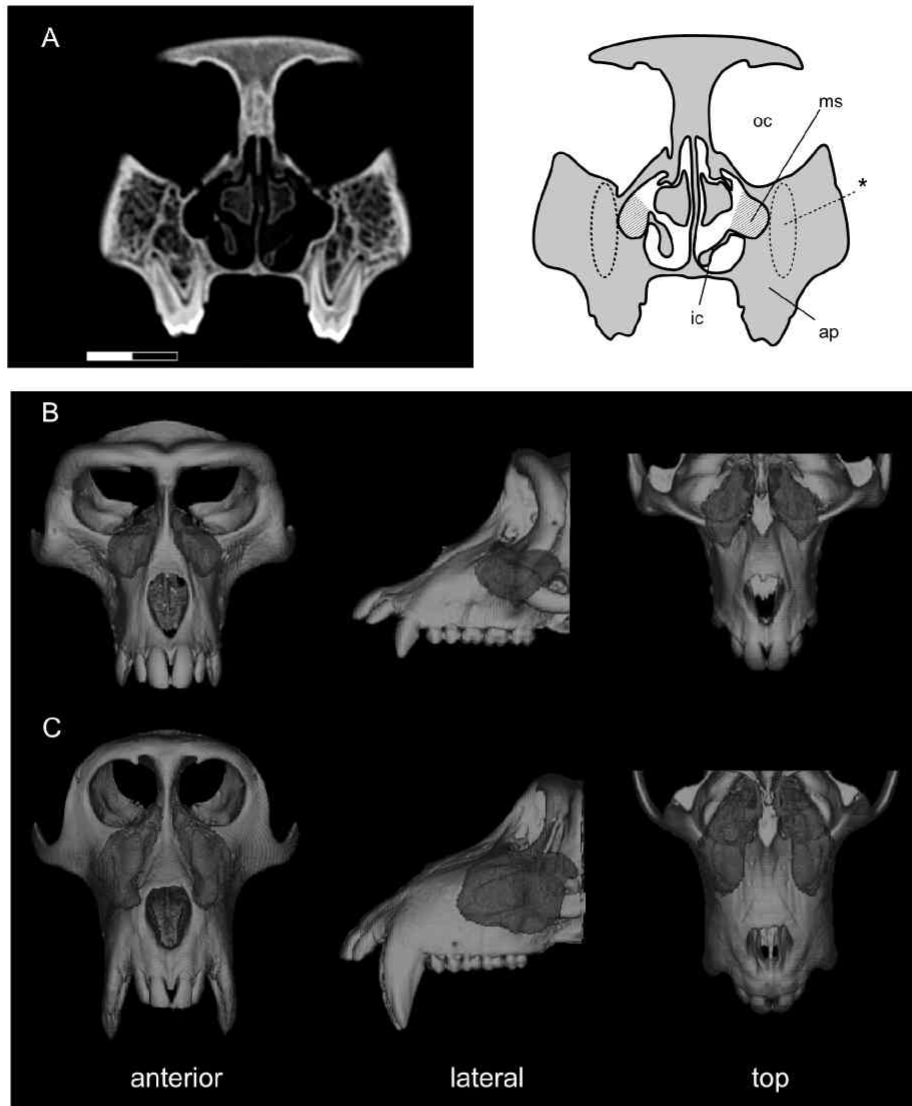
**Figure 2.** Coronal CT images at the level of M$^2$ and three-dimensional reconstructed images of *Macaca*. **A**, *Macaca fuscata* has a small maxillary sinus; the maxillary sinus (ms) pneumatizes the medial restricted part of the maxilla, and the cancellous bones (*) occupy the lateral half. **B**, *Macaca nigra* has a small maxillary sinus; the maxillary sinus (dark grey) pneumatizes the restricted part of the maxilla, and cancellous bones occupy the lateral half of the maxilla and the region of the maxillary tuberculum. **C**, *Macaca nemestrina* has a relatively large maxillary sinus in the genus; the maxillary sinus expands to the lateral wall of the maxilla, but cancellous bones occupy the region of the maxillary tuberculum. Scale in centimeters. Abbreviations: ap, alveolar process; ic, inferior concha; oc, orbital cavity.

received considerable attention, because these data are potentially applicable to phylogenetic analyses, the identification of unclassified fossil primates, and systematic analyses.

The inner structure of the facial cranium, including the paranasal sinuses, has been examined using sectioned crania or X-ray photos (de Beer, 1937; Cave and Haines, 1940; Cave, 1967; Negus, 1958; Hershkovitz, 1977; Lund, 1988; Swindler, 1999). The traditional methods of investigating three-dimensional anatomy are limited by the unavailability of large samples or difficulties in the detection of targeted structures. In recent decades, medical imaging techniques, such as computer tomography (CT) and magnetic resonance imaging (MRI), and the software for the anatomical analyses of the tomographic images provided
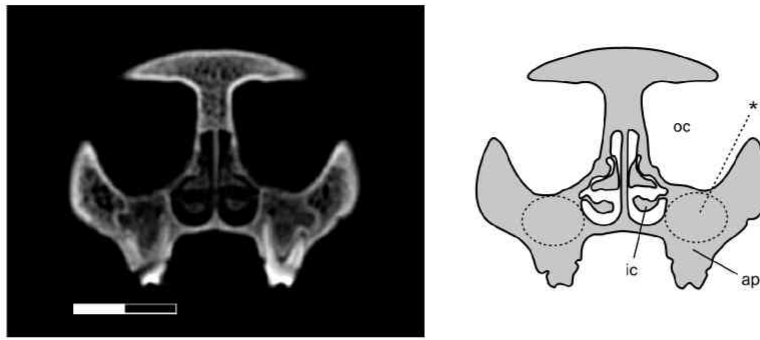
**Figure 3.** A Coronal CT image at the level of M$^2$ in an adult male of *Chlorocebus aethiops*. The maxillary body is filled with cancellous bone (*) in non-macaque cercopithecines, excluding baboons. Scale in centimeters. Abbreviations: ap, alveolar process; ic, inferior concha; oc, orbital cavity.

by these instruments, have been introduced into primatology. They have facilitated the nondestructive three-dimensional examination of inner bony structures using large samples (Nishimura *et al.*, 1999). In this way, our knowledge of the morphological variation in the paranasal sinuses of primates has been increasing, especially in the anthropoid primates.

In paleoprimatology, most of the studies concerning the paranasal sinuses focus on the morphological variation in the maxillary sinus and its phylogenetic significance (Rae, 1999; Rae and Koppe, 2004; Rossie, 2005). The maxillary sinus is found in many groups of mammals (Paulli, 1900; Moore, 1981; Novacek, 1993; Rae and Koppe, 2004), and it was probably present in the last common ancestor of the eutherians (Novacek, 1993). It usually occupies the maxilla, superior to the orbital cavity and inferior to the alveolar processes of the cheek teeth. Fragmented or rarely complete maxillae of fossil primates are discovered relatively often, together with the dentition, and these specimens potentially provide valuable information about maxillary sinus morphology. In recent decades, CT has been used to scan the inner structures (such as the brain capacity, teeth, or inner ear) of fossil primates, including humans (e.g., Conroy and Vannier, 1984; Conroy *et al.*, 1998; Silcox, 2003; Kunimatsu *et al.*, 2004). Knowledge of the morphological variation of the maxillary sinus and its phylogenetic significance is expected to facilitate the phylogenetic analysis of enigmatic fossil primates in the future.

This paper begins with a brief description of the anatomy and definitions of the maxillary sinus. I then survey the variation in the three-dimensional morphology of this sinus and its phylogenetic significance in extant and fossil anthropoid primates. Finally, the potential utility of the maxillary sinus in the phylogenetic analyses of fossil primates is discussed, together with other issues that are yet to be resolved.

## Maxillary sinus

The maxillary sinus had been defined as a paranasal sinus occupying the maxilla. However, in cladistics, the characters used for phylogenetic analysis must be defined to ensure interspecies homology. The homology of a feature is determined by its homologous
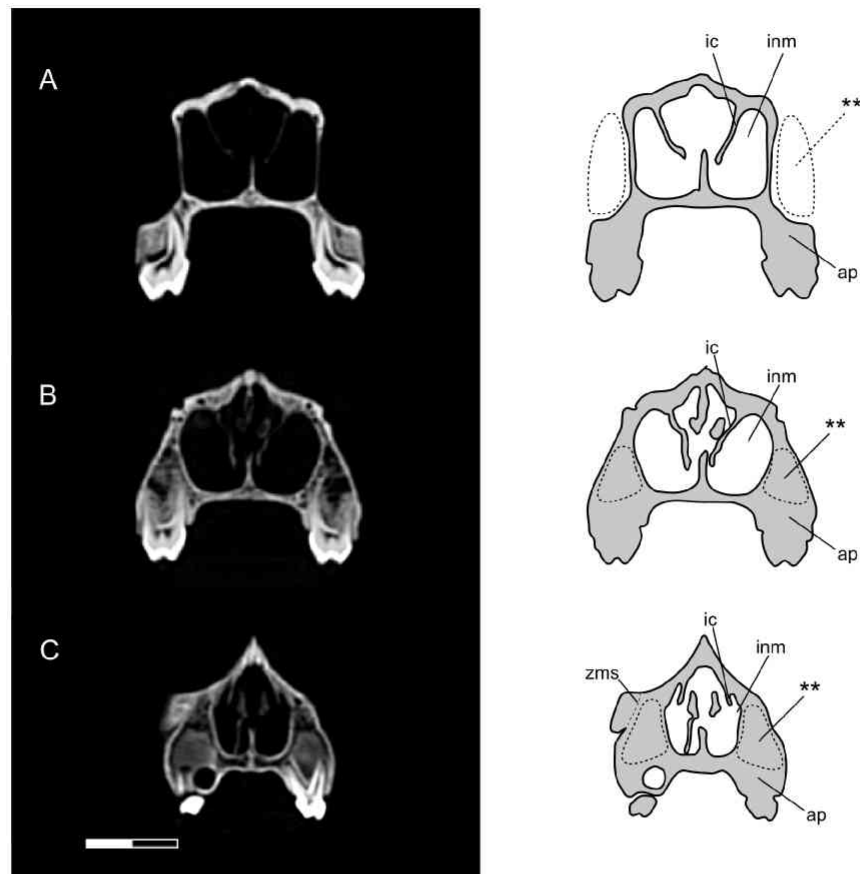
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**Figure 4.** Coronal CT images in *Papio hamadryas*. **A**, at the level of $M^2$ in a sub-adult male. The cancellous space (dotted-lining area) is lacked in the maxillary body superior to the alveolar process (ap), and the alveolar processes of the molars lie outside the rostrums, producing a distinctive maxillary fossa (*) The inferior nasal meatus (inm) occupies a substantial region in the lateral part of the nasal cavity. **B**, at the level of $M^1$ in a juvenile male. The inferior nasal meatus occupies a substantial region in the lateral part of the nasal cavity, but the cancellous bones occupy the region superior to the alveolar process (**). **C**, at the level of $P^4$ in a young juvenile female. This animal has the cancellous region seen in all other cercopithecids except the macaques (**). Scale in centimeters. Abbreviation: zms, zygomaxillary suture.

developmental origin and subsequent developmental patterns, not by similarities in its shape and situation in the adult. In this section, I provide a brief description of the development of the maxillary sinus, the precise definition of this sinus, and the conventional definition used for its identification in extant and fossil specimens.

## Development of the maxillary sinus

The paranasal sinus develops through the primary and secondary pneumatization of the nasal accessory cartilage and the bony elements surrounding the nasal cavity, respectively (de Beer, 1937; Moore, 1981; Moss-Salentijn, 1991; Weiglein, 1999; Witmer, 1999; Maier, 2000). Primary pneumatization occurs principally in the fetal period, and secondary pneumatization occurs in the postnatal to adolescent periods (Crelin, 1976; Spaeth *et al.*, 1997; Weiglein, 1999).

The maxillary sinus develops prenatally as a small epithelial diverticulum in the maxillary recess, a part of the cartilaginous nasal capsule in the region homologous to the

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adult middle meatus. (*Note*: This maxillary recess was named after the maxillary sinus that develops from it, but this feature itself is defined independently of the maxillary sinus and maxilla.) This primary pneumatization is probably shared by all mammalians, regardless of the presence or absence of the maxillary sinus in the adult (Rossie, 2003, 2006).

After the primary pneumatization, the diverticulum postnatally invades the region in which the cancellous bones of the bony elements neighboring the maxillary recess (usually the maxilla) are resorbed. This process is the secondary pneumatization. In the secondary pneumatization, the expansion of this sinus is achieved through the resorption of the cancellous bones by osteoclasts that line the exterior surface of the epithelial diverticulum (de Beer, 1937; Witmer, 1997). This fact suggests that the secondary pneumatization is triggered by the contact of the epithelial diverticulum lining the maxillary recess with the cancellous region of the bone neighboring the maxillary recess though an ostium, *viz.* a region that is not ossified to form the bony wall of the compact bones (Rossie, 2003, 2006). Although the genetic and physiological foundations of secondary pneumatization remain unclear, the maxillary sinus probably varies in shape or is lost as the result of modifications to these foundations, e.g., differences in the distribution of osteoclasts and osteoblasts on the external surfaces of epithelial diverticula, or the formation of compact bones that prevent such contact.

**Definitions of the maxillary sinus**

Based on the development of the maxillary sinus, it is defined in precise homology-based terms: the maxillary sinus is a paranasal sinus formed by the invasion of the epithelial diverticulum lining the maxillary recess into the region in which the cancellous bones of the bone neighboring the maxillary recess are resorbed (Cave 1967; Maier, 2000; Rossie, 2003, 2006). Therefore, even if this diverticulum invades bones other than the maxilla, the product is called a 'maxillary sinus' (*Note*: No such a maxillary sinus has been found elsewhere).

The maxillary sinus is identified in extant species in this sense, based on the determination of its developmental origin and patterns. However, in most studies, this sinus has been conventionally identified by its ostium opening to the middle nasal meatus and not to any other space, because this ostium marks the site from which secondary pneumatization begins (Cave and Haines, 1940; Cave, 1967; Koppe and Ohkawa, 1999; Rae and Koppe, 2003). This criterion has been adopted in paleoprimatological studies (Rae *et al.*, 2002; Rossie *et al.*, 2002; Rossie, 2005). In future, the feature defined by this criterion may be identified as another sinus or feature. However, in this paper, I survey the anatomical variation in the maxillary sinus, defined by this criterion in the literature, unless otherwise specified.

**Morphological variation in the maxillary sinus in anthropoids**

There are few studies of the variation in maxillary sinus anatomy of prosimians, including tarsiids (Kollmann and Papin, 1925; Negus, 1958). In contrast, the varied anatomy

of this sinus, including its presence or absence, is recognized in anthropoids. This variation depends on modifications both to the process of secondary pneumatization, and to the morphology of the surrounding bony elements. Here, the features of the three-dimensional anatomy of the maxillary sinus are surveyed in hominoids, cercopithecoids, and platyrrhines. The factors producing these features are then discussed for each group.

## Maxillary sinus in hominoids

The extant members of Hominoidea consists of two families (Table 1), Hominidae including humans, *Pan*, *Gorilla*, and *Pongo*, and Hylobatidae including *Hylobates*, *Nomascus*, *Bunopithecus*, and *Symphalangus*. In humans, the maxillary sinus pneumatizes the entire maxilla to occupy a space between the orbital floor and the alveolar processes of the premolars and molars (Crelin, 1976; Spaeth *et al.*, 1997; Weiglein, 1999). This is the case in all extant apes (Figure 1; Cave and Haines, 1940; Cave, 1967; Koppe and Ohkawa, 1999; Rae and Koppe, 2000).

In hominoids, including humans, the maxillary sinus often invades the alveolar process and zygomatic process, and expands to pneumatize the neighboring frontal and palatine bones (Cave and Haines, 1940; Koppe and Ohkawa, 1999). The volume of this sinus is believed to differ among *Pan*, *Gorilla*, and *Pongo* (Ward and Kimbel, 1983; Groves, 1986; Ward and Brown, 1986; Begun, 1992; Gebo *et al.*, 1997; Ward, 1997). However, a CT study of the volume of this sinus provided no evidence for this supposition (Rae and Koppe, 2000). Although there are few instances in humans, hon-human hominids often show a large confluent sinus expanding within the maxillary, ethmoidal, sphenoidal, and frontal bones in older subjects, which is formed by the resorption of the bony boundary between the maxillary, ethmoidal, sphenoidal and frontal sinuses (including an extension into the frontal bones of the maxillary sinus) (see Figure 1; Cave and Haines, 1940; Koppe and Ohkawa, 1999).

Thus, despite slight differences in anatomy, all hominoids have a maxillary sinus that pneumatizes the entire maxilla, and their maxillary sinuses *per se* show few differences between species.

## Loss of the maxillary sinus in cercopithecoids excluding *Macaca*

Cercopithecidae are generally classified as in Table 1, according to the results of molecular biological studies (Disotell, 1996, 2000). The subtribe Macacina includes only the genus *Macaca*, and the subtribe Papionina comprises such genera as *Papio* (baboons) and *Cercocebus* (mangabeys). The two subtribes constitute the tribe Papionini. No maxillary sinus is found in cercopithecoids, except for *Macaca* (Paulli, 1900; Koppe and Ohkawa, 1999; Rae and Koppe, 2003).

*Macaca* are unique among cercopithecoids in having a maxillary sinus. In contrast to hominoids, their maxillary sinus pneumatizes a restricted region of the maxilla (Figure 2;

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**Table 1.** The classification of anthropoids. From Harada *et al.* (1995), Disotell (1996, 2000), Schneider *et al.* (1996), Barroso *et al.* (1997), Horovitz *et al.* (1998), von Dornum and Ruvolo (1999), and Canavez *et al.* (1999).

Infradorder Catarrhini
    Superfamily Hominoidea
        Family Hominidae
        Family Hylobatidae
    Suferfamily Cercopithecoidea
        Family Cercopithecidae
            Subfamily Cercopithecinae
                Tribe Cercopithecini
                Tribe Papionini
                    Subtribe Macacina
                    Subtribe Papionina
            Subfamily Colobinae
Infraorder Platyrrhini
    Superfamily Ceboidea
        Family Cebidae
            Subfamily Callitrichinae
            Subfamily Cebinae
            Subfamily Aotinae
        Family Pithecidae
            Subfamily Pitheciinae
            Subfamily Callicebinae
        Family Atelidae
            Tribe Atelini
            Tribe Alouattini

Koppe and Ohkawa, 1999; Koppe *et al.*, 1999a). The sinus extends to the level of the molars, but cancellous bones occupy the region of the maxillary tuberculum (most posterior part of the maxilla) (Figure 2A, B). The maxillary sinus expands laterally to the medial half of the maxilla, and the cancellous bones occupy the lateral half in many species (Figure 2A, B), although the sinus expands to the lateral wall of the maxilla in some species (e.g., *Macaca nemestrina;* Figure 2C; Koppe and Ohkawa, 1999). It is unclear why the entire maxilla is not pneumatized in *Macaca*, despite a lack of physical obstacles such as morphological modifications to the maxilla or its surrounding bony elements (Koppe and Nagai, 1997; Koppe *et al.*, 1999b). Such a configuration may have resulted from a modification to the process of secondary pneumatization, such as a decrease in osteoclasts or an increase in osteoblasts on the external surface of the sinus epithelium during pneumatization.

No other cercopithecoids have a maxillary sinus, so the cancellous bones occupy the entire maxilla in these species (Figure 3; Koppe and Ohkawa, 1999; Rae *et al.*, 2002; Rae and Koppe, 2003). There is no obstacle between the middle nasal meatus and the cancellous region of the maxilla, excluding the bony medial wall (compact bones) of the maxilla. This suggests that the compact bones are ossified to form this bony wall before the resorption of the cartilaginous maxillary recess. This modification precludes the formation of the ostium that allows contact between the epithelial diverticulum of the maxillary recess and the

cancellous bones of the maxilla.

Among cercopithecoids with no maxillary sinus, *Papio* and *Theropithecus* are unique in having a negligible cancellous region in the maxilla (Figure 4A; Koppe and Ohkawa, 1999). Their nasal cavity occupies the entire snout, extending laterally to the lateral wall of the snout and to the zygomaxillary suture. Their inferior meatus occupies a substantial region in the lateral part of the nasal cavity, and the inferior concha extends from the superior part of the nasal lateral wall (Koppe and Ohkawa, 1999; Rossie, 2006). Although subadult subjects also show a negligible cancellous region in the maxilla (Figure 4A), younger subjects have the cancellous region seen in all other cercopithecoids except *Macaca* (Figure 4B, C). This indicates that the cancellous bones are resorbed in the juvenile to adolescent periods in *Papio* and *Theropithecus*. This feature may be associated with the enlargement of the inferior meatus into the region in which the cancellous bone of the maxilla is resorbed. However, this feature is associated with a unique configuration of the alveolar processes of the molars, which grow to lie outside the rostrums, producing a distinctive maxillary fossa (Figure 4). This means that the resorption of the cancellous bone results in a narrow rostrums relative to the width of the dentition. This preliminary finding suggests that the maxillary cancellous region is lost and is not invaded by the inferior meatus in this group. Although the adaptive advantages are unclear, this loss may be related to the skull strength associated with the long faces of this group (Preuschoft *et al.*, 1986) or may conserve the bony volume in their uniquely long rostrums.

Thus, cercopithecoids have no or a small maxillary sinus, in contrast to that of the hominoids. This variation is probably attributable to modifications in the pneumatization processes that form the maxillary sinus, but not to physical obstacles caused by anatomical modifications to the surrounding bony elements.

## Varied maxillary sinuses in platyrrhines

The phylogenetic relationships among the platyrrhine genera have been the subject of debate (e.g., Schneider and Rosenberger, 1996). Based on molecular biological studies (Harada *et al.*, 1995; Schneider *et al.*, 1996; Barroso *et al.*, 1997; von Dornum and Ruvolo, 1999; Canavez *et al.*, 1999) and incorporating morphological data (Horovitz *et al.*, 1998), the updated classification of platyrrhines is shown in Table 1. Atelids and pitheciids are more closely related to each other than to cebids. In the subfamily Pitheciinae, *Cacajao* and *Chiropotes* are more closely related to each other than to *Pithecia*. *Saimiri* in the subfamily Cebinae, *Cacajao*, and *Chiropotes* lack a maxillary sinus, but all other platyrrhines have this sinus (Koppe *et al.*, 2005; Nishimura *et al.*, 2005; Rossie, 2006). The maxillary sinuses of this group are more varied than those of the catarrhines (Nishimura *et al.*, 2005).

The entire maxilla is pneumatized by the maxillary sinus in the atelids, *Cebus* (subfamily Cebinae), and *Callicebus* (subfamily Callicebinae), as in the hominoids (Figures 5, 6; Nishimura *et al.*, 2005; Rossie, 2006). In some subjects, the sinus invades the alveolar or
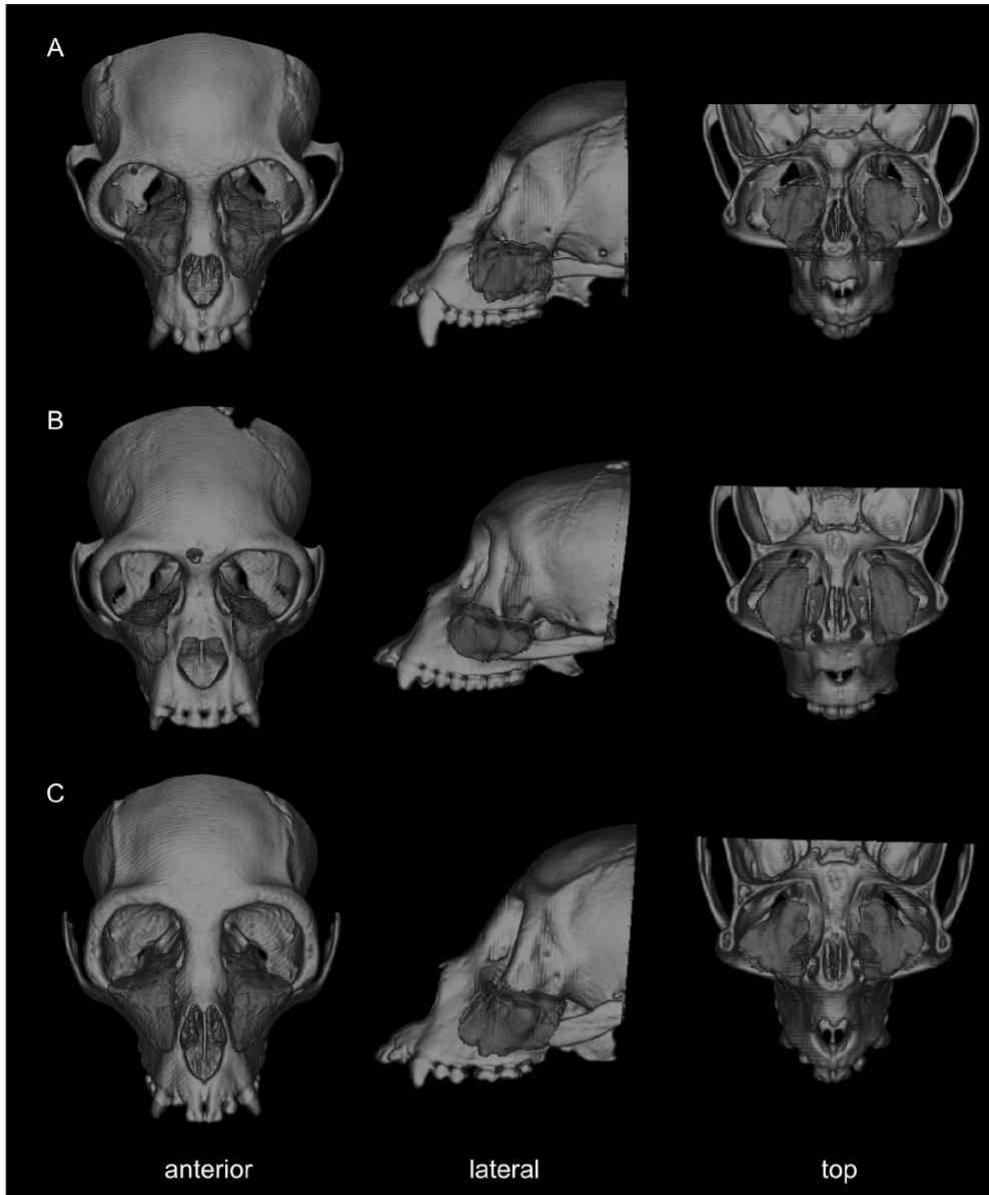
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**Figure 5.** Three-dimensional reconstructed images of crania indicating the maxillary sinus pneumatizing the entire maxilla between the orbital floor and alveolar process. The maxillary sinus is indicated in colored dark grey. **A**, *Ateles geoffroyi*; **B**, *Lagothrix lagotricha*; **C**, *Brachyteles arachnoides*; **D**, *Callicebus moloch*; **E**, *Cebus apella*. Not to scale.

zygomatic processes, and expands to the neighboring palatine or frontal bones. In *Alouatta* (tribe Alouattini), the maxillary sinus is confluent with the neighboring sinuses, including the ethmoidal and sphenoidal sinuses, to form a large confluent sinus, as seen in some non-human hominids (Figure 6; Koppe *et al.*, 2005; Nishimura *et al.*, 2005; Rossie, 2006).

In the callitrichines and *Aotus* (subfamily Aotinae), the maxillary sinus pneumatizes only the medial part of the maxilla (Figure 7; Nishimura *et al.*, 2005; Rossie, 2006). Although the sinus rarely expands to reach the maxillary tuberculum, it pneumatizes the maxilla at the level of the molars. In *Aotus* and smaller callitrichines (*Cebuella* and *Callithrix*; Smith and Jungers, 1997), the orbital floor approximates the alveolar processes of the premolars
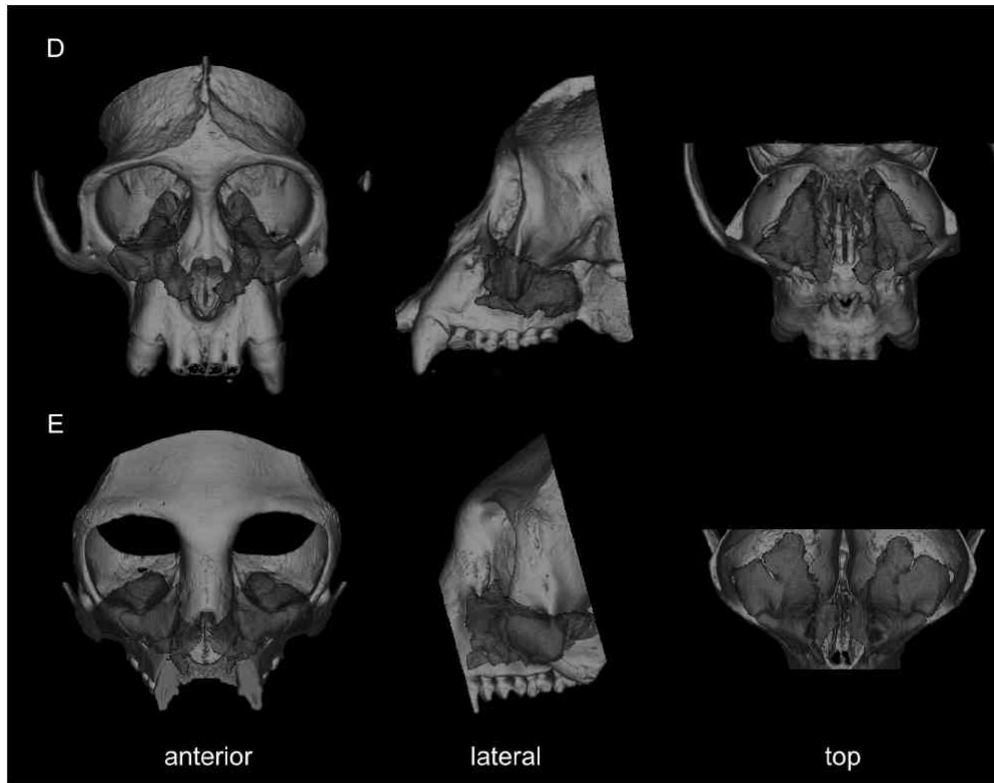
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**Figure 5 (continued).** Three-dimensional reconstructed images of crania indicating the maxillary sinus pneumatizing the entire maxilla between the orbital floor and alveolar process. The maxillary sinus is indicated in colored dark grey. **D**, *Callicebus moloch*; **E**, *Cebus apella*. Not to scale.

and molars, resulting in little space in the lateral half of the maxilla (Nishimura *et al.*, 2005; Rossie, 2006). Thus, there is little space into which the maxillary sinus might invade. In contrast, the larger callitrichines (*Saguinus* and *Leontopithecus*; Smith and Jungers, 1997) have a sinus that expands to the lateral half of the maxilla, between the orbital floor and the alveolar processes of the molars (Rossie, 2006). However, in most larger callitrichines, this space is narrow, so the sinus reaches the level of the medial roots of the molars (Nishimura *et al.*, 2005; Rossie, 2006).

The way of the maxillary pneumatization in *Pithecia* is unique among anthropoids; the entire maxilla is pneumatized by both the maxillary sinus and another cavity that expands from the inferior meatus (Figure 8; Nishimura *et al.*, 2005). Although neonate animals exhibit little pneumatization beyond the region of the maxillary recess, there is an evidence for secondary pneumatization by the maxillary sinus in young juvenile animals. However, even at later developmental stages, the lateral parts of the maxilla are filled with cancellous bone. In the juvenile to adult periods, another cavity rapidly expands from the inferior meatus to occupy the anterolateral part of the maxilla. This cavity physically restricts the further expansion of the maxillary sinus. Thus, the maxillary sinus expands to occupy the posteromedial part of the maxilla in the adult.

Among the platyrrhines with no maxillary sinus, *Cacajao* have an inferior meatus that extends superiorly to reach the orbital floor, and occupies the area between the middle meatus
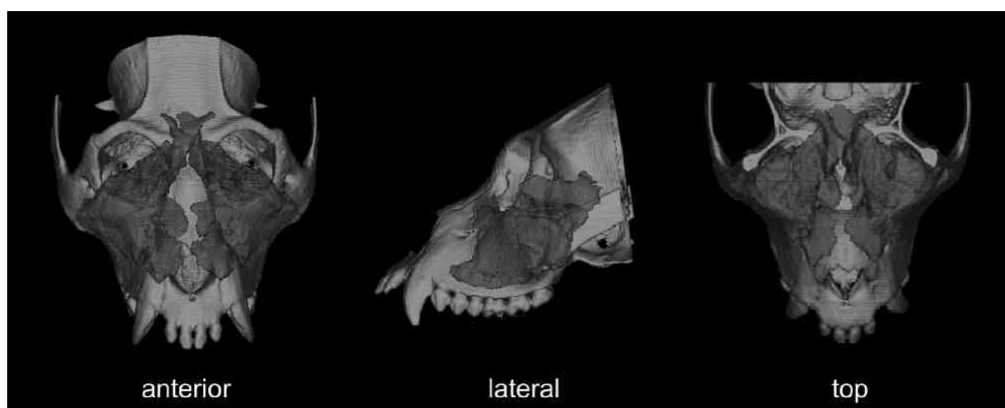
**Figure 6.** Three-dimensional reconstructed images of crania indicating the maxillary sinus confluent with the other sinuses in *Alouatta caraya*. The maxillary sinus occupies the entire maxilla between the alveolar process and orbital cavity and is confluent with the ethmoidal and sphenoidal sinuses. The confluent sinuses are colored dark grey.

and the maxilla (Figure 9A; Nishimura *et al.*, 2005; Rossie, 2006). This feature is known as an 'expanded inferior meatus' (Rossie, 2006), and physically precludes contact between the maxillary recess and the cancellous region of the maxilla. This may also be the case in *Chiropotes* (Nishimura *et al.*, 2005). In contrast, *Saimiri* have no obstacle between the middle meatus and the maxilla during growth (Figure 9B; Rossie, 2006). Although the maxillary recess maintains contact with the maxilla, no maxillary sinus develops in this animal. This is probably caused by similar modifications to the processes of secondary pneumatization as are observed in cercopithecoids, excluding *Macaca* (Rossie, 2006).

Thus, the anatomy of the maxillary sinus varies in platyrrhines, depending on the species. This variation possibly resulted from modified processes of secondary pneumatization, as seen in the hominoids and cercopithecoids, and by the physical obstruction of modified bony elements surrounding the maxilla. These obstacles include the proximity of the orbital floor and alveolar process in the callitrichines and *Aotus*, a second cavity expanding from the inferior meatus into the maxilla in *Pithecia*, and the expanded inferior meatus in *Cacajao* and *Chiropotes*. These obstructions modify or prevent maxillary sinus development. Thus, platyrrhines display various factors that cause wide variation in the anatomy of the maxillary sinus compared with that of the hominoids and cercopithecoids.

## Phylogeny of the maxillary sinus anatomy of anthropoids

Figure 10 summarizes the variation in maxillary sinus anatomy in the anthropoids. It shows the varied anatomy of this group and the similar features that occur independently in some separate lineages. Various physiological or morphological factors have produced this anatomical variation. In this section, the phylogenetic significance of the anthropoid maxillary sinus is discussed, taking these factors into consideration. The maxillary sinuses of fossil primates are then surveyed to test this hypothesis. Lastly, the potential utility of maxillary sinus anatomy in the phylogenetic analysis of enigmatic fossil anthropoids is discussed, together with related issues that are yet to be resolved.

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## Derived feature of the maxillary sinus

Among the anthropoids, cercopithecoids (excluding *Macaca*), *Saimiri*, and *Cacajao-Chiropotes* lack a maxillary sinus. Different evolutionary processes have probably contributed independently to this loss in cercopithecoid, *Saimiri*, and *Cacajao-Chiropotes* lineages. In the *Cacajao-Chiropotes* lineage, an expanded inferior meatus physically prevents the initiation of secondary pneumatization (1' in Figure 10; Nishimura *et al.*, 2005; Rossie, 2006). In contrast, in cercopithecoid and *Saimiri* lineages, the compact bones probably ossify fully to form a bony wall between the maxillary recess and the cancellous region of the maxilla. This bony wall prevents the epithelial diverticulum contacting the cancellous bones of the maxilla, resulting in a failure of secondary pneumatization (2' and 2" in Figure 10; Rossie, 2003; 2006). Phylogenetically, the two lineages are distantly related and, consequently, the genetic or physiological foundations of these processes may be nonhomologous. Even if this is true, the maxillary sinus was lost independently in these three lineages, because the sinus is common to all other lineages of the anthropoids (Koppe and Ohkawa, 1999; Rae, 1999; Rossie, 2003, 2006; Nishimura *et al.*, 2005).

Among cercopithecoids, *Macaca* species are unique in having a maxillary sinus. Their sinus does not pneumatize the entire cancellous region of the maxilla, despite the lack of any physical obstacle. The maxillary sinus of macaques may be nonhomologous to those of all other anthropoids. Briefly, they may be independent in genetic terms (Rossie, 2003). This issue requires further study. However, many scholars support the idea that the maxillary sinus was lost in a common ancestor of cercopithecoids, although the genetic foundations of secondary pneumatization were retained in this group. These were expressed again, so that the maxillary sinus was reacquired in an ancestor of *Macaca* (3 in Figure 10; Koppe and Ohkawa, 1999; Rae, 1999).

*Pithecia* has a maxillary sinus, in contrast to their phylogenetic relatives, *Cacajao* and *Chiropotes*. The cavity that expands from the inferior meatus into the maxilla in *Pithecia* may be homologous to the expanded inferior meatus in *Cacajao* (and probably that in *Chiropotes*), despite differences in form. If this is true, the expanded inferior meatus is one of the derived features shared by the pitheciines (1 in Figure 10; Nishimura *et al.*, 2005). Evolutionary diversification may have caused the inferior meatus to expand superiorly, precluding secondary pneumatization in the *Cacajao-Chiropotes* lineage (1' in Figure 10; Nishimura *et al.*, 2005; Rossie, 2006) and to expand laterally to pneumatize the maxilla in the *Pithecia* lineage (1" in Figure 10; Nishimura *et al.*, 2005), although the primitive structure and the functional reasons behind this diversification are unclear.

In many callitrichines and *Aotus*, the orbital floor approximates to the alveolar process, and this situation physically precludes the expansion of the maxillary sinus into the lateral half of the maxilla. However, this physical obstacle probably arose independently in both lineages, under different evolutionary processes (Nishimura *et al.*, 2005). Morphological
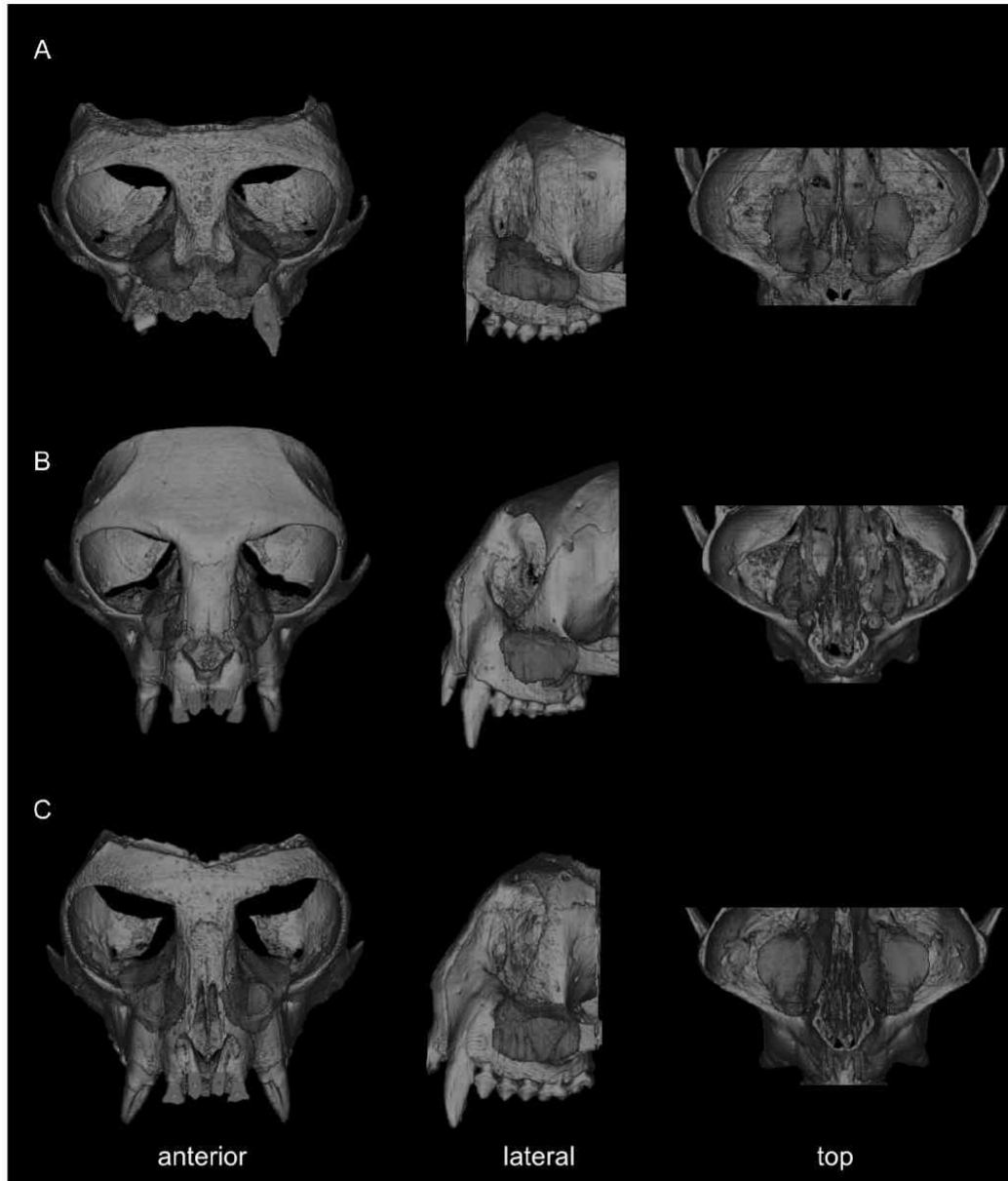
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**Figure 7.** Three-dimensional reconstructed images of the cranium indicating the restricted maxillary sinus. The maxillary sinus is colored dark grey. **A**, *Callimico goeldii*; **B**, *Saguinus labiatus*; **C**, *Leontopithecus rosalia*; **D**, *Callithrix jacchus*; **E**, *Cebuella pygmaea*; **F**, *Aotus trivirgatus*. Not to scale.

and behavioral features of extant and fossil platyrrhines indicate that callitrichines are 'phyletic dwarfs', in that a general reduction in body size appeared in this group as a derived characteristic (Kinzey *et al*., 1975; Ford, 1980; Sussman and Kinzey, 1984; Levitch, 1987; Plavcan and Gomez, 1993; Kay, 1994). In primates, there is a negative allometric relationship between orbital and body sizes; smaller species have larger orbits relative to their body (or cranial) size (Schultz, 1940; Kay and Kirk, 2000). This suggests that phyletic dwarfism produced the relatively larger orbits of callitrichines (4 in Figure 10; Nishimura *et al*., 2005). The eye anatomy and behavior of owl monkeys reflect the diurnal ancestry of this group; the reacquisition of extremely large eyes is associated with a nocturnal habitat (5 in Figure 10;
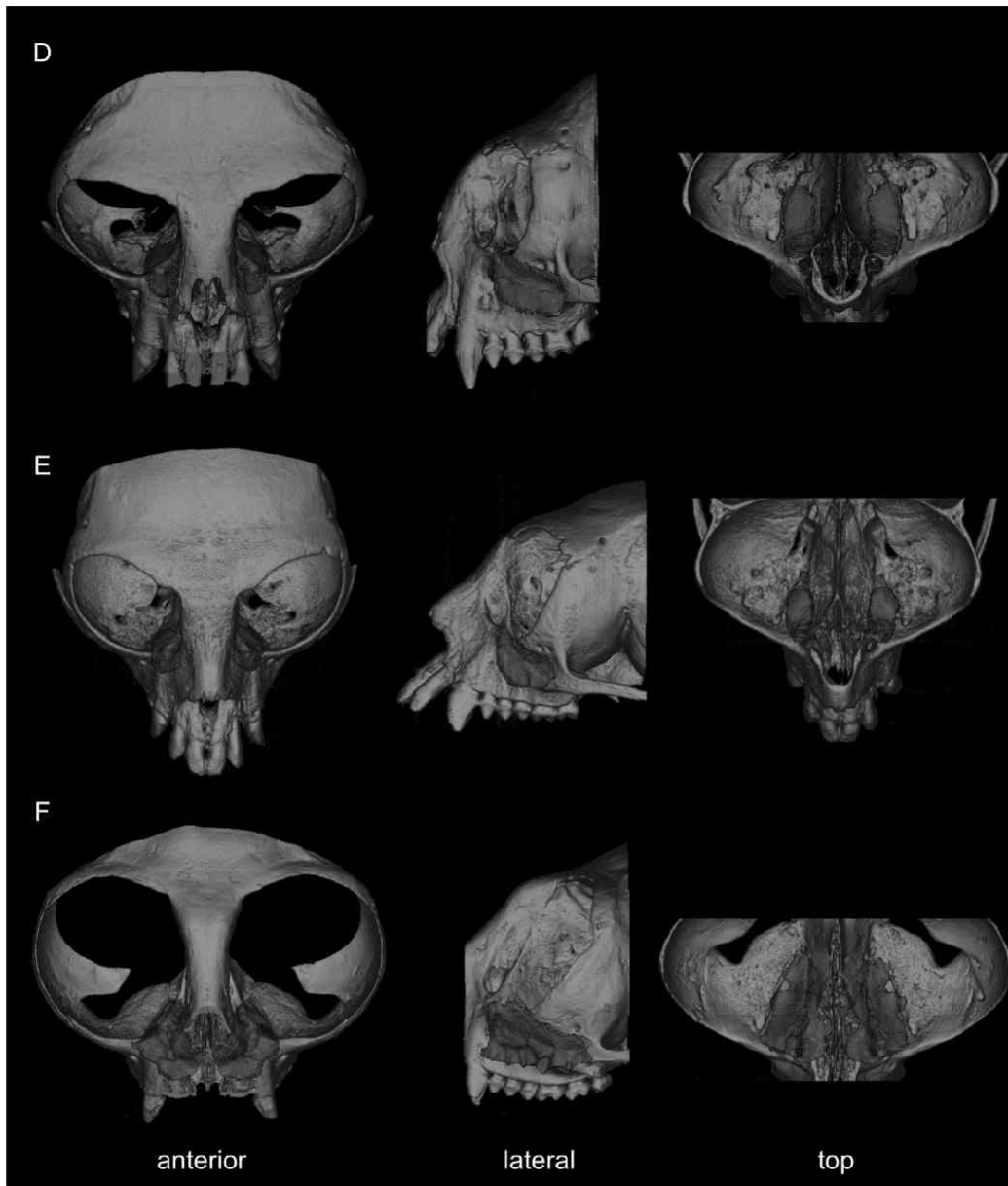
**Figure 7 (continued).** Three-dimensional reconstructed images of the cranium indicating the restricted maxillary sinus. The maxillary sinus is colored dark grey. **D**, *Callithrix jacchus*; **E**, *Cebuella pygmaea*; **F**, *Aotus trivirgatus*. Not to scale.

Wright, 1994; Heesy and Ross, 2001). Thus, it is likely that their large orbits relative to their cranial size arose independently in the callitrichines and *Aotus*, precluding the expansion of the maxillary sinus into the lateral half of the maxilla in both lineages (Nishimura *et al.*, 2005).

## Primitive condition of the maxillary sinus in anthropoids

Hominoids and all platyrrhines except the above mentioned have a maxillary sinus that pneumatizes the entire maxilla superior to the orbital floor and inferior to the alveolar process. In the non-human hominids and *Alouatta*, the bony wall between the maxillary, ethmoidal,
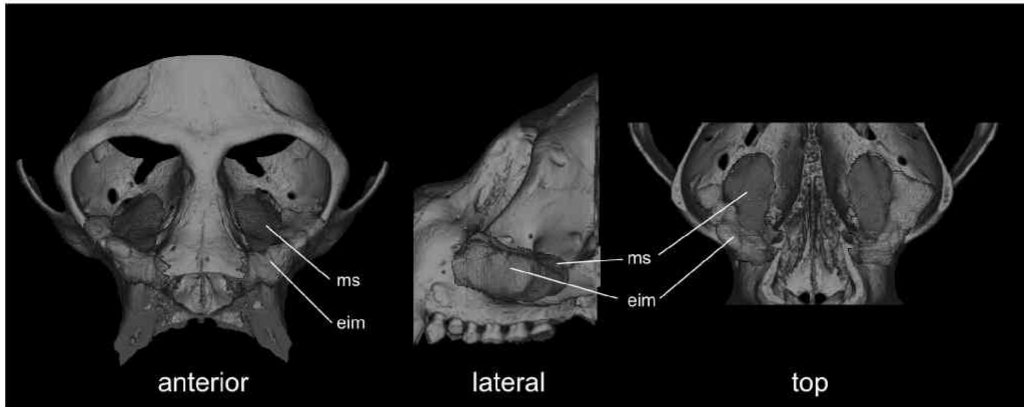
Nishimura



**Figure 8.** Three-dimensional reconstructed images of the cranium indicating the maxillary sinus and the expanded inferior nasal meatus in *Pithecia sp*. The inferior meatus (eim) expands, running from a narrow opening in the bottom of the lateral wall, over the anteroinferior aspect of the maxillary sinus (ms), and occupies the anterolateral part of the maxilla.

and sphenoidal (and frontal in non-human hominids) sinuses develops to be resorbed, resulting in a single large confluent sinus. On the other hand, although the callitrichines, *Aotus*, and *Pithecia* have physical obstacles to any further expansion of the maxillary sinus, their sinuses pneumatize the entire region of the maxilla, excluding the region that is affected by the obstruction. These facts suggest that the maxillary sinus potentially pneumatizes the entire maxilla, if there are no physical obstacles to secondary pneumatization. The extant callitrichines are phyletic dwarfs (Kinzey *et al.*, 1975; Ford, 1980; Sussman and Kinzey, 1984; Levitch, 1987; Plavcan and Gomez, 1993; Kay, 1994), and therefore the diurnal common ancestor of the extant anthropoids probably had a larger body size than them. This means that there was a large space between the orbital floor and the alveolar process in the ancestor. Consequently, it is likely that a maxillary sinus that pneumatizes the entire maxilla is the primitive condition of the extant anthropoids (Nishimura *et al.*, 2005; Rossie, 2006). This implies that the superfamily Hominoidea, the family Atelidae, the subfamily Callicebinae, and *Cebus* are lineages in which the primitive condition has been retained. Thus, various forms of the maxillary sinus have arisen independently from this condition in all other lineages, under the influence of different factors.

**Studies of the maxillary sinus form in fossil primates**

The morphology of the maxillary sinus has been examined in fossil primates, in surface views of complete or fragmented fossils in which the sinus is exposed. Recently, CT studies have examined the inner structures of well-preserved fossils to identify the maxillary sinus by the criterion used here (Rae *et al.*, 2002; Rossie *et al.*, 2002; Rae and Koppe, 2004; Rossie, 2005). These studies are expected to provide critical information with which to test the existing phylogenetic hypothesis of the maxillary sinus (Rae *et al.*, 2002; Rossie, 2005). Here, these studies are reviewed to test the existing hypothesis.

There is no CT study of the maxillary sinus in fossil hominoids. However, diagnoses from fragmented specimens have indicated that *Proconsul*, *Morotopithecus*, *Rangwapithecus*,
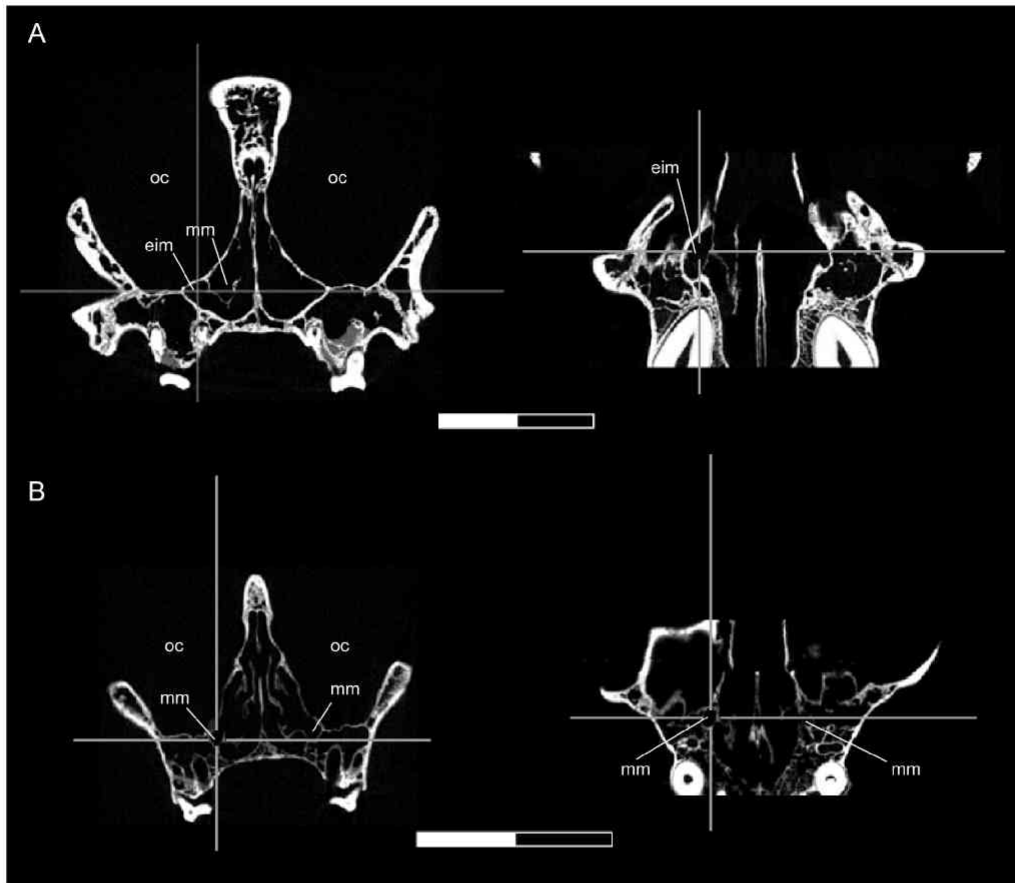
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**Figure 9.** CT images of the original coronal section (left) and the reformatted axial (right) sections in platyrrhines without maxillary sinus. **A**, *Cacajao rubicundus*. The nasal accessory structures had been destroyed on the left side (right on the CT images). The inferior meatus (eim) extends superiorly to the floor of the orbital cavity (oc), to occupy an area between the middle meatus (mm) and the medial surface of the maxilla. **B**, *Saimiri sciureus*. This genus has no maxillary sinus, although the maxilla and the middle meatus (mm) are in contact with each other. Scale in centimeters.

and *Afropithecus* from early Miocene had a maxillary sinus that pneumatized the entire maxilla, as seen in extant hominoids (Rossie, 2005). This suggests that this superfamily has maintained the primitive condition of maxillary sinus anatomy in the anthropoids.

Among the stem lineages of cercopithecoids, a well-preserved cranium of *Victoriapithecus* from early to middle Miocene was examined with CT (Rae *et al.*, 2002). CT scans showed that this genus lacked the maxillary sinus and that its maxilla was filled with cancellous bone, as in extant cercopithecoids, excluding *Macaca* and *Papio-Theropithecus*. A CT study of early Oligocene *Aegyptopithecus*, a stem lineage of the catarrhines, showed that this animal had a sinus that pneumatized the entire maxilla (Rossie *et al.*, 2002; Rossie, 2005). Despite the diagnoses of fragmented fossils, *Limnopithecus* and *Dendropithecus*, stem lineages of the catarrhines from early Miocene, probably had a similar form of maxillary sinus (Rossie, 2005; *Note*: Although these two genera are often classified as stem lineages of the hominoids, the classification of Rossie [2005] is accepted in this paper. However, the conclusion drawn here is unaffected by this controversy). This evidence supports the hypothesis that a maxillary sinus that pneumatizes the entire maxilla is the primitive
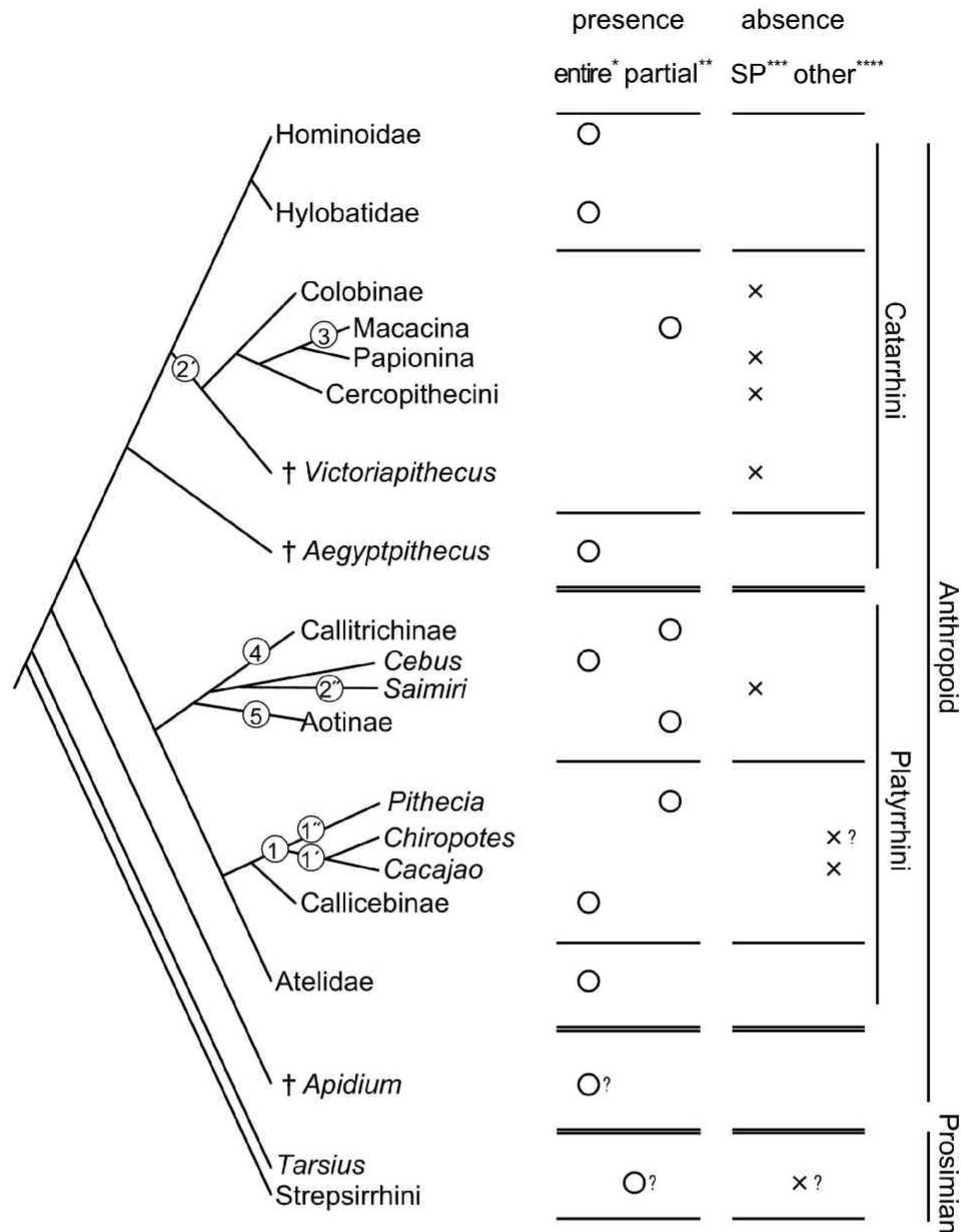
**Figure 10.** Variation in the morphology of the maxillary sinus among anthropoids, using the criterion used in the present study. This cladogram is based on Disotell (1996) for catarrhines and Horovitz *et al.* (1998) for platyrrhines. † indicates a fossil species. A right table explains the form of the maxillary sinus in each genus. *, a maxillary sinus occupying the entire maxilla; **, a maxillary sinus occupying a part of the maxilla; ***, a loss of the maxillary sinus is attributable to modifications to the processes of the secondary pneumatization; ****, a loss of the maxillary sinus is attributable to modifications to the surrounding bone elements. Circled numbers indicate evolutionary events: 1, an expanded inferior meatus; 1', an expanded inferior meatus extending superior to reach the orbital floor; 1", an expanded inferior meatus pneumatizing the maxilla; 2' and 2", losses of the maxillary sinus are attributable to the modifications to the processes of the secondary pneumatization; 3, reacquisition of the maxillary sinus; 4, a maxillary sinus pneumatizing the medial part of the maxilla (attributable to the reduction in the body size); 5, a maxillary sinus pneumatizing the medial part of the maxilla (attributable to the enlarged eye). The maxillary sinus pneumatizing the entire maxilla is likely a primitive condition in anthropoids

condition of the catarrhines, and that the cercopithecoid lineage lost the maxillary sinus after its divergence from the hominoid lineage.

Fossil platyrrhines have been scanned with CT (Kay *et al.*, 2004), but there is no information regarding the anatomy of the maxillary sinus comparable to that of extant

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species. On the other hand, a preliminary CT study showed that *Apidium* (early Oligocene), a stem lineage of the anthropoids, had a maxillary sinus that pneumatized the entire maxilla (Rae and Koppe, 2004). This fact strongly supports the hypothesis that this form of the maxillary sinus is the primitive condition of the anthropoids.

The identification and analysis of the maxillary sinuses of one specimen of *Victoriapithecus* (Rae *et al.*, 2002), two specimens of *Aegyptopithecus* (Rossie *et al.*, 2002; Rossie, 2005), and one specimen of *Apidium* (Rae and Koppe, 2004) have been performed with the criterion used for extant species. These studies provide critical evidence supporting the existing phylogenetic hypothesis of the maxillary sinus in anthropoids. Furthermore, all other studies of fossil anthropoids provide evidence supporting this hypothesis, although they were not based on the interspecies homology-based criterion.

CT will soon be readily available for paleoprimatological research even in developing countries, in which many primate fossils have been discovered. Therefore, in future, the maxillary sinus anatomy of all other primate fossils is possibly to be examined with CT using an interspecies homology-based criterion. Such studies are expected to provide valuable information for the discussion of maxillary sinus phylogeny. Moreover, they may reveal an unknown form in fossil species that stimulates a new phylogenetic hypothesis.

**Potentials and perspectives for phylogenetic analysis**

Our increasing knowledge of the variation in maxillary sinus anatomy is expected to facilitate the future phylogenetic analysis of unclassified fossil primates (Rae, 1999; Rae and Koppe, 2004; Rossie, 2005). The identification and phylogenetic evaluation of these fossils have been based principally on the diagnosis of features on the fossil surface, such as dentition and facial forms. CT readily visualizes the inner structures of fossils. However, most studies have examined features in which any variation is already well documented (e.g., teeth or inner ears; Kunimatsu *et al.*, 2004; Silcox, 2003). Consequently, there has been little increase in our knowledge of the variation in the inner cranial structures of extant species. The maxillary sinus is one of the few features that will facilitate phylogenetic analysis (Rae, 1999; Rae and Koppe, 2004).

Many issues remain to be solved, for strengthening the potentials. For instance, more information is required about the intra- and interspecies variability of maxillary sinus forms. The distribution of the various forms of maxillary sinuses among the primates, especially the New World monkeys, had been controversial (Cave and Haines, 1940; Cave, 1967; Negus, 1958; Hershkovitz, 1977; Lund, 1988; Swindler, 1999). Although CT studies have generally resolved this issue, these controversies might reflect existing intra- or interspecies variations. Secondly, the form of the maxillary sinus changes dramatically during growth (Koppe *et al.*, 1999b; Nishimura *et al.*, 2005; Rossie, 2006), and information about these changes has yet to be collected. Lastly, pathologies in the formation of the maxillary sinus must be considered. One case report describes maxillary sinus atelectasis–the failure of sinus formation–in a wild-

born silvery Javan gibbon, *Hylobates moloch* (Koppe *et al.*, 2006). Data on the frequency of maxillary sinus pathologies and anatomical modifications to the surrounding structures will contribute to more reliable diagnoses of the presence or absence of the maxillary sinus in any given fossils.

There is little information on the three-dimensional anatomy of the maxillary sinus in prosimians or in any other non-primate mammalians. Although the criterion for its identification is unclear, some lorisids and lemurs have been reported to lack a maxillary sinus (Kollmann and Papin, 1925; Negus, 1958). Future studies of maxillary sinus variability among the prosimians are expected to provide critical information for the discussions of the phylogenetic modification of this sinus in primates. Such information will facilitate the phylogenetic analysis of enigmatic primate fossils, and may contribute to our understanding of the evolution of the surrounding features. Anatomically, modifications to the anatomy of the maxillary sinus are inevitably associated with the morphology of the surrounding bony elements, so these modifications have contributed to the evolution of facial morphology (Rae and Koppe, 2004). For example, maxillary sinus modifications may be associated with the formation of the bony cups of the orbits, which are a derived feature in the anthropoids. These orbits are formed by postorbital closure, which separates the orbit from the temporal fossa behind it. It principally involves the inferior extension of the greater wing of the sphenoid bone. This rearrangement might have been associated with another event, wherein the orbital floor drifted upward, becoming approximate to the greater wing. In *Aotus* and callitrichines, the maxillary sinus anatomy is strongly related to the orbital anatomy, e.g., to the relatively larger orbits of these animals (Nishimura *et al.*, 2005; Rossie, 2006). The maxillary sinus atelectasis of *Hylobates* is associated with the depression of the orbital floor (Koppe *et al.*, 2006). Future studies of maxillary sinus anatomy in prosimians may also provide important suggestions for the evolutionary processes involved in postorbital closure in the anthropoids.

## Conclusion

In this paper, I have surveyed the morphological variation in the maxillary sinus and its phylogenetic significance in the anthropoids, which have been revised with the advent of CT scanning. There are various forms of maxillary sinus among anthropoids, including its complete absence. This variation is probably attributable to modifications to the process of secondary pneumatization and to the morphology of the surrounding bony elements. These data suggest that a maxillary sinus that pneumatizes the entire maxilla is the primitive condition in the anthropoids. Unfortunately, the functions of the paranasal sinus are still unclear, so the selective advantage of each form remains controversial. However, the derived forms have probably arisen independently in different lineages, and have resulted in the diversification of maxillary sinus forms seen in the extant anthropoids. Updated studies of the maxillary sinus in fossil primates support this phylogenetic hypothesis. Although there are many issues still to be resolved, the maxillary sinus is one of the few features that should

facilitate a phylogenetic analysis of the fossil primates in the future. However, our basic knowledge of the relationships of the inner and surface features of the cranium, (e.g., the maxillary sinus and surrounding structures) among extant primates is increasing only slightly even now. Such studies may provide critical evidence to support the idea that a maxillary sinus that pneumatizes the entire maxilla arose with postorbital closure, a derived feature in the anthropoids. Further studies of maxillary sinus anatomy in extant and fossil primates are expected to facilitate the classification and phylogenetic evaluation of enigmatic anthropoid fossils in the near future.

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## Appendix 1: Specimens used and parameters of the images acquired

| Specimens | Sex | Institution[1] | ID No. | Scanner[2] | Resolution | FOV |
|---|---|---|---|---|---|---|
| **Catarrhines** | | | | | | |
| *Pan troglodytes* | m | MNB | 83661 | hCT | 0.26 | 134 |
| *Chlorocebus aethiops* | m | PRI | 2209 | hCT | 0.2 | 102 |
| *Macaca nemestrina* | m | PRI | 3055 | hCT | 0.35 | 180 |
| *Macaca nigra* | m | PRI | 1527 | hCT | 0.2 | 102 |
| *Papio hamadryas* | m | PRI | 1540 | hCT | 0.3 | 154 |
| *Papio hamadryas* | m | PRI | 4231 | hCT | 0.3 | 154 |
| *Papio hamadryas* | f | KAS | 187 | hCT | 0.2 | 154 |
| **Platyrrhines** | | | | | | |
| *Ateles geoffroyi* | m | PRI | 1766 | hCT | 0.2 | 102 |
| *Brachyteles arachnoides* | m | PRI | 4690 | hCT | 0.2 | 102 |
| *Lagothrix lagotricha* | m | PRI | 4626 | hCT | 0.2 | 102 |
| *Alouatta caraya* | m | PRI | 2121 | hCT | 0.2 | 102 |
| *Pithecia sp.* | m | PRI | 4646 | pQCT | 0.11 | 60 |
| *Cacajao rubicundus* | m | JMC | 2950 | pQCT | 0.11 | 75 |
| *Callicebus moloch* | m | PRI | 2048 | pQCT | 0.07 | 50 |
| *Leontopithecus rosalia* | m | JMC | 1487 | pQCT | 0.07 | 40 |
| *Saguinus labiatus* | m | PRI | 662 | pQCT | 0.07 | 40 |
| *Callimico goeldii* | m | JMC | 5270 | pQCT | 0.07 | 45 |
| *Callithrix jacchus* | m | PRI | 1996 | pQCT | 0.05 | 30 |
| *Cebuella pygmaea* | m | JMC | 404 | pQCT | 0.04 | 14 |
| *Cebus apella* | m | PRI | 7133 | pQCT | 0.2 | 80 |
| *Saimiri sciureus* | m | PRI | 934 | pQCT | 0.1 | 50 |
| *Aotus trivirgatus* | m | PRI | 2036 | pQCT | 0.08 | 50 |

Scale is in millimeters. In catarrhines, *Chlorocebus aethiops* and *Macaca* crania were from adult individuals with fully erupted M[3]. Crania of *Pan troglodytes* and *Papio hamadryas* (PRI #1540) were from the individual with partially erupted M[3]. The two crania of *Papio hamadryas*, PRI #4231 and KAS #187, were from the individuals with the fully errupted M[2] and with deciduous dentitions, respectively. All platyrrhine specimens were from adult individuals, with the last upper molar fully erupted.
[1] Abbreviations for the institutions; MNB, Museum für Naturkunde Berlin (Germany); JMC, Japan Monkey Centre; KAS, Laboratory of Physical Anthropology, Department of Zoology, Graduate School of Science, Kyoto University; PRI, Primate Research Institute of Kyoto University.
[2] Abbreviations for the CT scanners; hCT, helical CT scanner; pQCT, peripheral Quantitative CT scanner (see Appendix 2).

## Appendix 2: CT scan and image processing

Variation in the anatomy of the maxillary sinus was examined using noninvasive CT scannig. Serial CT images of the dry crania were obtained by one of two methods (Appendix 1). The smaller specimens were scanned using a peripheral Quantitative CT (pQCT, a high-resolution mode) scanner (XCT Research SA+, Norland and Stratec) with the smaller collimator of the $\mu$Scope mode (0.25 x 0.50 mm) at Primate Research Institute of Kyoto University. Each specimen was placed on a wooden stage and the coronal plane of the cranium was held perpendicular to the plane of the line of X-ray beams using adhesive tape. The specimens were scanned with a scanning resolution ranging from 0.04 x 0.04 to 0.20 x 0.20 mm per pixel with same thickness, no gap between the slices, a field of view ranging from 25 to 80 mm, a tube voltage of 50 kV, tube current of 0.50 mA, and a CT speed ranging from 2.25 to 11.5 mm/s. These parameters were chosen based on the size of each specimen (Appendix 1). The CT images acquired had a pixel matrix raging from 359 x 359 to 718 x 718.

The larger specimens, excluding *Pan troglodytes*, were scanned using a helical CT scanner (XVision TSX-002/4I, Toshiba Medical Systems Co.) at the Laboratory of Physical Anthropology, Graduate School of Science, Kyoto University. The specimens were placed on the scanner table in the same way as for the pQCT examination. The overview scans were made with a field of view of 180 mm, a tube voltage of 120 kV, a tube current of 100 mA, and a table speed of 1.0 mm per rotation. The serial CT images were reconstructed from the original volume data through the procedure known as zoom reconstruction, which differs completely from the magnification of an existing image (see Spoor *et al.*, 2000). The serial images acquired had a pixel matrix of 512 x 512, with a field of view of 102, 154 or 180 mm and a 0.2 mm interval between slices (Appendix 1).

A cranium of *Pan troglodytes* was scanned using a helical CT scanner (Somatom AR.T., Siemens) at the Institut für Anatomie, Ernst Moritz Arndt Universität Greifswald, Germany. The specimens were placed on the scanner table in the same way as for the pQCT examination. The overview scans were made with a field of view of 500 mm, a tube voltage of 120 kV, a tube current of 50 mA, and a table speed of 1.0 mm per rotation. The serial CT images were reconstructed from the original volume data through the procedure known as zoom reconstruction, which differs completely from the magnification of an existing image (see Spoor *et al.*, 2000). The serial images acquired had a pixel matrix of 512 x 512, with a field of view of 134 mm and a 0.7 mm interval between slices (Appendix 1).

INTAGE 3.1 software (KGT Inc., Japan) and Amira 3.1.1 (TGS Inc., USA) was used for reconstructions of the three-dimensional (3D) images of the adult cranium, demonstrating the shape and configuration of the maxillary sinus and the other structures. At first, the area of the sinus and the other structures were segmented and traced on the coronal images. Next, the traced regions were colored, and the remaining regions were blacked out. The original and colored images were processed to make 3D images and calculate volumes.