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# MAXILLARY AND FRONTAL SINUSES IN EURASIAN MIOCENE HOMINOIDS: PHYLOGENETIC IMPLICATIONS

## SENOS MAXILAR Y FRONTAL EN HOMINOIDEOS DEL MIOCENO DE EURASIA: IMPLICACIONES FILOGENÉTICAS

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### ABSTRACT

The paranasal sinuses (maxillary, frontal, ethmoidal and sphenoidal) are cavities in the facial skeleton of vertebrates. The study of maxillary and frontal sinuses in Eurasian Miocene hominoids constitutes a very useful tool in phylogenetic analysis. In this work, the available evidence of these structures in fossil great apes of the Vallès-Penedès (*Anoiapithecus*, *Hispanopithecus* and *Pierolapithecus*) is reviewed. The results are relevant for the study of the phylogenetic position of these genera. Differences between these primates, mainly in the frontal sinus features, confirm the relationship of *Hispanopithecus* with pongines. The configuration of *Anoiapithecus* and *Pierolapithecus* fits with that of great apes, with *Anoiapithecus* displaying a more primitive character state in the frontal sinus.

**Keywords:** *Pierolapithecus*, *Anoiapithecus*, *Hispanopithecus*, paranasal sinuses, great apes.

### RESUMEN

Los senos paranasales (maxilar, frontal, etmoidal y esfenoidal) son cavidades del esqueleto facial de los vertebrados. El estudio de los senos maxilar y frontal en los hominoideos del Mioceno de Eurasia constituye una herramienta muy útil en análisis filogenéticos. En este trabajo, se revisa la evidencia disponible de estas estructuras en los grandes simios antropomorfos fósiles del Vallès-Penedès (*Anoiapithecus*, *Hispanopithecus* y *Pierolapithecus*). Los resultados son relevantes para el estudio de la posición filogenética de estos géneros. Las diferencias entre estos primates, principalmente en las características del seno frontal, confirma la relación de *Hispanopithecus* con los ponginos. La configuración de *Anoiapithecus* y *Pierolapithecus* concuerda con la de los grandes simios antropomorfos, presentando *Anoiapithecus* un estado de carácter más primitivo en el seno frontal.

**Palabras clave:** *Pierolapithecus*, *Anoiapithecus*, *Hispanopithecus*, senos paranasales, grandes simios antropomorfos.

### 1. INTRODUCTION

The paranasal sinuses are empty spaces inside the facial skeleton that conform the nasal cavities. The size and shape of these pneumatized cavities (ethmoidal, sphenoidal, maxillary and frontal) are studied in order to understand their function, evolution and application in phylogenetic reconstruction (Fig. 1). The function of the sinuses include breathing by warming air during respiration; acting as a defence against diseases caused by bacteria; and constituting a hard structure that resist traumas due to impacts (Rae and Koppe, 2004). In this study, we deal mainly with the maxillary and frontal sinuses characteristics.

The maxillary sinus is a pyramidal cavity situated in the maxillary bone and located in the laterals of the na-

sal cavity (Márquez, 2008). Being present in eutherian ancestors, it represents an important taxonomical tool (Rae and Koppe, 2004). Extant cercopithecoids (Old World monkeys) generally lack any sign of paranasal sinuses. There are some exceptions, such as *Macaca*, which displays a maxillary sinus (Márquez, 2008), as well as *Papio* and several other taxa, which display a recess one. In fact, the maxillary sinus of macaques is variable in size, being related to latitudinal and temperature gradients—the sinus being smaller in species from northern and colder zones (Rae and Koppe, 2004). Regarding the Hominoidea (apes and humans), the maxillary sinus is well developed in both hylobatids (gibbons and simians) and extant hominids (great apes and humans), being the largest of all the cavities (Koppe and Ohkawa, 1999).

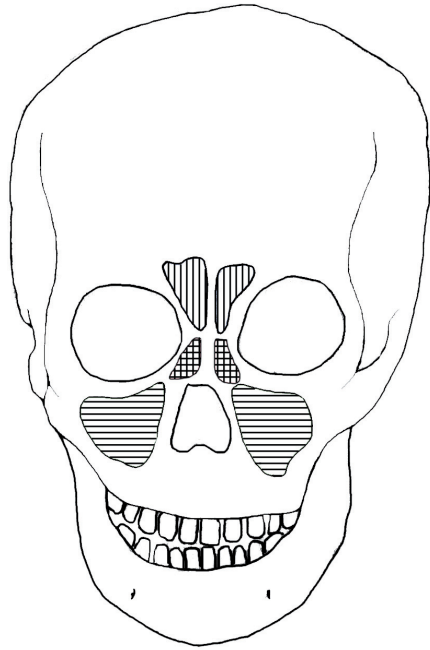


Figure 1. Location of the paranasal sinuses in hominoids: maxillary (horizontal lines), ethmoidal (grid) and frontal (vertical lines). All of them can vary in morphology, size and number.

The formation of the frontal sinus is ontogenetically related to ethmoidal pneumatization. Among extant hominoids, its presence is restricted to the Hominae (African apes and humans), so that it might represent a synapomorphy of this clade (Rae and Koppe, 2004). African apes and humans thus display a large frontal sinus that spreads out through the squama of the frontal bone, is divided by a septum into two parts and penetrates on the upper orbital rims in a variable degree. On the other hand, *Pongo* and *Hylobates* lack a true frontal sinus, the latter therefore being a potentially very useful feature in phylogenetic analysis (Koppe and Ohkawa, 1999).

Modern humans generally display a frontal sinus, but this structure is lacking in some *Homo sapiens* populations from Australia, Sudan and several Arctic zones (Rae and Koppe, 2004). This may be attributable to a combination of climatic and functional reasons. The great pneumatization displayed by Neandertals (*Homo neanderthalensis*) has been interpreted as an adaptation to cold conditions, although this hypothesis is contradictory with the recent evidences on the volume of the maxillary sinus in Inuits as well as macaques (Rae and Koppe, 2004). In *Homo rhodesiensis* from Broken Hills (Zambia), the volume of the frontal sinus is quite similar to that of *Homo sapiens* and African great apes (Spoor and Zonneveld, 1999).

## 2. METHODOLOGY

Nowadays, the most effective method to observe cranial pneumatization in mammals is computed tomography (CT). This technique has become generalized owing to medical and industrial applications. The application of this kind of methodologies in palaeontology is actually

one of the most useful tools to investigate and get new data in extinct organisms. Among others, it can be used to define the boundaries of the paranasal sinuses and their degree of pneumatization (Koppe *et al.*, 2005). CT therefore enables a level of resolution high enough to investigate the paranasal cavities with non-destructive methods. The resolution obtained with medical CT permits one to measure the degree of pneumatization as well as visualize the size and shape of the several sinuses without distortion (Spoor *et al.*, 2000). In addition, in order to explain the variability of the sinuses and apply this knowledge in forensic science and palaeontology, statistical techniques can be also applied (Márquez, 2008). In this study, we relied on both the direct observations on fossils, casts and skull of extant primates, as well as on the interpretation of CT images for fossil taxa such as *Pierolapithecus*. The descriptions of the sinuses is based mainly on their presence and morphology (size and shape).

## 3. THE FRONTAL AND MAXILLARY SINUSES IN MIOCENE HOMINOIDS FROM EURASIA

The development of the frontal and maxillary sinuses in Miocene European hominoids is quite diverse, thus providing a potentially useful feature to be considered in phylogenetic analyses. In three different genera of the European Miocene, the preserved facial material is complete enough to enable the observation of the sinus pattern: *Anoiapithecus*, *Pierolapithecus* and *Hispanopithecus* (Moyà-Solà and Köhler, 1993, 1995, 1996; Moyà-Solà *et al.*, 2004, 2009a,b; Köhler *et al.*, 2001).

The fossil great ape *Hispanopithecus laietanus*, from the late Miocene of the Vallès-Penedès Basin (Spain), displays a large maxillary sinus, which supports the hypothesis that it belongs to the great-ape-and-human clade (Moyà-Solà and Köhler, 1995). The phylogenetic affinities of this taxon, however, have been very controversial, with several authors considering it a stem pongine (Moyà-Solà and Köhler, 1993, 1995, 1996; Köhler *et al.*, 2001), and others considering it a stem hominine (Begun *et al.*, 1997; Begun, 2009). Interestingly, *Hispanopithecus laietanus* displays no frontal sinus, showing only an ethmoidal sinus close to nasion, which supports a phylogenetic relationship to the *Pongo*-clade (Moyà-Solà and Köhler, 1995). On the contrary, Begun (1995a,b, 2009) has repeatedly described *Hispanopithecus* as possessing a large frontal sinus that invades the interorbital area. That would support the contention by this author (e.g., Begun, 2009) that *Hispanopithecus* is a stem member of the African-ape-and-human clade. Nevertheless, Begun's description of the *Hispanopithecus laietanus* stems in fact from an incorrect identification of the ethmoidal sinus as the frontal sinus; the former partially fills the interorbital space in *Hispanopithecus*, whereas no frontal sinus can be observed at all.

Regarding the putative stem great ape *Pierolapithecus catalaunicus*, from the middle Miocene of Spain, the

maxillary sinus is restricted, not arriving even to the roots of molars. A similar condition is observed in other late Miocene genera, such as *Anoiapithecus brevirostris*, at least on the basis of currently available evidence (Moyà-Solà *et al.*, 2009a).

No frontal sinus can be recognized in *Pierolapithecus*, which merely displays a somewhat porous area in the interorbital region (Fig. 2) (Pérez de los Ríos *et al.*, in press). This would suggest a closer relationship to pongines than previously suspected or, alternatively, that the lack of frontal sinus is not a synapomorphy of the *Pongo*-clade but instead a symplesiomorphy of crown hominids. Interestingly, a sinus in the ethmoidal region is clearly present in *Pierolapithecus*, between the porous area of the frontal sinus and the actual maxillary sinus. However, whether it is a true ethmoidal sinus or an upper expansion of the maxillary sinus, as it occurs in *Pongo* (Koppe and Ohkawa, 1999), cannot be addressed on the basis of the currently available evidence.

*Anoiapithecus brevirostris*, finally, clearly displays a distinct frontal sinus occupying all the frontal squama, but restricted to the interorbital region, whereas the upper part of the maxillary sinus can be observed on the preserved maxillary processes. The preserved maxillae of *Dryopithecus fontani* (Moyà-Solà *et al.* 2009b) merely show the presence of a relatively restricted maxillary sinus.

In respect to other Eurasian taxa, the pongine *Sivapithecus*, from the middle to late Miocene of Indo-Pakistan, displays a maxillary sinus development similar to *Pongo*, where it extends up to the P<sup>4</sup>, but being splitted by the interorbital pillar, which is an autapomorphy of this taxon (Rae, 1999). *Sivapithecus* further lacks a frontal sinus (Begun, 2009), which agrees with the consideration of this taxon as a member of the *Pongo* clade, on the basis of many other cranial features. On the contrary, *Ankarapithecus meteai*, from the middle to late Miocene of Turkey, displays a frontal sinus that completely expands through the orbital region completely filling the glabella and spreading through the orbital crest (Kappelman *et al.*, 2003). This taxon is usually considered a stem pongine, owing to the possession of several cranial features that are more primitive than in both *Sivapithecus* and *Pongo*. If correct, this might indicate that the lack of frontal sinus is not a shared-derived feature of all the Ponginae, but merely a synapomorphy of a more restricted (e.g., *Sivapithecus-Pongo*) clade within this group.

#### 4. DISCUSSION

The distribution of paranasal sinuses in cercopithecoids makes it difficult to reconstruct the ancestral condition for hominoids, cercopithecoids, and catarrhines as a whole. The absence of paranasal sinuses in most cercopithecoids could indicate that the lack of these structures represents the ancestral catarrhine condition, and that these structures independently evolved along several lineages, such as the case of the maxillary sinus in macaques and some

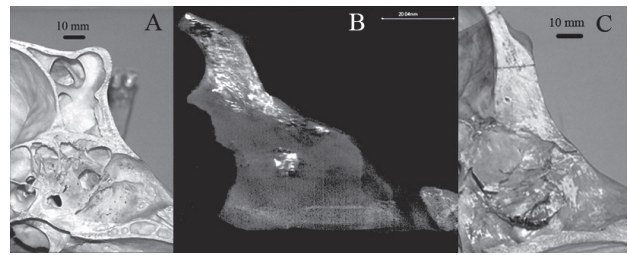


Figure 2. Sagittal sections through the glabella of several hominoids, showing the condition of the frontal sinus: A: *Pan troglodytes*, well-developed frontal sinus; B: *Pierolapithecus catalaunicus*, porous frontal sinus (CT-scan); C: *Pongo pigmaeus*, lack of frontal sinus.

hominoids. The primitive condition for hominoids is the presence of a large maxillary sinus, more developed in great apes than in hylobatids (Rae, 1999). Regarding the frontal sinus, its presence has been considered symplesiomorphic for catarrhines as a whole (Kappelman *et al.*, 2003), being restricted to an area underlying the glabella (Moyà-Solà and Köhler, 1995; Rossie *et al.*, 2002).

Regarding the extinct hominoids discussed in this paper, the high diversity of sinus patterns among the European taxa is very striking. *Hispanopithecus* displays a large maxillary sinus and lacks a frontal sinus, although showing a sinus in the ethmoidal region. This configuration fits well with the previous proposal of this taxon as a stem Ponginae (Moyà-Solà and Köhler, 1993, 1995, 1996; Köhler *et al.*, 2001) and stands clearly at odds with Begun's (2009) contention that this taxon is most likely a stem Homininae. The latter, in fact, results from an inaccurate description of the frontal sinus of this taxon, among other reasons, owing to a confusion with the ethmoidal sinus. In *Pierolapithecus* and *Anoiapithecus*, two opposed patterns can be observed. In *Pierolapithecus* a total lack of frontal sinus is accompanied by a reduction of the maxillary sinus as well. On the contrary, in *Anoiapithecus* a large frontal sinus is present. The restricted development of the maxillary sinus has been interpreted as a primitive feature that might reflect the ancestral hominid condition (Moyà-Solà *et al.*, 2009a), which would have been later retained by pongines but further enlarged in hominines. That would fit well with the previous proposal of *Pierolapithecus* and *Anoiapithecus* as putative stem great apes (Moyà-Solà *et al.*, 2004, 2009a).

Nevertheless, the lack of frontal sinus in *Pierolapithecus*, which merely shows a porous area under the glabella (Pérez de los Ríos *et al.*, in press)—similar to the condition displayed by hylobatids—is more difficult to interpret. At first glance, the lack of frontal sinus in *Pierolapithecus* might be interpreted as indicating a closer phylogenetic relationship with *Pongo*, thus being a stem pongine instead of a stem hominid. This is however contracted by the more developed frontal sinus present in the clearly more derived pongine *Ankarapithecus* (see Kappelman *et al.*, 2003), suggesting that the loss of the frontal sinus might only characterize the more derived pongines, such as *Sivapithecus*. If this were the case, the condition displayed by *Pierolapithecus* might be merely homoplas-

tic. This issue is further complicated by the presence of an intermediate-sized frontal sinus in *Anoiapithecus*, which is a feature diagnostic of extant African great apes and humans, although it might alternatively represent the ancestral hominid condition.

## 5. CONCLUSIONS

The development of the maxillary and frontal sinuses may represent a very useful tool in primate phylogenetic analyses, although an accurate description and identification is required and the issue is further complicated by the potential homoplastic similarities between several taxa. The discussion presented here leads us to conclude that the evidence from *Hispanopithecus* is more consistent with considering this taxon a stem pongine rather than a stem hominine.

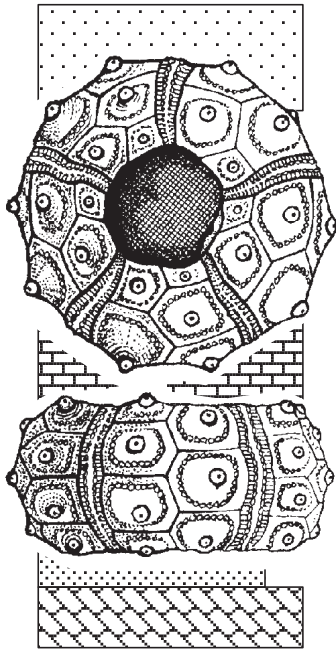
On the other hand, the evidence reported here for putative stem great apes from Spain suggests that *Anoiapithecus* shows a more primitive condition than *Pierolapithecus*, which might be interpreted as a stem pongine. Nevertheless, it should be taken into account that, like other features, the development of paranasal sinuses is very subject to homoplasy (false homology). Hence, deciphering the phylogenetic affinities of any taxon should rely not only on one trait but on all the morphological evidence available from several anatomical regions.

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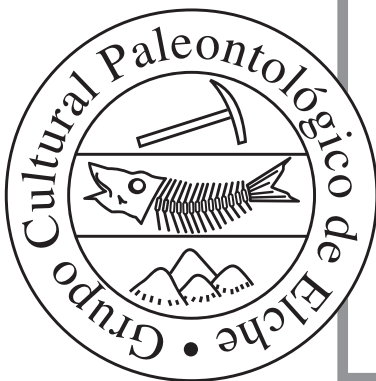


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