Comparative anatomy of the frontal sinuses in the primitive sabre-toothed felid *Promegantereon ogygia* (Felidae, Machairodontinae) and similarly sized extant felines

Anatomía comparada de los senos frontales en el félido dientes de sable primitivo Promegantereon ogygia (Felidae, Machairodontinae) y felinos actuales de tamaño similar

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ABSTRACT

In the present work, the frontal sinuses of the sabre-toothed felid *Promegantereon ogygia* are analysed, in comparison to those of the extant felines *Acinonyx jubatus, Puma conocolor* and *Panthera pardus,* of similar body weight. The study was carried out using 3D virtual models obtained from CT Scan images, a non-destructive technique that has revealed as a powerful tool for accessing to all kind of intracranial information. Our study shows that the frontal sinuses of *P. ogygia* were more similar to those of *P. concolor*, both in the presence of several struts reinforcing the dorsal part, and in the development of a remarkable caudal expansion. This caudal expansion would act as a thermal insulator of the brain, and would indicate a more open environment than previously supposed for this species, whereas the struts would be related to biomechanical stresses produced during the "canine shear-bite", the killing method of the machairodontines.

Keywords: frontal sinus, pneumatisation, skull, Felidae, Felinae, Machairodontinae.

RESUMEN

En el presente trabajo, se analizan los senos frontales del félido dientes de sable *Promegantereon ogygia*, en comparación con los de los felinos actuales *Acinonyx jubatus, Puma conocolor* y *Panthera pardus*, de similar peso corporal. El estudio se llevó a cabo utilizando modelos virtuales 3D obtenidos por tomografía axial computerizada, una técnica no destructiva que se ha revelado como una poderosa herramienta para acceder a todo tipo de información intracraneal. Nuestro estudio muestra que los senos frontales de *P. ogygia* eran más similares a los de *P. concolor*, tanto en la presencia de varios puntales óseos de refuerzo de la parte dorsal, y en el desarrollo de una notable expansión caudal. Esta expansión caudal actuaría como un aislante térmico del cerebro, y podría indicar un entorno más abierto de lo que se supone para esta especie, mientras que los puntales óseos se relacionarían con tensiones biomecánicas producidas durante el mordisco típico de los macairodontinos, el método de ataque de los machairodontinos.

Palabras clave: seno frontal, pneumatización, cráneo, Felidae, Felinae, Machairodontinae.

Introduction

The cranial sinuses are air-filled spaces located within the skull of Vertebrates, highly variable in shape and development among the different groups. The study of these structures is very interesting for the analysis of cranial morphology and functional anatomy, but their functionality has been widely debated and several hypotheses have been proposed (Blanton & Biggs, 1968; Blaney, 1990;

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Witmer, 1997). Frontal sinuses are included in a complex system of cranial cavities (pneumatisations) called paranasal sinuses, which include, besides the frontal sinuses, all the sinuses located within the ethmoidal, maxilar and sphenoidal bones (Barone, 2010; Evans, 1993; Joeckel, 1998; Edinger, 1950). These cavities may extend to adjacent bones, such as the temporal bone (Sherwood, 1999). In Mammals, the paranasal sinuses derive from diverticula of the nasal cavity formed by means of a pneumatisation process. Thus, these sinuses are connected with the nasal cavity, and covered with a thin epithelial tissue, which is a continuation of the nasal mucosa. The maxillary sinus derives from the respiratory portion of the nasal cavity, whilst the ethmoidal, frontal and sphenoidal sinuses, derive from the olfactory portion of the nasal cavity (Witmer, 1997, 1999). The most widely accepted hypothesis for the origin of the cranial pneumatisation states that this process is produced when the mucous epithelial tissue from the nasopharyngeal cavity expands into different cranial bones, which are close to the nasal cavity; this mucosa is very rich in osteoclasts, which are responsible for the resorption of the cranial bony tissue (Witmer, 1997; Smith *et al.*, 2005). This process of bone remodelling is restricted by several structural and biomechanical constrains, which are different depending on the bone in which the cavity is being developed. Thus, in the case of frontal sinuses, they grow as separate left and right entities from the middle nasal meatus, as their development is confined laterally by the orbits, and rostro-caudally by the inner and outer tables of the frontal bone (Zollikofer & Weissmann, 2008).

Besides, this process of pneumatisation requires certain equilibrium between bone resorption and deposition, in order to keep the sinus biomechanically stable (Sherwood, 1999; Witmer, 1997). This equilibrium results in a sinus structure with chambers and bony struts, the latter supporting the cavity, as they are located in areas of high biomechanical demands (Witmer, 1997).

Several hypotheses have been proposed to explain the function of these cranial pneumatisation, most of them related to physiology or architecture, development and biomechanics of the skull, such as: imparting resonance to the voice (Cleland, 1862; Bignon, 1889; Leakey & Walker, 1997; Dyce *et al.*, 2002), protection of the brain from shocks (Rui *et al.*, 1960; Schaffer & Reed, 1972; Davis *et al.*, 1996), reducing cranial weight (Cleland, 1862;

Paulli, 1900; Nemours, 1931; Shea, 1936; Buhler, 1972; Davis *et al.*, 1996), increasing surface area of olfactory mucosa (Braune & Clasen, 1877; Negus, 1957, 1958), humidifying and warming the inspired air (Proetz, 1922, 1938; O'Malley, 1924; Gannon *et al.*, 1997), thermoregulation of the brain (Bignon, 1889; Bremer, 1940; Proetz, 1953; Verheyen, 1953; Dyce *et al.*, 2002), or producing nitric oxide gas (Lundberg *et al.*, 1994). Nevertheless, no one of these hypotheses is completely satisfactory or widely applicable. For example, a function related to respiratory physiology (humidifying and warming the inspired air) has been refuted based on the evidence that the sinus epithelium is almost devoid of glandular tissue and the *sinus ostium* (the opening that connects a sinus to the nasal cavity itself) is situated out of the path of the respiratory currents (Proetz, 1953; Blanton & Biggs, 1968; Witmer, 1997). The humidification and warming of the inspired air is provided by the epithelium of the maxilloturbinates, which is placed in the line of the respiratory current (Hillenius, 1992). Besides this, for other authors the paranasal sinuses are simply functionless structures resulting from a process of unnecessary bone tissue removal, followed by deposition of necessary bone to maintain a strong structure that supports biomechanical stress (Weidenreich, 1941; Edinger, 1950; Witmer, 1997).

Anyway, in order to assess the functionality of the paranasal pneumatisation, it is necessary to study the different groups of sinuses as separated entities, with similar formation processes, but with different structural constrains and physiological features. Thus, although primarily paranasal sinuses could have been formed as a result of a bone remodeling process, they have probably developed a set of secondary functions, different in each group of vertebrates.

General morphology of the frontal sinuses in mammals

The frontal sinuses are located between the external and internal tables of the frontal bone. These two tables contact by means of several struts developed along the sinus, forming an irregular transverse partition; rostrally and medially, the nasofrontal opening connects the sinus with the nasal cavity (Barone, 2010; Evans, 1993). The sinuses are subdivided into a series of chambers by a variable number of bony struts, which can be from more or

less cylindrical structures to bony sheets. Some species have relatively simple frontal sinuses, with a low number of struts, such as felids; others develop complex frontal sinuses, such as some bovids, whose sinuses have a great number of struts and a complicated system of interconnected chambers (Farke, 2010). There are also intermediate morphologies, such as that seen in canids, which show frontal sinuses divided in three chambers (rostral, medial and lateral) and a relatively high number of struts (Barone, 2010; Evans, 1993).

The frontal sinuses are invaded by prolongations of the ethmoturbinate bones. The turbinate bones are complex bony scrolls developed within the nasal cavity, derived from the ossification of the ethmoid bone. There are three groups of turbinates, defined by the name of the bones where they are fixed: ethmoturbinates, nasoturbinates and maxilloturbinates (Hillenius, 1992; Kardong, 2002). Besides, ethmoturbinates can be divided in endoturbinates and ectoturbinates, based upon how far they extend medially toward the nasal septum; the maxilloturbinates are covered by respiratory epithelium, and are located in the rostro-ventral portion of the nasal cavity, in the path of the respiratory airflow; on the contrary, nasoturbinates and ethmoturbinates are primarily, but not entirely covered by olfactory epithelium, and are situated in the dorsocaudal part of the nasal cavity (Negus, 1958; Moore, 1981; Hillenius, 1992). Maxilloturbinates, nasoturbinates and ethmoturbinates serve to increase the surface of both olfactory and respiratory tissues and are partially separated by a thin sheet of bone (Negus, 1958; Moore, 1981; Hillenius, 1992). The ethmoturbinates occupy the rostral and medial parts of the frontal sinus, the caudal part being almost empty; a slight prolongation connects this caudal portion with the nasal cavity. The epithelium covering the frontal sinuses is lined with a thin layer of ephithelium of the ethmoturbinates (Evans, 1993).

the 3D morphology of these cavities, mostly because these structures usually have complex shapes, with prolongations and connections to other cavities. Also, the very nature of the destructive techniques drastically reduces the available fossil skulls, so they were used only when relatively large samples were available.

The development of non-invasive and non-destructive methods like computerized axial tomography (CT Scan, CAT) and 3D virtual reconstructions generated from CT data, has facilitated the access to new information on the endocranial structures, as they provide with precise morphological information without damaging the skulls. Due to this, the use of these techniques in anatomical studies of cranial internal morphology has greatly increased in the last two decades (Brochu, 2000; Colbert *et al*., 2005; García *et al*., 2007; Jin *et al*., 2007; Dong, 2008; Silcox *et al*., 2009).

In recent years, most studies on frontal or paranasal sinuses have been focused on extant and fossil primates, including hominids, and many of these on maxillary sinus (Rae & Koppe, 2003, 2004; Márquez *et al*., 2008). More recently, the frontal sinus of extant Bovidae (Farke, 2007, 2010) or the cranial sinuses of theropod and ceratopsian dinosaurs (Witmer & Ridgely, 2008; Farke, 2010) have been described in detail. In carnivoran mammals, most of the studies have been focused on the frontal sinuses of fossils and extant Hyaenidae, due to their exceptional development. In fact, this group shows unique frontal sinuses, caudally elongated, and skulls with domed-forehead, whose function has been related to the dissipation of stresses produced when cracking bones (Joeckel, 1998; Tanner *et al*., 2008; Tseng *et al*., 2011). There are other groups of carnivorans such as ursids, percrocutids, and borophagine canids, and members of the Creodonta, whose frontal sinuses have been recently described (Joeckel *et al*., 1997; García *et al*., 2007; Tseng, 2009; Tseng & Wang, 2010).

Previous studies on the frontal sinuses of fossil vertebrates

Classically, the study of frontal sinuses in fossil vertebrates, and in general, of any intracranial cavity, was based on destructive methods (i. e.: cutting the skulls) or X-ray techniques (Negus, 1958; Paulli, 1900; Edinger, 1950). Nevertheless, these methods do not provide complete information on

Frontal sinuses in Felidae

The available information on the morphology of the frontal sinuses in Felidae is quite scarce. Classical anatomical studies use to include short descriptions of the frontal sinuses of the domestic cat (*Felis catus*), although never in detail (Reighard & Jennings, 1901; Negus, 1954; Barone, 2010). The frontal sinus of *F. catus* (fig. 1) is described as a
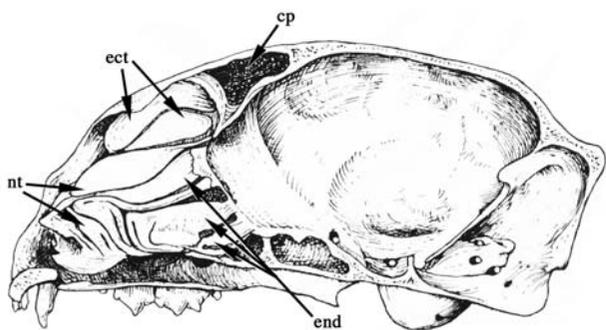
Fig. 1.—Sagittal section of the skull of *Felis catus* showing some of the intracranial structures discussed in the text (modified from Barone, 2010): cp, caudal portion of the frontal sinus; ect, ecto-turbinates filling the rostral portion of the frontal sinus; end, endo-turbinates; nt, nasoturbinates.

simple cavity, with a small rostral portion, and a caudal portion equivalent to the lateral and medial frontal sinuses of canids (Barone, 2010). The rostral portion is invaded by the first ethmoturbinates, whereas the caudal portion is almost empty, but showing a slight prolongation of the ethmoturbinates in its rostral portion (fig. 1) (Barone, 2010; Negus, 1954). Nevertheless, we have to consider that this is a domestic form, and might not reflect the general morphology of wild small felines.

Concerning fossil felids, the classical work by Merriam & Stock (1932) briefly describes the frontal sinuses of the sabre-toothed felid *Smilodon fatalis* indicating the existence of a large caudal portion, and a rostral portion containing the upper scrolls (ectoturbinates) of the ethmoturbinate (fig. 2); these authors also describe the frontal sinuses of the feline *Panthera atrox*, but just indicating that "the frontal sinus is of large size" in relation to that of *S. fatalis*. Joeckel & Stavas (1996) described the frontal sinuses of the bar-bourofelid (a felid-related family of carnivorans) *Barbourofelis fricki* as being relatively larger and more caudally extended than those of extant felids, this latter feature also present in *S. fatalis*; for these authors, this caudal displacement of the sinus would be caused by the hyper-development of the upper canines in both *B. fricki* and *S. fatalis*, which also would be indicating certain degree of paral-lelism in the development of this structure in these species. Also, Joeckel & Stavas (1996) describe the frontal sinus of the sabre-toothed felid *Machairo-dus* as extending into the sagittal crest, but they do not provide any reference supporting this. Recent-ly, Christiansen & Mazák (2008) have inferred rel-

atively large frontal sinuses in the primitive chee-tah *Acinonyx kurteni*, from China, although based on the external anatomy of the frontal bone, which is greatly inflated.

All of these fossils felids are relatively derived species within their lineages, and the morphology of the frontal sinus in primitive forms remains undescribed. In the case of the primitive sabre-toothed felid *Promegantereon ogygia*, an animal of similar body weight to those of the extant *P. concol-or* or *P. pardus*, the only available data came from very fragmentary fossils. The discovery in 1991 of the Batallones-1 fossil site in central Spain (Morales *et al.*, 2000, 2004) changed this situation, as cranial and post-cranial fossils of many individu-als of *P. ogygia* have been recovered in the excava-tions of 1991-2008, which has allowed several stud-ies on the functional anatomy, palaeoecology and systematics of this species (Salesa *et al.*, 2005, 2006, 2010a, 2010b). Some other aspects of its palaeobiology, such as the development, function or physiology of the intracranial cavities remained completely unknown, in spite of the excellent col-lection of skulls of this species recovered from Batallones-1. Thus, in the present paper we carry out the first study of the frontal sinuses of this prim-itive member of the Smilodontini, providing valu-able data for future comparisons with other sabre-toothed felids, in order to understand the evolution of these cavities in Felidae.

Material and methods

Material

The skull of *Promegantereon ogygia* (BAT-1'06 F6-57) analysed in this study belongs to the excep-tional collection from the Batallones-1 fossil site (Late Miocene, Vallesian, MN 10, Madrid) housed at the collections of the Museo Nacional de Cien-cias Naturales-CSIC (Madrid, Spain). This skull is one of the most complete and less deformed within the sample from Batallones-1, and was discovered during the excavations of 2006. Although CT Scan of other skulls of *P. ogygia* from Batallones-1 were performed, the fossils were severely flattened, the frontal sinuses being so collapsed that the speci-mens were not suitable for the present study.

For comparison, skulls of the following extant species of Felinae were used: one male *Panthera par-dus* (MAV-4882), one male *Puma concolor* (MAV-
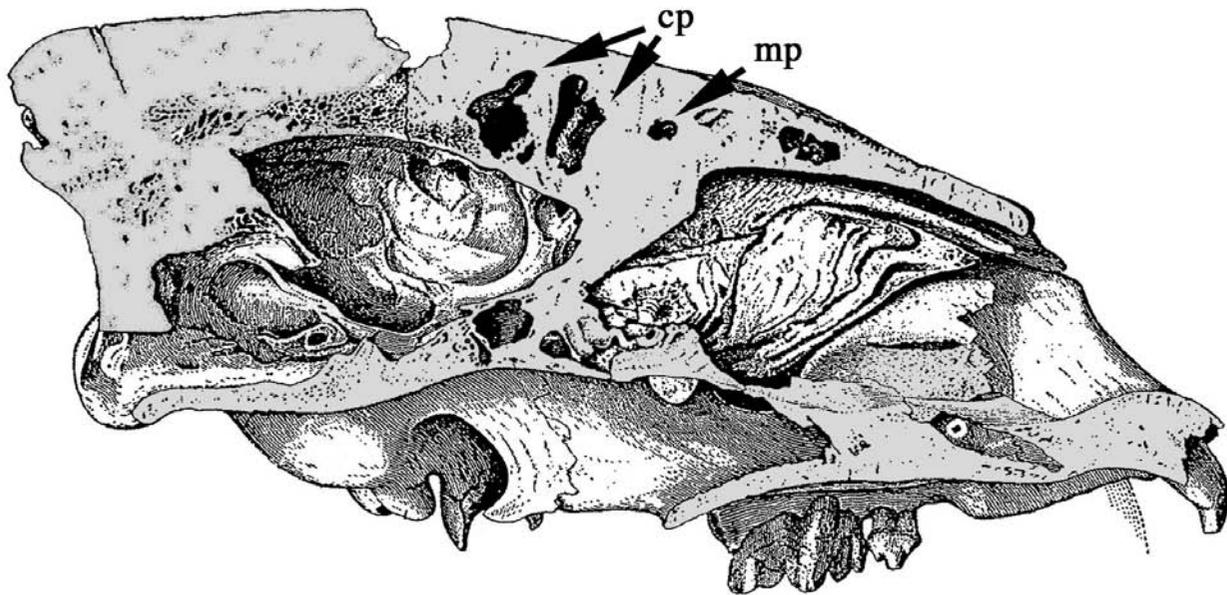
Fig. 2.—Sagittal section of the skull of *Smilodon fatalis* from Rancho La Brea (Los Angeles, USA) showing the development of the frontal sinus (modified from Merriam & Stock, 1932): cp, caudal portion of the frontal sinus; mp, medial portion of the frontal sinus.

3686), and one *Acinonyx jubatus* (MNCN-3438) of unknown sex. These specimens belong to the collections of the Museo Anatómico de la Universidad de Valladolid (Valladolid, Spain) (with the acronym MAV) and Museo Nacional de Ciencias Naturales-CSIC (Madrid, Spain) (with the acronym MNCN), and were chosen due to their similarity in size with *P. ogygia*, which eliminates any allometric effect in our study. The skull of *P. pardus* was scanned with its soft tissue, as it was also used for dissection.

Acquisition and processing of data

The skulls of *P. ogygia*, *P. concolor* and *A. jubatus* were scanned in coronal orientation on a Philips Brilliance 64 CT Scan at the Hospital Nuestra Señora de América (Madrid, Spain), with the following parameters: a slice thickness of 0.67 mm, and an inter-slice spacing of 0.33 mm, which generated a matrix size of 768 x 768 pixels. Scanner energy was 120 kV and 101mA for extant skulls, and 250 mA for the skull of *P. ogygia*. The head of *P. pardus*, with soft tissue, was scanned on a General Electric 64 CT at the Hospital Clínico Universitario (Valladolid) with the following parameters: slice thickness and inter-slice spacing of 0.625 mm, the matrix size was 512 x 512 pixels and scanner energy was 120 kV and 127.80 mA.

The acquired CT Scan data consist in a series of slices in coronal view, the number of which varies in each specimen depending on the size of the skull. These slices were obtained in DICOM format and were used for reconstructing and creating a 3-dimensional virtual model.

Processing of data

The slices obtained were imported into Mimics 9 (Materialise N. V.) software package, in which each slice is processed individually by a process of thresholding and a combination of manual and automatic segmentation. With this method, any internal structure of the skull can be clearly observed, and a 3D reconstruction of the frontal sinuses can be created through a virtual filling of this cavity.

Comparative description of frontal sinuses of *Puma concolor*, *Panthera pardus* and *Acinonyx jubatus*

The frontal sinus of *P. concolor*, *P. pardus* and *A. jubatus*, as that of other felids, is located between the external and internal tables of the frontal bone, developed following the shape of this bone, extending from the nasal process of the frontal bone to its
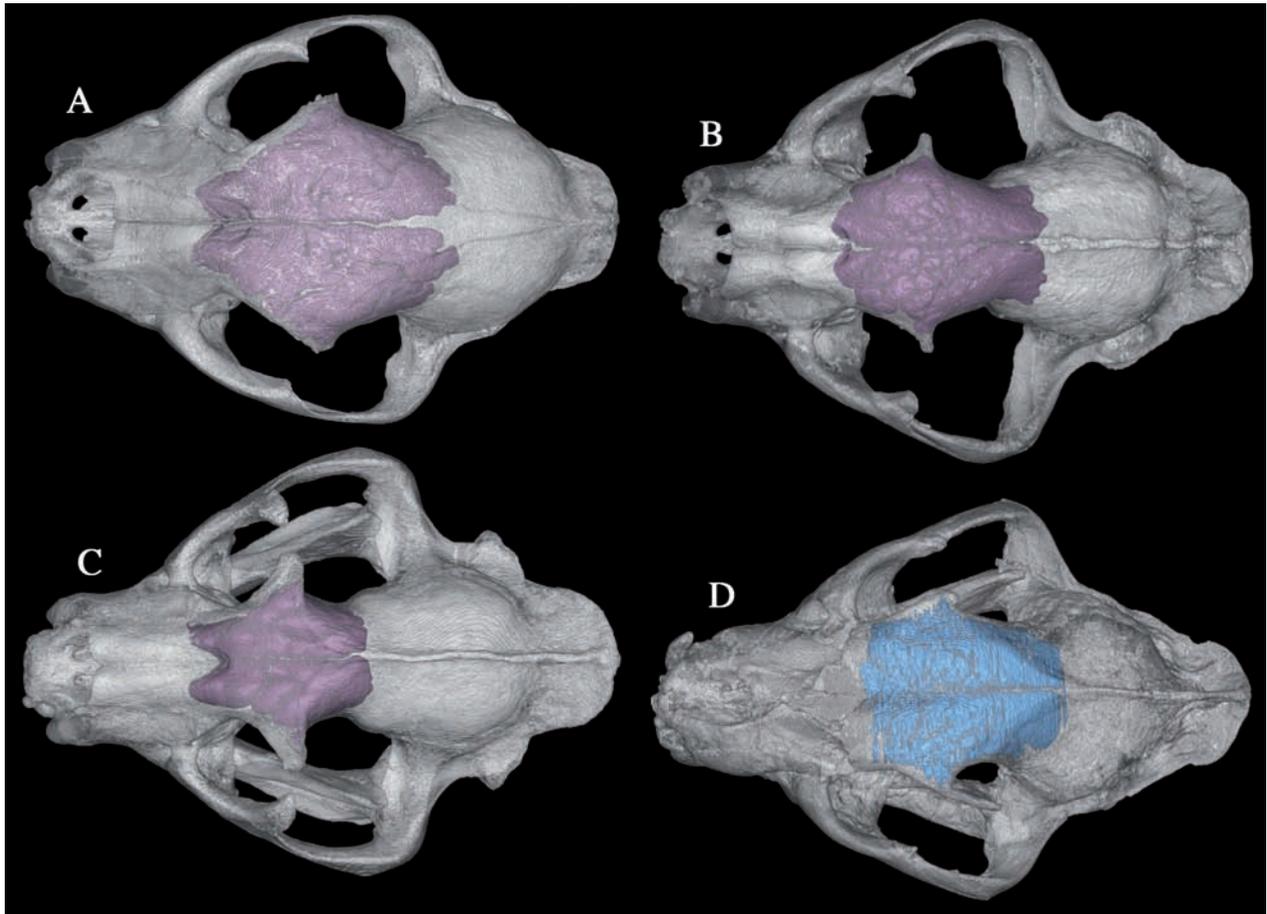
Fig. 3.—Digital reconstructions in dorsal view of the skulls of *Acinonyx jubatus* (A), *Puma concolor* (B), *Panthera pardus* (C) and *Promegantereon ogygia* (D), showing the virtual reconstruction of the volume occupied by the frontal sinus.

fronto-parietal suture (fig. 3). It shows a little developed rostral portion, although relatively larger than that of *F. catus*, and a caudal widening that follows the supraorbital margin, penetrating into the zygomatic process of the frontal bone (fig. 3). The development of the frontal sinus is similar in both sides, separated by means of the *septum sinuum frontalium*, which coincides with the interfrontal suture. The extension of the sinuses over the brain cavity is similar in three species, covering only its rostral portion. However, in *A. jubatus* and *P. concolor* the sinus extends more caudally than in *P. pardus* (fig. 3)

The internal table of the medial portion of the frontal sinus is irregular and discontinuous. The ethmoturbinates invade this region, developing several prolongations, being difficult to distinguish the ventral boundary of the sinus in this part. So, these ethmoturbinates prolongations constitute the ventral border of the sinus, separating it from the nasal cavity.

The rostral portion of the sinus is small and digitiform; it extends rostro-caudally, being filled with ethmoturbinates. Both *A. jubatus* and *P. concolor* show a small rostral extension, absent in *P. pardus*, which reaches the level of the frontal process of the nasal bone. This extension should not be strictly considered part of the frontal sinus, but just an internal concavity of the nasal bone, not derived from a pneumatisation process, named "recess" (Rossie, 2006; Farke, 2010). Therefore, we consider that in *A. jubatus*, *P. pardus* and *P. concolor* the rostral portion of the frontal sinus reaches the level of the fronto-nasal suture, and not beyond this (fig. 3).

Caudally to the rostral part of the frontal sinus, there is a reduced medial portion, hardly distinguishable from the rostral portion. Nevertheless, this portion is also occupied with ethmoturbinate
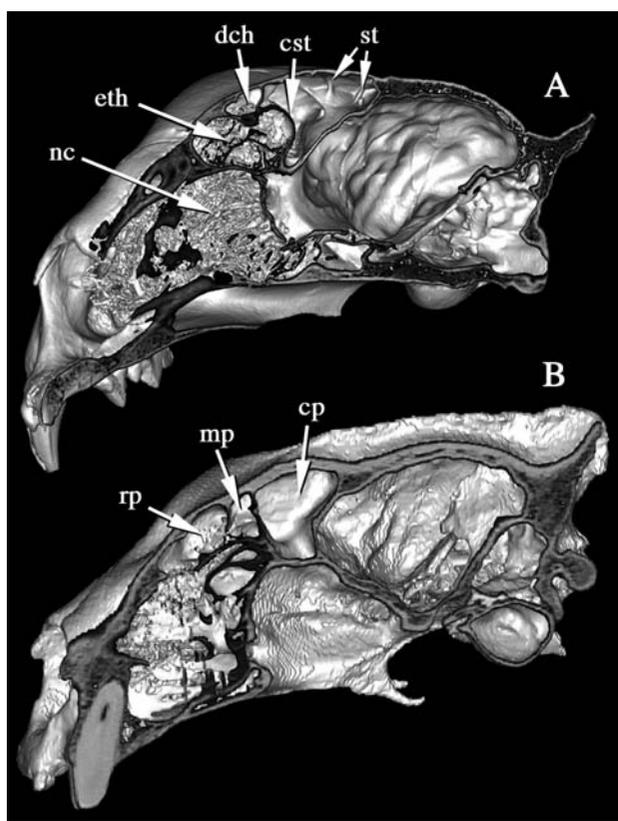
Fig. 4.—Sagittal sections of the virtual reconstructions of the skulls of *Puma concolor* (A) and *Panthera pardus* (B), showing the main structures and cavities within the frontal sinus: rostral portion (rp); medial portion (mp); caudal portion (cp); nasal cavity (nc) filled with the turbinates and the ethmoturbinates (eth); caudal strut (cst) separating the caudal portion from the rest of the sinus; dorsal chambers (dch); struts in the caudal end of the frontal sinus (st).
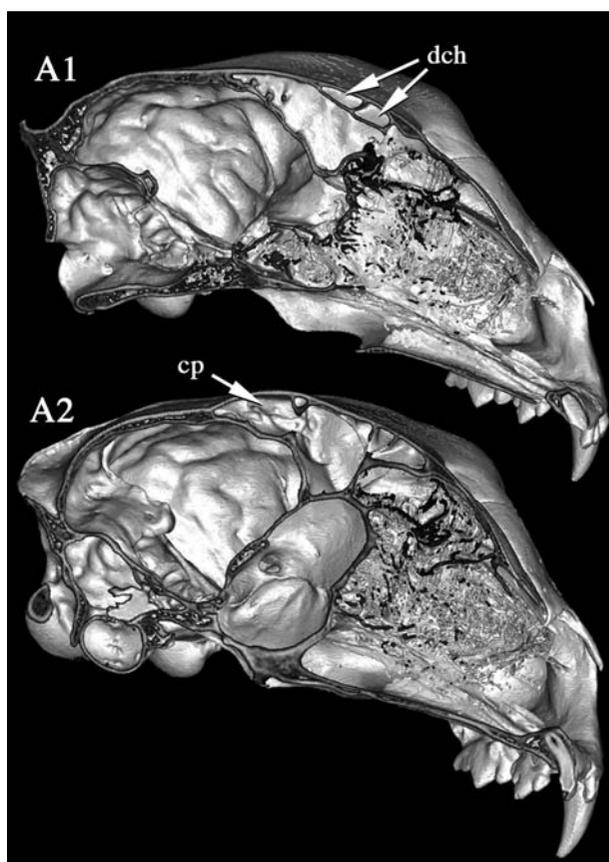

Fig. 5.—Two sagittal sections at different levels of the virtual reconstruction of the skull of *Acinonyx jubatus*. A1, dorsal chambers (dch) developed in the dorso-medial part of the sinus; A2, large caudal portion (cp) of the frontal sinus communicated with the dorsal chambers.

prolongations, even to a higher degree than in the rostral part in the three species. In *P. pardus,* this medial portion is more differentiated from the rostral one than in *A. jubatus* and *P. concolor*, having less ethmoturbinate prolongations inside (fig. 4B). These two later species show a nasal cavity totally occupied by dense packets of scrolling turbinates (ethmoturbinates, nasoturbinates and maxilloturbinates). Although in these three species, prolongations of the ethmoturbinates penetrate in the medial portion of the frontal sinus, in *A. jubatus* and *P. concolor* they show a greater development than in *P. pardus*, almost occupying the whole cavity of this portion (figs 4-5). There are few and small struts in the rostral and medial portions of the frontal sinus.

The caudal portion of the frontal sinus is the largest of the 3 portions, and it is well separated from the others by means of a sheet-like caudal strut. Unlike the rostral and medial portions, the ethmoturbinates do not invade massively the caudal portion, this cavity being almost empty, and its ventral boundary is clearly defined, formed by the ventral table of the frontal sinus (figs 4-5). This caudal portion is communicated with the nasal cavity through a slight prolongation of one of the ethmoturbinates. Both *A. jubatus* and *P. concolor* have relatively larger frontal sinus than *P. pardus,* with a caudal portion longer caudally (figs 3, 6). The *squama frontalis* (in the frontal bone) of these latter species has a vaulted shape, especially in *A. jubatus*, and is in that part of the frontal where the caudal portion of the frontal sinus is located (fig. 6).

Although *A. jubatus, P. pardus* and *P. concolor* have relatively simple frontal sinuses, with few bony struts, *A. jubatus* and *P. concolor* show a

great number of struts than *P. pardus*. Most of the struts are placed in the rostral and caudal extremes of the caudal portion of the sinus, at the level of the zygomatic process of the frontal bone, and in the caudal end of the sinus (figs 4-5). Also, both *A. jubatus* and *P. concolor* have a set of small chambers in the dorso-medial part of the sinus, and in the dorso-rostral part of the caudal portion of the sinus, resulted from the interconnection of the small struts situated in those parts (figs 4A-5). In *A. jubatus* these chambers are connected to the caudal portion of the sinus, whilst in *P. concolor* the chambers are isolated due to the more caudal situation of the caudal strut (figs 4A-5); also, in this latter species, the strut is curved, with a concave rostral face and a convex caudal one, producing an increase in the volume of the medial portion at expenses of the caudal one.

Finally, in dorsal view, the different development of the frontal sinus can be observed, with *P. pardus* showing a clearly shorter sinus than *A. jubatus* and *P. concolor*. Besides this, whereas in *P. pardus* and *A. jubatus* the sinus gradually becomes narrower caudally, in *P. concolor* the sinus shows a marked post-orbitary constriction (fig. 3).

Morphology of the frontal sinus in *Promegantereon ogygia*

The studied skull of *P. ogygia* from Batallones-1 shows a good state of preservation, although unfortunately, as in most of the fossil skulls of mammals, the ethmoturbinates are not preserved. Its internal cavities keep the three-dimensional structure except for a small collapsed area near the naso-frontal suture, which prevents the description of the rostral portion of the sinus. In spite of this, and although no 3D reconstruction can be made of this portion, the fronto-nasal suture, the predictable rostral limit of this portion, is visible.

The extension of the frontal sinus in *P. ogygia* is directly correlated with the extension of the frontal bone, as in the studied felines; it is limited rostrally by the naso-frontal suture, and caudally by the fronto-parietal suture. In dorsal view, the frontal sinus, which has a very reduced rostral portion, follows the morphology of the frontal bone, extending caudally and penetrating into the zygomatic process of the frontal; then, the sinus narrows following the shape of the post-orbitary constriction of the frontal, and finishes at the level of the fronto-parietal suture (fig. 3D).

The internal table of the frontal bone in the caudal portion of the sinus is well preserved, but in the medial and rostral portions this table is so fragmentary that it cannot be described. The caudal portion of the frontal sinus is the best preserved of the three portions. The *septum sinuum frontalium*, which divides both left and right sides, is well developed, and coincides with the interfrontal suture, as in other felids. In the caudal end of the sinus, several struts are seen.

The general shape of the sinus of *P. ogygia* is similar to that of *P. concolor*. In dorsal view it extends more caudally, and it is wider than that of *P. pardus*, although it is caudally shorter and narrower than that of *A. jubatus*, in accordance with the morphology of the frontal bone (fig. 3). However, the caudal end of the sinus in *P. ogygia* does not show any trace of constriction and posterior widening, and the caudal strut, which separates the caudal portion from the rest of the sinus, is more or less straight, unlike the curved strut seen in *P. concolor*.

In the medial portion of the sinus there are several struts within the sediment filling the cavity; some of them seem to keep their original position, whilst others just maintain their connection to the dorsal wall of the sinus. These struts are similarly located as in the compared species, but they are relatively more abundant than in *P. pardus*, resembling to morphology seen in *P. concolor* and *A. jubatus*. Nevertheless, nothing more can be said on their degree of complexity or on the possible existence of chambers.

Discussion

As in other groups of mammals, the size and morphology of the frontal sinuses of felids are closely correlated to those of the frontal bone. This intracranial cavity is relatively simple in felids, and does not show great variability in both extension and development. Nevertheless, within the studied species, some differences in relative size and number of struts are found, with *A. jubatus* showing the relatively largest frontal sinuses. Also, this species shows a typical dome-shaped skull, linked to larger frontal sinuses than those of other felids, and characterised by an inflated caudal portion with a higher number of small struts in its dorso-medial part, which interconnect forming several small chambers (figs 4A-5). This latter feature is shared by *P. concolor*, which also shows a vaulted frontal bone,
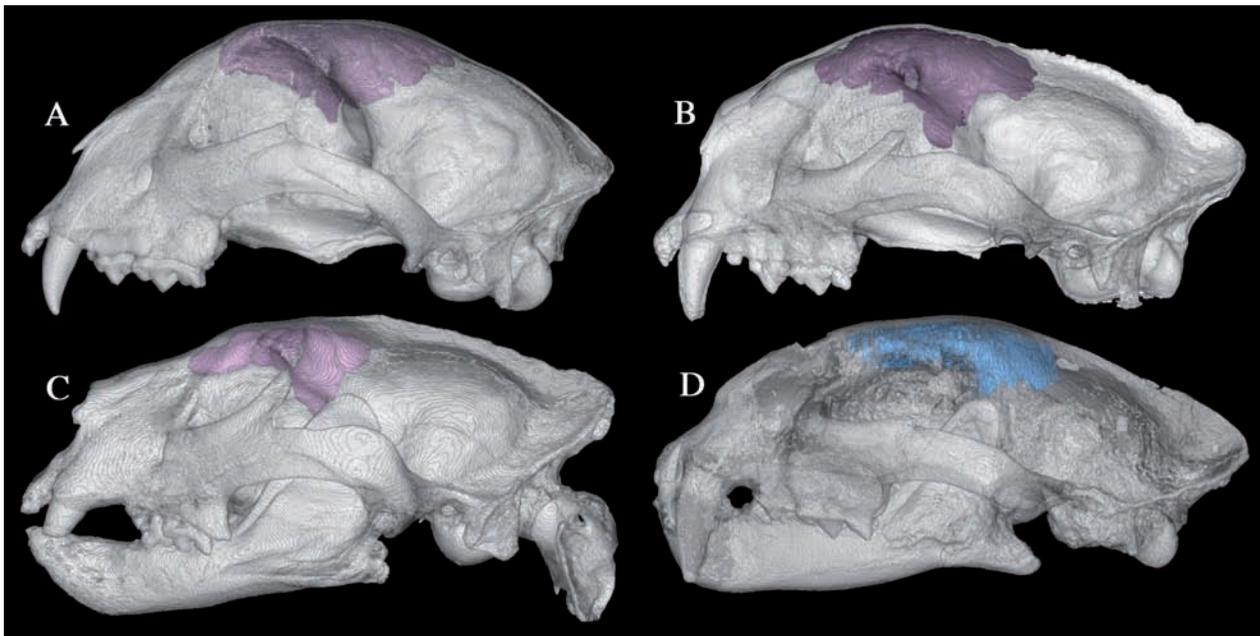
Fig. 6.—Digital reconstructions in lateral (left) view of the skulls of *Acinonyx jubatus* (A), *Puma concolor* (B), *Panthera pardus* (C) and *Promegantereon ogygia* (D), showing the virtual reconstruction of the volume occupied by the frontal sinus.

although lacking the dome-shaped skull observed in *A. jubatus*. On the other hand, the frontal sinuses of *P. pardus* are rostro-caudally shorter, with a less developed caudal portion, and lacking the chambered dorso-medial portion. In these features, the sinus of *P. pardus* resembles that of *Felis catus*, probably reflecting the primitive condition for Felidae. At this respect, it is remarkable that the frontal sinus of *P. ogygia* shares the caudal elongation seen in *P. concolor* and *A. jubatus*, and even the sabre-toothed felid could have had the chambers observed in the dorso-medial part in these two species, or at least a higher number of struts than *P. pardus*. This similarity between *P. ogygia*, *P. concolor* and *A. jubatus* cannot be easily explained, as there is no consensus on the function of the frontal sinuses. Anyway, the caudal development and the chambered region could have derived independently in both groups, as they are not closely related.

As mentioned before, the function of the frontal sinus in felids, or mammals in general, has not been satisfactorily explained. Negus (1957, 1958) proposed an olfactory function for the frontal sinuses of Carnivora, as the surface of the olfactory epithelium is increased by the complex system of scrolled ethmoturbinates, which are housed in the sinus cavity; following this, the presence of empty frontal sinuses would be explained by a reduction in the complexity of the ethmoturbinates. For other authors (Rui *et al*., 1960; Witmer, 1997) frontal sinuses would be primarily empty cavities, and macrosmatic mammals (those with well developed olfactory sense) would have experimented a secondary expansion process of the ethmoturbinates into the sinus cavities. Nevertheless, as shown by our analysis, both *A. jubatus* and *P. concolor* have well developed ethmoturbinates, but they only occupy the medial portion of the sinus, the inflated caudal portion almost lacking ethmoturbinates. This would clearly disagree with this "olfactory hypothesis", as would the fact that these two species do not show differences in their sense of smell in relation to other felids.

Other proposed functions for the large frontal sinus of *A. jubatus* are the warming and humidification of the inhaled air that penetrates in the respiratory system (Krausman & Morales, 2005; Lecastre & Flamarion, 2010) and the thermoregulation of the brain and related sense organs (Bignon, 1889; Bremer, 1940; Proetz, 1953; Verheyen, 1953; Dyce *et al*., 1987). The former hypothesis has been convincingly refuted (Proetz, 1953; Blanton & Biggs, 1968; Shea, 1977; Witmer, 1997), whilst the other could be more plausible at least for some groups (Bignon, 1889; Bremer, 1940; Proetz, 1953; Verheyen, 1953; Dyce *et al*., 1987). In this latter hypothesis, the air

chamber formed by the sinus would act as thermal insulator of the central nervous system, and thus the observed differences in relative size and caudal expansion in the frontal sinuses of *P. concolor*, *A. jubatus*, *P. ogygia* and *P. pardus* would imply differences in the capacity for brain thermal insulation, with *P. pardus* having the shortest sinus, and thus this function relatively reduced. *Acinonyx jubatus* are found in low-structured habitats, such as savannas or grasslands with some shrub coverage (Alderton, 1998; Bothma & Walker, 1999; Nowak, 2005), whereas *P. pardus* and *P. concolor* can occupy a range of very different habitats, from arid savannas to dense tropical forests (Currier, 1983; Johnson *et al.*, 1993; Alderton, 1998; Bothma & Walker, 1999; Nowak, 2005). Nevertheless, recent studies on molecular phylogeny show *A. jubatus* and *P. concolor* as closely related taxa (Mattern & McLennan, 2000; Yu & Zhang, 2005; Johnson *et al.*, 2006), and their sharing of a long frontal sinus, although having strong physiological implications, would be reflecting their inheritance from a common open habitat-dweller ancestor (Van Valkenburgh *et al.*, 1990; Hemmer *et al.*, 2004) with high capacity for brain thermal regulation. The morphology observed in *P. ogygia*, more similar to those of *P. concolor* an *A. jubatus* than that of *P. pardus*, poses an interesting question on its palaeoecology, as the inferred habitat for this machairodontine felid is a more or less closed habitat (Salesa *et al.*, 2006). A possible explanation may be associated with the progressive aridification process that occurred during the Vallesian and Turolian of Europe (Fortelius *et al.*, 2002), which led to the predominance of savannas over wooded habitats. The caudally expanded frontal sinus of *P. ogygia* would be reflecting an adaptation to these new climatic conditions, where the insolation was higher than in wooded habitats. Nevertheless, the frontal sinus of *P. ogygia*, and those of all the analysed felids, extends as far as the level of the fronto-parietal suture, this is, the sinus expands caudally following the development of the frontal bone. According to this, any environmental explanation for this expansion should be established with caution, even if we consider that the derived *Smilodon fatalis*, the last Smilodontini, associated to relatively open environments (Gonyea, 1976; Kurtén & Werdelin, 1990; Stock & Harris, 1992; Coltrain *et al.*, 2004), shows this caudal expansion in the frontal sinus as much developed as *P. ogygia* (fig. 2).

The other observed difference in the frontal sinus of the analysed felids, this is, the presence in *A. jubatus* and *P. concolor* of several struts in the dorso-medial part of the frontal sinus, absent in *P. pardus*, could be related to the necessity of a reinforcement in the larger cavities of the two former species, due to the greater tensions and biomechanical demands that a more inflated sinus requires (Witmer, 1997). This dorso-medial part of the frontal sinus is damaged in the analysed specimen of *P. ogygia*, but it could have contained several struts, as indicated in the descriptions above. Nevertheless, these struts would not be reinforcing a large dorso-medial part of the sinus, as this is not inflated, but they could be necessary if great tensions occurred in this part when the animal killed its prey. The killing technique employed by the sabre-toothed felids, the so-called "canine shear-bite", based on a strong flexion movement of the head (Emerson & Radinsky, 1980; Akersten, 1985; Turner & Antón, 1997; Antón & Galobart, 1999) could imply an increase in the stress experimented by the frontal bone, and thus the need for some kind of reinforcement in this area. Several cranial and dental features support the development of this killing technique in *P. ogygia* (Salesa *et al.*, 2005), and thus, it could be possible for these struts to have played a role in resisting the tensions generated during the machairodont bite. The results of the present study on the size and shape of the frontal sinus in *P. ogygia* are not enough to support this interpretation, and the use of different techniques for assessing the resistance of the skull of this species would be highly valuable. One of these methods, the Finite Element Analysis has been recently used to quantitatively assess the biomechanical performance of the skull of *S. fatalis* during the bite, showing that a moderate stress is produced in the frontal bone during this action (McHenry *et al.*, 2007: fig. 4C). Future studies on the skulls of *P. ogygia* from batallones-1, using this methodology, will help to elucidate the functional implications of the observed morphology of frontal sinuses and related structures in this primitive sabre-toothed felid.

Conclusions

The morphology of the frontal sinuses of *P. ogygia* has revealed as being more derived than could be expected considering that this species is one of the most primitive of the machairodontines. The caudal expansion of the sinus could be reflecting a

more open habitat than previously inferred for this species, whereas the presence of several struts in the dorso-medial part of the sinus would indicate a reinforcement of the frontal bone in relation to the canine shear-bite. Nevertheless, the present work must be considered as a first approach to these aspects of the palaeobiology of this primitive sabre-toothed felid, and further studies are need in order to complete our results.

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