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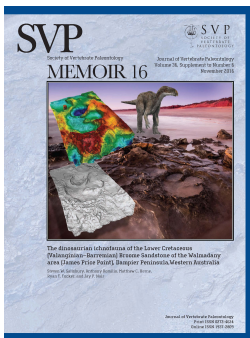
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UNIQUE FRONTAL SINUSES IN FOSSIL AND LIVING HYAENIDAE (MAMMALIA, CARNIVORA): DESCRIPTION AND INTERPRETATION

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ABSTRACT—Unique, caudally elongated frontal sinuses 2' (terminology of Paulli, 1900c) are present in the living hyaenine hyaenids (*Crocota crocuta*, *Parahyaena brunnea*, *Hyaena hyaena*) and in at least four fossil hyaenids (*Adcrocuta eximia*, *Hyaenotherium wongii*, *Palinhyena reperta*, and *Ictitherium viverrinum*). In *Crocota crocuta*, *Parahyaena brunnea*, *Hyaena hyaena*, and *Adcrocuta eximia*, the elongated frontal sinuses completely overlie the brain cavity, a condition apparently unique in the history of the Carnivora. Elongated frontal sinuses are conspicuously absent in the extant aardwolf (*Proteles cristatus*), however. The cladogenetic distribution of these fossil and living hyaenid species is broad enough to indicate a persistent difference in skull architecture between proteline and hyaenine hyaenids through time. The elongated frontal sinuses in all hyaenids examined in this study except for *Proteles* is an impressive pattern, and its potential function is unlikely to be related to shock dissipation, brain cooling, olfaction, or maximization of muscle attachment area. With the application of basic structural engineering principles, however, the elongated frontal sinus can be modeled as a shell structure that provides better resistance to muscular load than the cantilever plate geometry of the typical plate-like mammalian sagittal crest.

INTRODUCTION

Adults of the three extant species of hyaenine hyenas, the spotted hyena (*Crocota crocuta*), brown hyena (*Parahyaena brunnea*), and striped hyena (*Hyaena hyaena*), have caudally elongated frontal (frontoparietal) sinuses that completely overlie the brain cavity (Figs. 1, 2C, D, 3). These elongated sinuses extend caudad far enough to actually overhang the occiput. Elongated frontal sinuses of the grade of development apparent in adult hyaenine hyenas are conspicuously absent in young juvenile hyenas (Fig. 2C). Elongated frontal sinuses are also absent in mature individuals of the aardwolf (*Proteles cristatus*), the fourth living hyaenid species (Fig. 3). Caudal elongation is one of two trends in frontal sinus evolution in hyaenids, the other being the anterior enlargement or "vaulting" (Werdelin, 1989) of the sinus directly dorsal and caudal to the orbits, which produces the characteristic profile of living hyaenine hyaenids.

The peculiar caudal extension of the frontal sinuses visible in *Crocota crocuta*, *Parahyaena brunnea*, and *Hyaena hyaena* is not limited to those living species alone, however. Elongated frontal sinuses also appear in at least four fossil hyaenids: *Adcrocuta eximia*, *Hyaenotherium wongii*, *Palinhyena reperta*, and *Ictitherium viverrinum* (Figs. 3, 4), species that appeared as early as the early late Miocene in the Old World (L. Werdelin, pers. comm.). The fossil hyaenid *Adcrocuta eximia* and the living hyaenids *Crocota crocuta*, *Parahyaena brunnea*, and *Hyaena hyaena*, which are closely related in a cladistic analysis (Werdelin and Solounias, 1991), appear to be the only carnivorans ever to elongate the frontal sinuses enough to overlie the brain cavity completely. These four species all have the characteristic modern non-proteline hyaenid lateral skull profile, which is produced by the enlarged anterior part of the frontal sinus and the resultant "vaulted" forehead (Werdelin, 1989; Werdelin and Solounias, 1991). Markedly enlarged anterior frontal sinuses and vaulted foreheads also appear in certain fossil canids presumed to be ecological vicars of living bone-cracking hyenas (Werdelin, 1989), but the skulls of these canids lack comparable caudal extension of the frontal sinuses.

The remaining three fossil hyaenid species discussed herein (*Ictitherium viverrinum*, *Hyaenotherium wongii*, *Palinhyena*

reperta) show lesser similarity to the modern hyaenine skull profile than *Adcrocuta eximia* does, although the skull (AMNH 129667) assigned by Werdelin and Solounias (1991) to *Palinhyena reperta* clearly resembles the modern hyaenine skull form, and may actually be a juvenile of *Adcrocuta eximia*.

Paulli (1900c:501) described the frontal sinus as "eine recht große pneumatische Höhle" (literally: "a right large pneumatic hole") in a young adult specimen of *Hyaena hyaena*; this caudally elongated sinus became sinus 2' in his terminology (Paulli, 1900c:figs. 4, 5, 8–10). Buckland-Wright (1969), however, appears to have been the first researcher to publish significant anatomical details of the caudally elongated frontal sinuses of living hyaenids. Subsequent work by Buckland-Wright (1971, 1978) and Werdelin (1989) discussed the possible architectural significance of anterior expansion of the frontal sinuses in carnivores, primarily by analyzing their potential role in the distribution of premolar biting stresses through the cranium. The evolutionary history of hyaenid frontal sinuses, however, has not been documented, and a comprehensive review and analysis of frontal sinuses in both living and fossil hyaenids is lacking. Consequently, the purposes of this study are to: 1) document the internal cranial morphology of selected fossil Hyaenidae; 2) provide a comprehensive comparison of cranial morphology in both fossil and living Hyaenidae; and 3) hypothesize the evolutionary significance of the elongated frontal sinus in the Hyaenidae. In approaching the evolutionary significance of the elongated frontal sinuses, I have attempted to examine possible functional relationships between the frontal sinuses, cranial architecture, ontogeny, the jaw musculature, and the olfactory apparatus.

MATERIALS AND METHODS

Computed tomography (CT) methods used in this study are similar to those used in Joeckel and Stavas (1996a, b), but several measurement methods were applied to both CT scan images and actual skulls. In order to assess any potential relationship of frontal sinus enlargement to increased muscle attachment area on the skull, I measured temporal area (i.e., the approximate attachment area of the temporalis muscle) on the skulls of representative species of carnivorans. These measure-

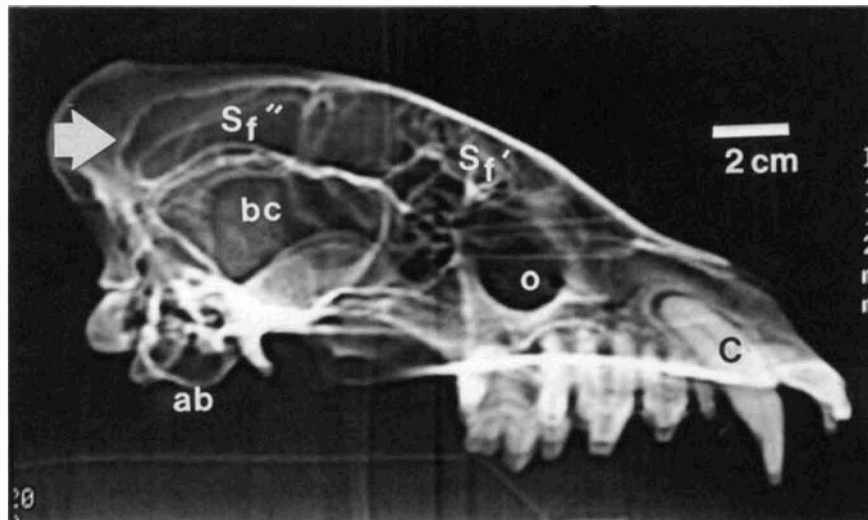


FIGURE 1. Skull of *Hyaena hyaena* (KU 82296, sex unknown), showing anterior part of frontal sinus (Sf') with bony trabeculae; caudally elongated part of frontal sinus (Sf''), or sinus 2' of Paulli (1900c), with maximum caudal extent marked by white arrow; brain cavity (bc), over which frontal sinus extends; orbit (o); auditory bulla (ab), and upper canine (C). Other abbreviations for anatomical features used in this paper: petrosal (P), pterygoid (Pt), sagittal crest (sc), sphenoid sinus (Ss), zygomatic arch (z).

ments were made by applying thin sheets of aluminum foil to each skull and then successively shaping the foil by hand and trimming it with a fine blade to produce an exact contact model of the temporal surface area of the skull. Each foil model was carefully removed from its skull, pressed flat, and optically scanned to produce a PICT computer graphics file. These PICT images were scaled to actual size and measured in "NIH Image," a free measurement program for the personal computer, circulated by the United States National Institutes of Health. Linear measurements (lengths and widths of sinuses) were made directly from CT scan images and conventional X-ray images of skulls, and from the skulls themselves using metric calipers, and area measurements of sinuses were made from images scanned as PICT files and analyzed in the computer graphics program Canvas[™]. Facial flexion measurements were made from both CT scan scout images (lateral images used to position the scanning interval through a given specimen) and conventional radiographs by replicating the basicranial and palatal axes on tracing paper using a straightedge, and then measuring the angle between these axes. In this method, the basicranial axis is relatively easy to represent as a straight line, but the palatal axis is more difficult to determine because the palate itself is concave, arching dorsad. Therefore, as a general rule, I drew the palatal axis as a straight line in the sagittal plane, extending from the caudal margin of the palate to the incisor alveoli at the termini of the premaxillaries. Tracings of the basicranial and palatal axes were optically scanned as PICT files and their angular orientations were measured using the line tool in Canvas[™].

Crania of living hyaenids and other carnivores were obtained from the American Museum of Natural History (AMNH), University of Nebraska State Museum (UNSM and UNSM-ZM), University of Kansas Mammalogy Collection (KU), and the Field Museum of Natural History (FMNH). The fossil hyaenid crania examined in this study are from the collections of the American Museum of Natural History (AMNH). Systematics used in this study follow the recent revisions of Werdelin and Solounias (1991).

RESULTS

I examined specimens from eight fossil and living hyaenid species (*Crocota crocuta*, *Hyaena hyaena*, *Parahyaena brun-*

nea, *Proteles cristatus*, *Adcrocuta eximia*, *Hyaenotherium wongii*, *Ictitherium viverrinum*, and *Palinhyena reperta*; see Appendix), which together represent much of the range of body size (Table 1) and morphological diversity expressed by the Hyaenidae since the middle Miocene (see Werdelin and Solounias, 1991). There are no easily recognizable hyaenids in the fossil record prior to 18 Ma (Hunt, 1996), so it is likely that the above species do, in fact, constitute an representative sampling of morphotypes. *Ictitherium viverrinum* is flat-skulled compared to modern hyaenids and *Hyaenotherium wongii* has a canid-like skull profile (Fig. 4), whereas *Adcrocuta eximia*, *Crocota crocuta*, *Hyaena hyaena*, and *Parahyaena brunnea* (Fig. 3) all have large, very robust skulls with strongly vaulted foreheads (sensu Werdelin, 1989; Werdelin and Solounias, 1991), broad palates, large premolars, and robust mandibles (the typical skull form of extant hyaenids excluding *Proteles*). *Palinhyena* was a small animal compared to modern non-proterline hyenas, but it has a skull form that grades towards the extant hyaenine hyaenid skull in its moderate expression of forehead vaulting (Werdelin and Solounias, 1991). Finally, the skull of *Proteles* has: 1) a generalized (i.e., not hyaenine-like) carnivorous lateral skull profile lacking a vaulted forehead; 2) a much-reduced dentition; and 3) weak dentaries compared to the robust ones of hyaenine hyenas. Relative to skull length, the attachment area of the temporalis muscle in hyaenids is greater than in the representative canids measured in the study, but it is not strikingly different from representatives of other carnivorous families (Felidae and Ursidae) having similar skull size (Fig. 5).

Facial flexion in the fossil and living hyaenids examined varies in all between $+8^\circ$ (*Palinhyena reperta*) and -16° (*Parahyaena brunnea*), but results show that facial flexion can vary widely within an individual species (Table 2). Almost all of the hyaenid specimens examined show low to moderate negative (ventrad) facial flexion. A near-adult specimen assigned by Werdelin and Solounias (1991) to *Palinhyena reperta* (AMNH 129667) shows the most positive facial flexion and also the least extension of the frontal sinus over the brain cavity among the adult hyaenids examined (except for *Proteles cristatus*); this specimen, however, is a juvenile. Likewise, *Ictitherium viverrinum* (AMNH 129665) shows the second most positive facial

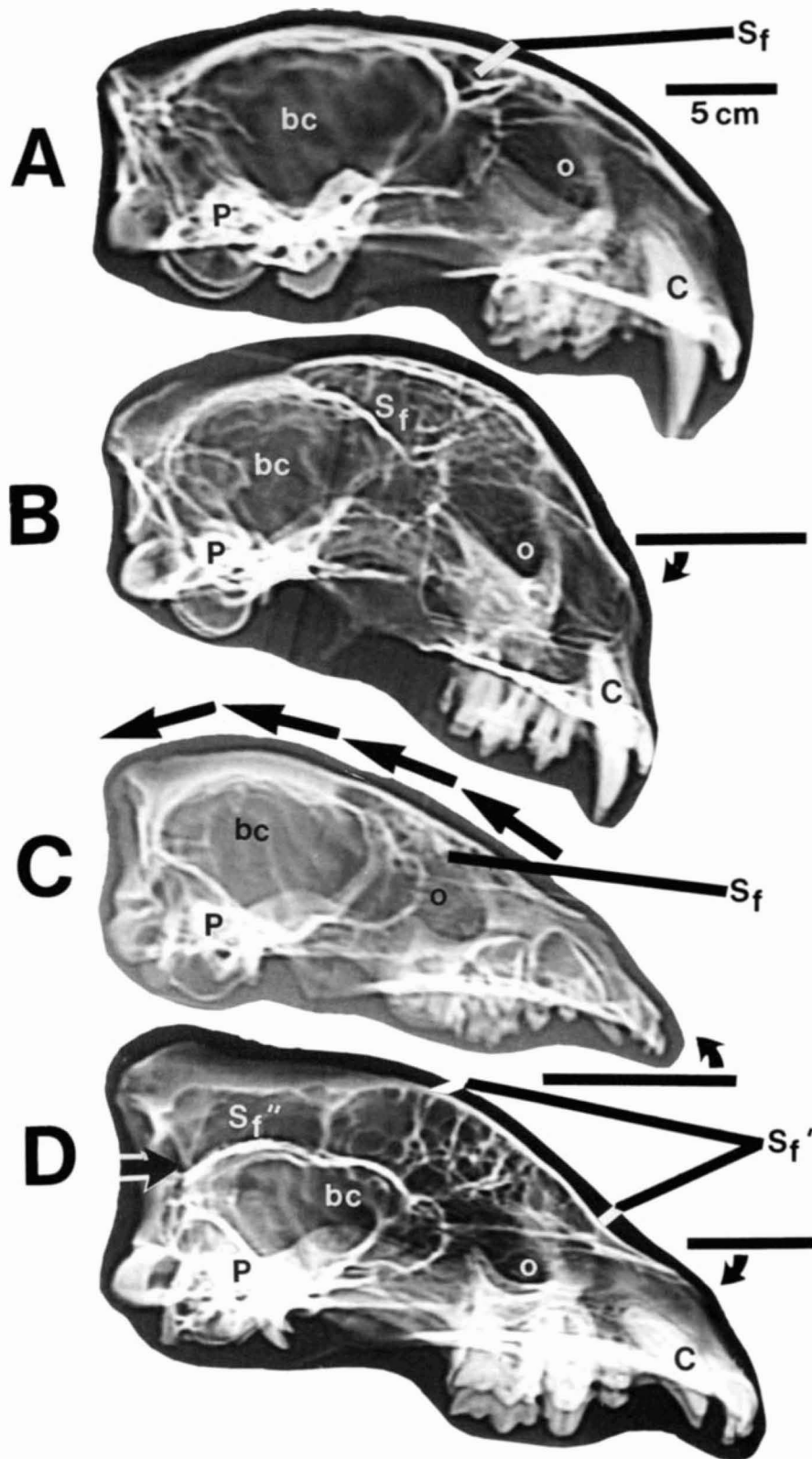


FIGURE 2. CT scout images of felids and hyaenids, oriented with basicranial axis approximately horizontal. **A**, skull of male *Panthera tigris* (ZM 14583), showing typical arrangement of frontal sinus (**Sf**) and brain cavity (**bc**) in aeluroid carnivorans. **B**, skull of cheetah (*Acinonyx jubatus*, ZM 16913, sex unknown), showing unusual arrangement of frontal sinus (**Sf**), which affects dome-like skull profile. **C**, skull of juvenile *Crocuta crocuta* (ZM 5102), showing frontal sinus (**Sf**) which has not yet elongated to overlie brain cavity (**bc**) but which will follow growth trajectory indicated by black arrows. **D**, skull of adult *Crocuta crocuta* (KU 145515, sex unknown), showing anterior part of frontal sinus (**Sf'**) with bony trabeculae and caudally elongated part of frontal sinus (**Sf''**), or sinus 2' of Paulli (1900c), extending over brain cavity (**bc**). Scale bars (shown with arrows in **B**, **C**, and **D**) all represent 5 cm.

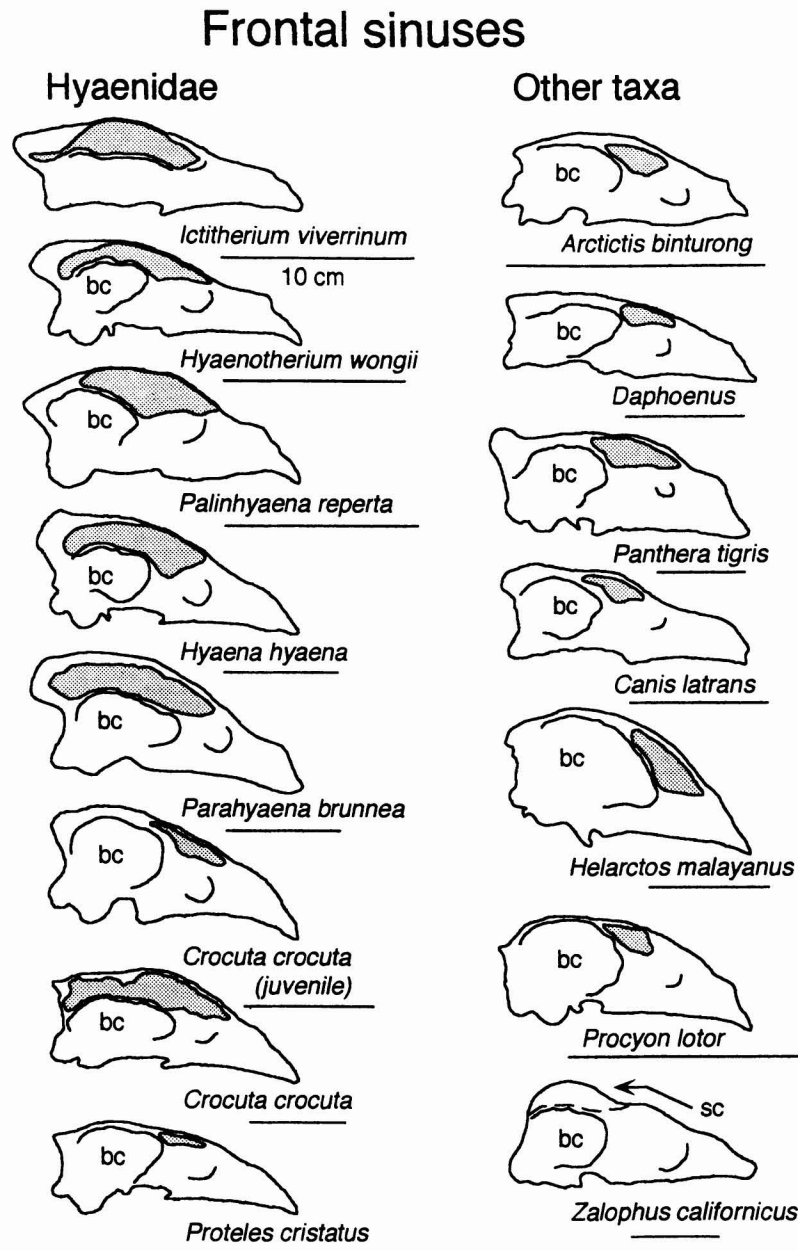


FIGURE 3. Frontal sinuses (shaded) in selected fossil and living carnivorans, traced from CT scout images. Note large, caudally elongated frontal sinuses in all adult hyaenids shown except for *Proteles cristatus*. *Zalophus californicus* (sea lion), diving marine mammal, lacks frontal sinus, and plate-like sagittal crest (sc) directly overlies the brain cavity (bc). Scale bars all represent 10 cm.

flexion and also the second least extension of the frontal sinus over the brain cavity (Figs. 3, 6).

Living Hyaenidae

In the living non-proteline (i.e., hyaenine) hyenas, the transverse cross-sectional area of the elongated frontal sinuses can exceed 45% of the transverse cross-sectional area of the brain, even in the posterior third of the skull (Fig. 7A–C). In this group, the elongated sinus 2' is generally a patent, albeit irregularly-shaped, space extending caudad from the olfactory chamber to the inion; it lacks any continuous transverse septa or consistent partitioning into separate sub-chambers. There may be an irregular "pocket" or sub-sinus toward the anterior end of sinus 2' (e.g., *Crocuta crocuta*, AMNH 114226) in some individuals. There is a thin floor of bone separating sinus 2'

from the brain cavity below, giving the paired elongated sinus the distinct appearance of a large attic atop the brain. The right and left sinuses are partially to completely (e.g., *Crocuta crocuta*, AMNH 169448) separated at the midline by a very thin bony partition. In one specimen (*Crocuta crocuta*, AMNH 114226), the right and left sinuses are not separated from each other posteriorly by such a partition. The right and left sinuses are frequently asymmetrical in the living hyaenine hyaenids, and there is considerable variation in the geometry of the sinuses between individuals. In some of the adult hyaenine hyenas examined, the walls of sinus 2' are smooth, but in others (e.g., AMNH 114226) they are densely and finely grooved, probably by blood vessels in life. This latter condition probably indicates active sculpting of bone in the walls of sinuses by resorption during particular intervals of time.

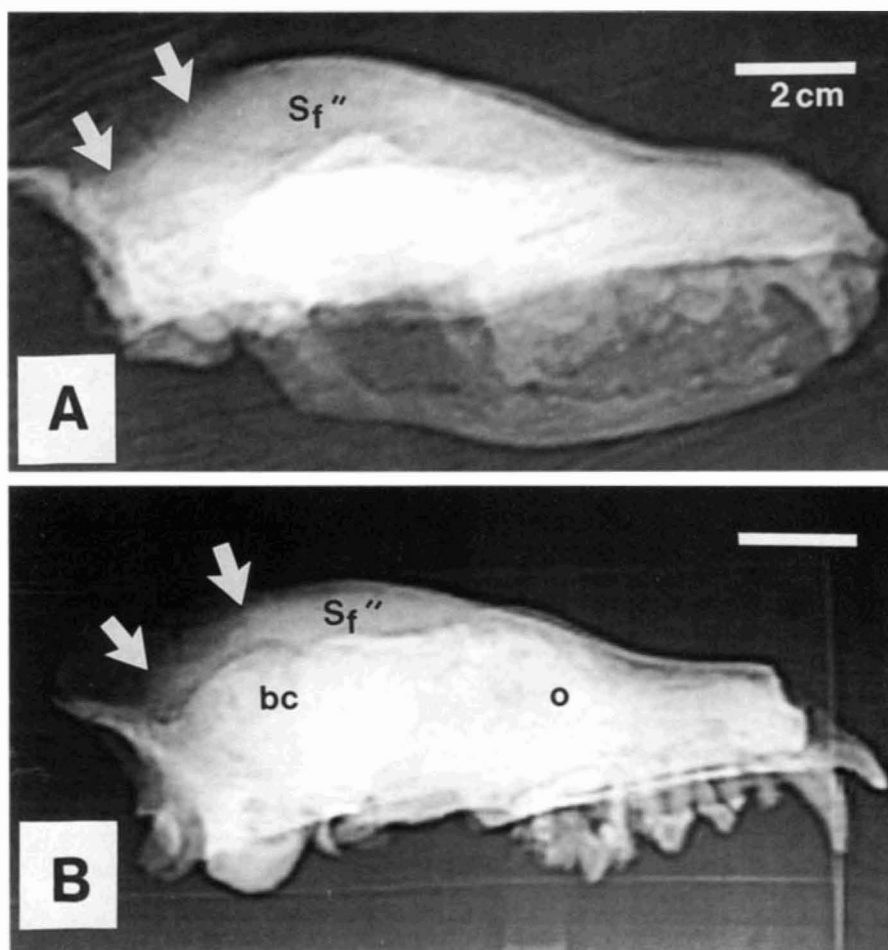


FIGURE 4. **A**, skull of fossil hyaenid *Ictitherium viverrinum* (AMNH 129665), showing caudally-elongated frontal sinus (Sf''). **B**, skull of fossil hyaenid *Hyaenotherium wongii* (AMNH 129666), showing caudally elongated frontal sinus (Sf''). In both specimens, posterodorsal extent of frontal sinuses indicated marked by white arrows, which lie partially on the plate-like part of the sagittal crest. Scale bars represent 2 cm.

Lateral CT scout images and conventional lateral radiographs of *Crocota crocuta*, *Parahyaena brunnea*, and *Hyaena hyaena* (but not *Proteles cristatus*) show that the enlarged anterior part of the frontal sinus ("vaulted forehead" of Werdelin, 1989) contains conspicuous bony trabeculae (Figs. 1, 2D), which are actually incomplete to complete partitions subdividing four to six bilaterally symmetrical divisions of the frontal sinus into which the scrolls of the ethmoturbinates partially extend. This geometry is actually much more complicated than that presented by Paulli (1900c), and, in fact, it is indecipherable from either his schematic illustrations or his descriptions.

TABLE 1. Condylbasal length in living and fossil hyenas; *Proteles cristatus* is only species lacking caudally elongated frontal sinuses.

Species	Condylbasal length (cm)
<i>Adcrocuta eximia</i> (AMNH 129664)	21.7
<i>Crocota crocuta</i>	18.25–25.0
<i>Hyaena hyaena</i>	20.6–22.4
<i>Hyaenotherium wongii</i> (AMNH 129666)	14.0
<i>Ictitherium viverrinum</i> (AMNH 129665)	12.5
<i>Palinhyena reperta</i> (AMNH 129667)	12.5
<i>Parahyaena brunnea</i>	22.1–22.9
<i>Proteles cristatus</i>	12.64–14.26

Fossil Hyaenidae

A specimen of *Ictitherium viverrinum* (AMNH 129665) has a transversely broadened brain cavity that matches the low profile of the skull (see Werdelin and Solounias, 1991). This skull is slightly damaged, but details of CT scans and the general symmetry of the skull, both externally and internally, indicate that the effects of diagenetic crushing are minor and that the head of the animal probably did have a very low profile in life (Fig. 4A). AMNH 129665 has nearly symmetrical left and right sinuses 2', each of which is roughly right triangle-shaped in transverse cross section through the sagittal crest (Fig. 8B). The sinuses extend caudad as far as the transverse level of the middle of the auditory bullae; the sinuses disappear caudad at the dorsal apex of the tentorium, at which point the left sinus is larger than the right sinus. There is a continuous median bony partition between the paired sinuses, and the floor of the sinuses (also the roof of the brain cavity) is nearly perfectly horizontal. Curiously, in AMNH 129665 the cross-sectional area ratio of the elongated frontal sinuses to the brain cavity is not the lowest among the hyaenids examined, despite its low skull profile and its lack of a vaulted forehead (Table 3).

A juvenile specimen with C1 just erupting (AMNH 129667), assigned by Werdelin (1988a) to *Palinhyena reperta*, has elongated sinuses 2', which extend to a point just caudad from the transverse level of the anterior end of the auditory bullae, dis-

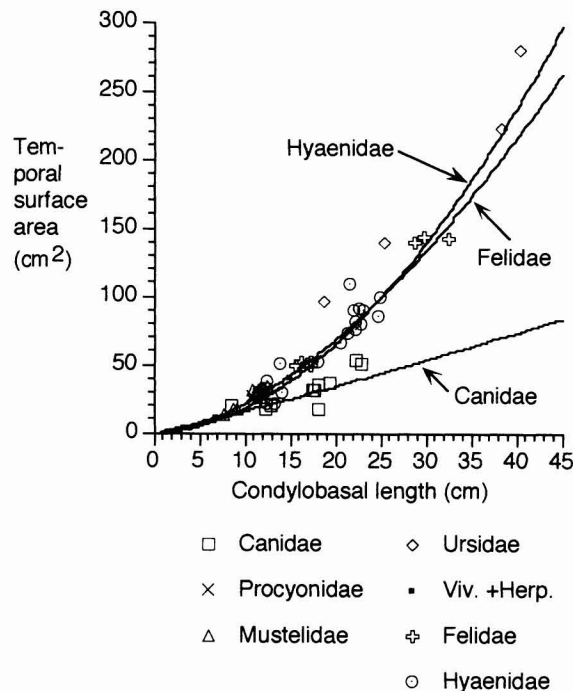


FIGURE 5. Plot of temporal surface area of skull versus condylobasal length in carnivorans (Viv. + Herp. = Viverridae + Herpestidae). Over measured ranges of skull ranges, there is no significant difference in temporal surface area between hyaenids and felids.

appearing anterior to the dorsal apex of the tentorium (Fig. 3). The forehead of this specimen is vaulted, however, and the anterior half of the frontal sinus complex contains partitioning bony trabeculae like those in living non-proteline hyaenids.

A specimen of *Hyaenotherium wongii* (AMNH 129666) has sinuses 2' that extend caudad to the inion and form a low "attic" over the braincase (Fig. 4B). In transverse cross section, however, these elongated sinuses in AMNH 129666 occupy relatively little area compared to the brain cavity, unlike the other fossil hyaenids and living hyaenids examined (Table 3).

A specimen of *Adcrocuta eximia* (AMNH 129664) shows the same grade of frontal sinus extension and enlargement as living non-proteline hyaenids (Figs. 7D, 8A): even in the posterior half of their length, the elongated frontal sinuses have a transverse cross-sectional area equivalent to as much as 45% of the transverse cross-sectional area of the brain cavity (Table 3).

The fossil hyaenid genera *Plioviverrops* and *Tungurictis* could not be examined in this study, yet the condition of the frontal sinuses in these genera would be of great interest because of the position of species belonging to these genera in the hyaenid phylogeny proposed by Werdelin and Solounias (1991). In a cladogram provided by Werdelin and Solounias (1991:fig. 38), *Plioviverrops* and *Tungurictis*, like *Proteles*, are excluded from a major clade of hyaenids that includes all of the fossil and living hyaenids examined by radiographic methods in the present study. It is impossible to determine from published photographs (Dietrich, 1927; Beaumont, 1969:pl. I; Hunt and Solounias, 1991:fig. 2) alone whether *Plioviverrops* and *Tungurictis* have elongated frontal sinuses, yet it appears unlikely that they do. In the very least, it can be said unequivocally that the skull forms of these genera are markedly less robust than those of living hyaenine hyaenids and their close fossil relatives.

TABLE 2. Facial flexion in living and fossil hyenas.

Species	Facial flexion
<i>Adcrocuta eximia</i> (AMNH 129664)	-6°
<i>Crocuta crocuta</i>	-3--10°
<i>Hyaena hyaena</i>	-3--5°
<i>Hyaenotherium wongii</i> (AMNH 129666)	-4°
<i>Ictitherium viverrinum</i> (AMNH 129665)	+5°
<i>Palinhyena reperta</i> (AMNH 129667)	+8°
<i>Parahyaena brunnea</i>	-7--16°
<i>Proteles cristatus</i>	-6--7°

Comparisons With Non-hyaenid Carnivorans

The relative posterior extent of the elongated sinus 2' in hyaenids can be expressed as the percentage of the length of the brain cavity that is overlain by the sinus (Fig. 9). The percentage overlap of the brain cavity by the frontal sinus in a variety of extant carnivorans measured in this study is 8–36%. *Proteles cristatus* fits well within this range, as does a neonatal *Crocuta crocuta*, which showed only 26% overlap (Fig. 9). The cheetah (*Acinonyx jubatus*) is considered separately because a specimen of that species demonstrated approximately 46% overlap of the brain cavity by the frontal sinus (Figs. 2B, 3, 9); cheetahs are already known to have an atypical frontal sinus and skull profile compared to other living felids (Joeckel and Stavas, 1996b). Despite even the anomaly presented by the cheetah, the elongated frontal sinuses of non-proteline hyaenids stand out among all other carnivorans examined in this study: the living and fossil non-proteline hyaenids examined all have overlap percentages $\geq 75\%$, and reaching 100% in adults of *Adcrocuta eximia*, *Crocuta crocuta*, *Hyaena hyaena* and *Parahyaena brunnea* (Fig. 9). The complete overlap of the brain cavity by the elongated sinus 2' in the latter group of species is accentuated by the extension of the parietals caudad so far as to overhang the occiput; the elongated sinus 2' actually proceeds caudad with the enclosing parietal bone.

The sagittal crests of primitive mammals (e.g., *Didelphis virginianus*) and many living carnivorans are simple bony ridges or plates extending dorsad from the midline of the skull. This normal type of sagittal crest-skull relationship contrasts with the pneumatized skull roof formed by the elongated sinuses 2' at the root of the sagittal crest in living hyaenine hyaenids. Sagittal crests in *Hyaenotherium wongii*, *Palinhyena reperta*, *Ictitherium viverrinum*, and *Adcrocuta eximia* all retain some

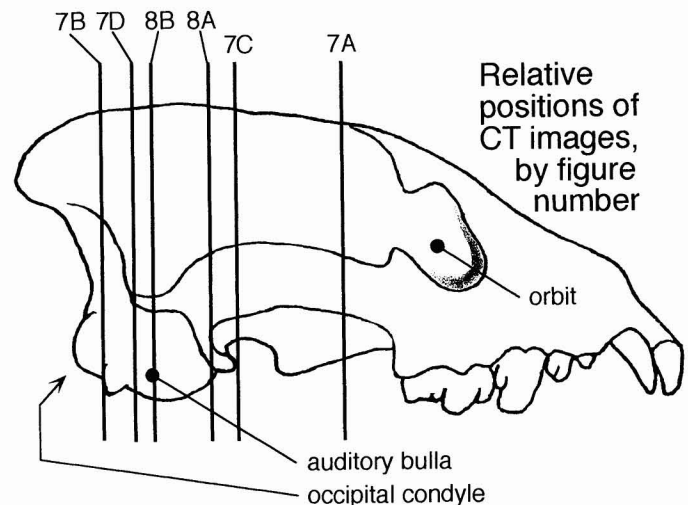


FIGURE 6. Approximate location of CT scan images presented in this study.

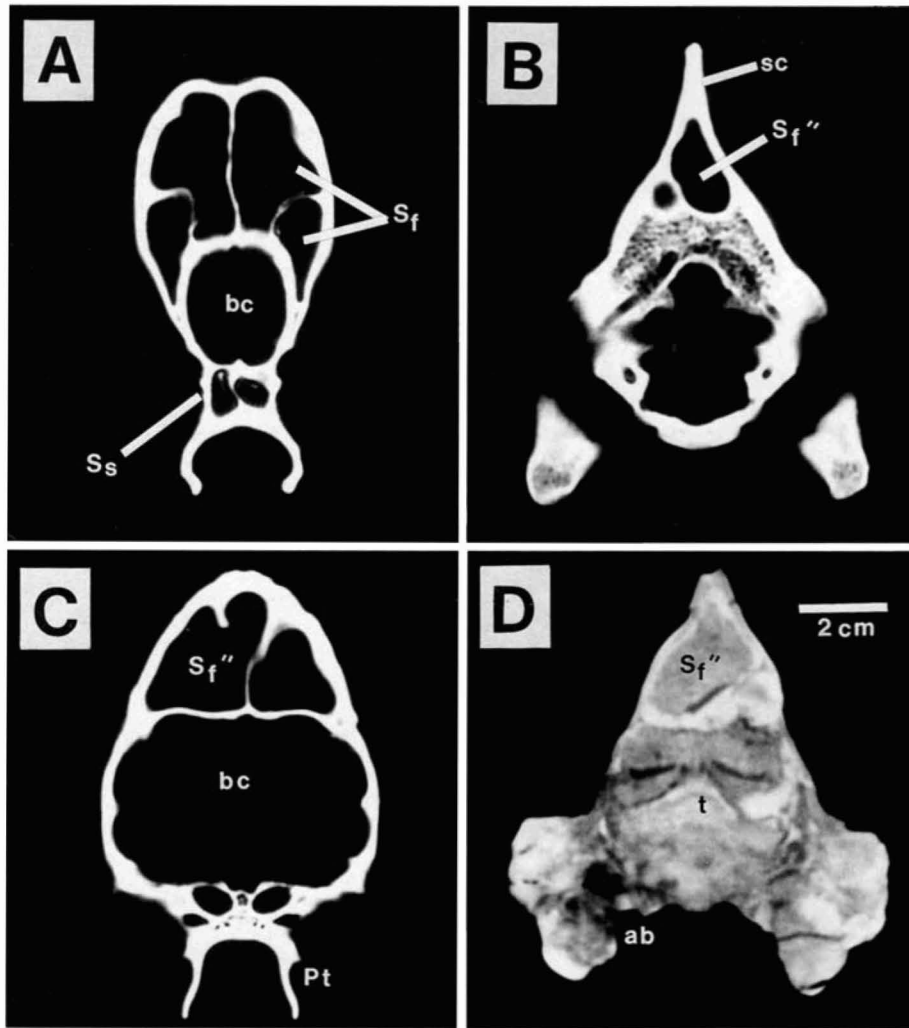


FIGURE 7. Transverse CT images of hyaenid frontal sinuses. **A**, anterior part of frontal sinus (**Sf**) in *Hyaena hyaena* (KU 82296), above anterior part of brain cavity (**bc**) formerly occupied by olfactory lobes. Note ethmoturbinate scrolls in sphenoid sinus (**Ss**). **B**, posterior, caudally elongate part of frontal sinus (**Sf''**) in *Hyaena hyaena* (KU 82296), a few mm anterior to foramen magnum, showing remnant of plate-like part of sagittal crest (**sc**) atop frontal sinus. **C**, posterior, caudally elongate part of frontal sinus (**Sf''**) in *Hyaena hyaena* (KU 82296), showing its "attic-like" geometry relative to brain cavity (**bc**). **D**, posterior, caudally elongate part of frontal sinus (**Sf''**) in fossil hyaenid *Adcrocuta eximia* (AMNH 129664) at position of tentorium (**t**) and posterior terminus of auditory bulla (**ab**). **A**, **B**, and **C** are approximately natural size. See Figure 6 for position of these images.

vestige of a normal sagittal crest, that is, a low, thin plate of bone extending dorsad from the parietals in the sagittal plane of the skull and joining posteriorly with the occipital crests at the inion, rather than a completely pneumatized skull roof. The skull roof in *Adcrocuta eximia* and *Palinhyena reperta* is partially pneumatized, and both of these species have markedly vaulted foreheads (Werdelin and Solounias, 1991). *Adcrocuta eximia* and the living hyaenine hyaenids have fully pneumatized parietals due to the extension of the frontal sinuses, and, hence, the sagittal crest is thin and plate-like only where the parietals extend caudad over the occiput.

Lateral CT scout images and conventional radiographs of the living non-proterline hyenas show that this enlarged anterior part of the frontal sinus ("vaulting" of Werdelin, 1989) contains partitioning bony trabeculae (Figs. 1, 2D); there is no obvious parallel to this variation on frontal sinus architecture in any of the other living Carnivora examined in this study, including several species of viverrids, felids, canids, mustelids, and ursids. Among the fossils examined in this study, scout images of *Adcrocuta eximia* (AMNH 129664) are too opaque to reveal

the contents of the anterior part of the frontal sinuses, although the same complex architecture seen in living hyaenine hyaenids might be expected in that species; the near-adult specimen (AMNH 129667) assigned to *Palinhyena reperta* by Werdelin and Solounias (1991), possibly a juvenile of *Adcrocuta eximia*, does show trabeculae within the anterior part of the frontal sinuses, and, indeed, a vaulted forehead, as well.

DISCUSSION

Overview of the Mammalian Frontal Sinus

As a general term, "frontal sinus" refers to any pneumatization or group of pneumatizations originating in the frontal bone as components of the paranasal sinus system—a complex of sinuses that includes not only the frontal sinuses but the maxillary sinuses as well (e.g., Evans and Christensen, 1979: 159). Edinger (1950) concluded: 1) that the parallel elaboration and enlargement of frontal sinuses in several mammalian taxa is predominantly a post-Eocene phenomenon, and 2) that frontal sinus geometries and relative sizes (i.e., frontal sinus size rel-

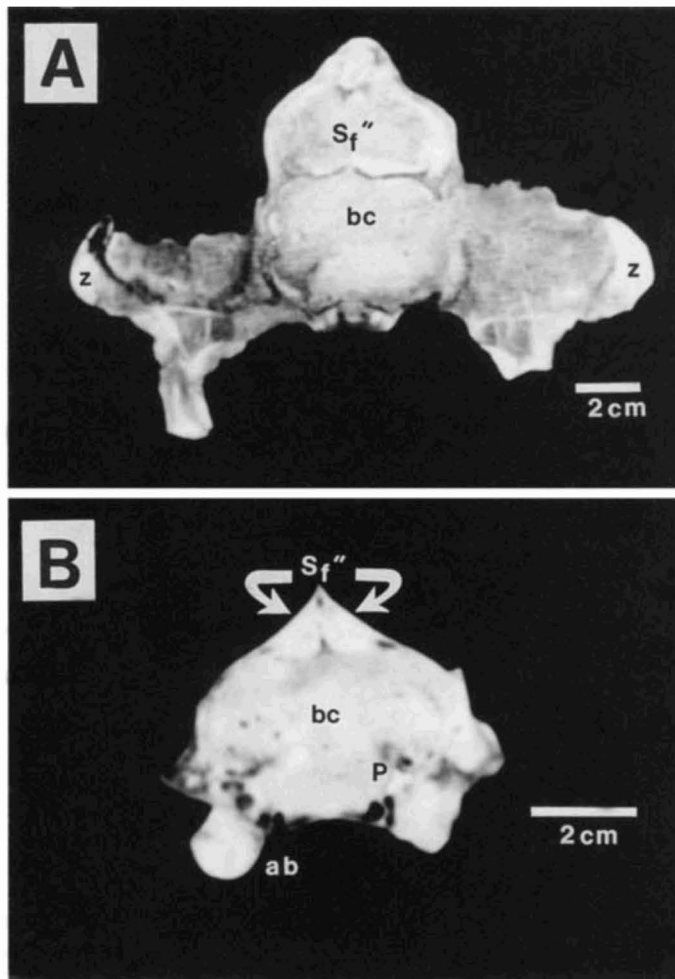


FIGURE 8. **A**, transverse CT scan image of fossil hyaenid *Adcrocuta eximia* (AMNH 129664) through posterior part of zygomatic arches (**z**) showing elongated frontal sinus (**Sf''**) above brain cavity (**bc**). **B**, transverse CT scan image of fossil hyaenid *Ictitherium viverrinum* (AMNH 129665) at position of auditory bullae (**ab**) and petrosal (**P**) showing paired, nearly symmetrical elongated frontal sinuses (**Sf''**) above brain cavity (**bc**). See Figure 6 for position of these images.

ative to overall skull size) are highly variable among both fossil and living mammals. Furthermore, Edinger (1950:486) maintained that cranial sinuses have no particular function, being, in her estimation, merely the result of "disharmonious growth of . . . the capsules of the brain and sense organs, the tooth apparatus, and the outer plates of the skull." In detailed studies of living mammals half a century before, Paulli (1990a, b, c) had already demonstrated the complexity of frontal sinus morphology and devised a numbering scheme for the paranasal sinuses, thereby abandoning the single term "frontal sinus" for

a system of sinus identification that is precise and intended to reflect the presumed homologies of different pneumatizations originating in the frontal bone. Because Paulli's numbering scheme for frontal sinuses is dependent on their position relative to different ethmoturbinals (more specifically, "endoturbinals"), it can be difficult to apply to fossils, in which the ethmoturbinals may be poorly preserved, difficult to see, or even missing entirely, and in which detailed, invasive (and therefore destructive) examination of rare skulls is, in the very least, not encouraged. Nonetheless, Paulli (1900c) established that the elongated frontal sinus of living hyaenids opens anteriorly between ectoturbinals 2 and 3, making it sinus 2' in his terminology (e.g., Paulli, 1900c:figs. 4, 5, 8–10), which is typically the largest of the two or three pneumatizations that make up each of the bilaterally paired frontal sinuses complex in carnivorans. It is of further note that the lateral part of ectoturbinal 2 extends slightly into sinus 2' both in the hyaenid specimen examined and illustrated by Paulli and in the two felids he examined (Paulli, 1900c:501–505), whereas in the several caniform carnivorans he examined, it is the medial part of ectoturbinal 3 that enters sinus 2' (Paulli, 1900c:figs. 4, 5, 8, 10). These observations already suggest a significant difference in ectoturbinal morphology between the caniform and feliform Carnivora worthy of further examination in the future.

To be sure, other carnivorans have large frontal sinuses (e.g., *Barbourofelis fricki* [Joeckel and Stavas, 1996b]), but the geometry of the elongated frontal sinuses in hyaenids appears to be unique. Even more greatly enlarged and elaborated frontal sinuses appear in other, non-carnivoran mammalian taxa, but almost all of these taxa, such as proboscideans (e.g., Zittel, 1925:fig. 335) and ground sloths (Stock, 1925; Joeckel and Stavas, 1997) are much larger than any fossil or living hyaenids.

Many ungulates have enlarged and elaborated sinuses (sometimes referred to as the "caudal frontal sinus") in the roof of the cranium that overlie part or all of the brain cavity (Flower, 1870; Edinger, 1950; Negus, 1958; Berg, 1974; Moore, 1981). In bovids, the "caudal frontal sinus" typically extends into the horns or is closely associated with other sinuses in the roof of the cranium (Berg, 1974:89, 94–96). Paulli (1900b) painstakingly documented the complexity of paranasal sinus elaboration in ungulates, which resulted in a somewhat confusing array of identifications for supposedly distinct and homologous pneumatic chambers. Sinuses in the skull roof of many ungulates are commonly presumed to strengthen the skull without adding significant weight and, in artiodactyls, to support the cranial appendages or protect the brain from shocks incurred through intraspecific combat. Since the first appearance of artiodactyl cranial appendages in the late Eocene, however, not all cranial appendage-bearing species have had such sinuses. Even two species within the same family of artiodactyls may show markedly different degrees of frontal sinus development. For example, there are very large sinuses in the frontals, parietals, and supraoccipitals of *Giraffa camelopardalis* that have been interpreted to cushion the shock of blows incurred during combat between males, but comparably enlarged sinuses are absent in

TABLE 3. Cross-sectional measurements (cm) for fossil hyaenas of elongated frontal sinuses 2' at transverse level of anterior end of auditory bullae.

Specimen	SH	SW	BH	BW	HR	AR
<i>Adcrocuta eximia</i> (AMNH 129664)	2.2	4.4	4.5	5.6	0.49	0.45
<i>Hyaenotherium wongii</i> (AMNH 129666)	1.1	2.1	4.1	5.1	0.27	0.09
<i>Ictitherium viverrinum</i> (AMNH 129665)	1.5	3.2	2.5	4.9	0.60	0.26
<i>Palinhyena reperta</i> (AMNH 129667)	1.4	2.8	3.7	5.0	0.38	0.10

SH = median sinus height, SW = sinus width at its base, BH = brain cavity height, BW = maximum width of brain cavity, HR = SH: BH, AR = ratio of total cross-sectional area of frontal sinuses to cross-sectional area of brain cavity.

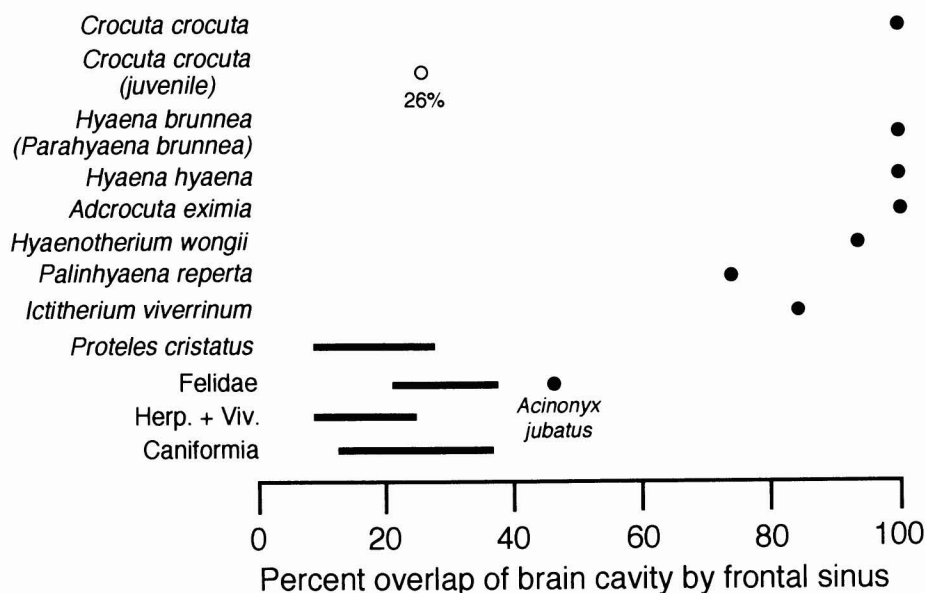


FIGURE 9. Length of frontal sinuses in different carnivoran taxa expressed in terms of percent of brain cavity overlapped dorsally by frontal sinus. Note striking difference between adult hyaenids and other carnivorans, but compliance of juvenile *Crocuta crocuta* with carnivoran norm.

the skull of *Okapia johnstoni*, which nonetheless has cranial appendages of proportionately similar size (Churcher, 1990).

It is apparent that there a number of different skull architectural strategies in mammals which involve enlargement and/or elaboration of the frontal sinuses, implying unique evolutionary histories and, quite possibly, unique fields of morphological adaptation. Thus, the question of the evolutionary significance of frontal sinuses in mammals, including any conjecture regarding function, remains wide open to further inquiry.

Edinger (1950:490) concluded that the post-early Tertiary evolution of frontal sinuses in Mammalia was due, in general, to the negative allometry of the brain cavity and eye and ear capsules relative to the skull during overall body size increase within an evolving lineage. Nonetheless, she was quick to point out that: 1) many large mammals of the early Tertiary did not have extensively pneumatized skulls as their modern equivalents in body size do; and 2) pneumatized skulls characterize some modern mammals that are considerably smaller than their early Tertiary relatives, which lack well-pneumatized skulls. Nearly a half-century later, Edinger's observations still indicate that the evolution of frontal sinuses in different mammalian clades has not been controlled by a single, uniform mechanism and therefore cannot be described by a single, explicit scenario (Edinger, 1950:486). It is difficult, though, to accept the long-standing interpretation that frontal sinuses have no function when they vary so extensively in size and shape and figure so prominently in the design of particular mammalian skulls. Cranial pneumatization, without a doubt, serves some function, albeit perhaps not an "active" or "discrete" one: cranial sinuses must be viewed as essential components of skull architecture.

Hyaenid Frontal Sinuses

The morphological contrast between neonatal and adult hyaenine hyaenid crania demonstrates that the development of elongated frontal sinuses in hyaenine hyaenids is associated with ontogenetic changes in the proportions of the skull, brain cavity, and nasal cavity during ontogeny (Fig. 3: *Crocuta crocuta* juvenile and adult). Reduction of the entire issue of elongated frontal sinuses to a matter of simple intrafamilial allometry alone (i.e., larger hyaenids having the most elongated fron-

tal sinuses and smaller hyaenids the least), however, is not only unsatisfying, but also incorrect. While the largest hyaenids do have the most caudally elongated frontal sinuses, each of the smaller hyaenids examined in this study, except for *Proteles cristatus*, has a frontal sinus that is more caudally elongated than the carnivoran norm (Fig. 3). This trend indicates a basic and persistent significance of the hyaenid elongated frontal sinus. It is essential, however, to reiterate the distinction between the caudal elongation of the frontal sinuses and their anterior enlargement (forehead-vaulting): most of the non-proteline hyaenids examined exhibit anterior enlargement to some degree, but all exhibit caudal elongation.

For heuristic purposes, six functional hypotheses are advanced herein to rationalize the function of caudally elongated frontal sinuses in non-proteline hyenas: 1) protection of the brain from external shock to the head; 2) brain-cooling; 3) olfaction; 4) enlargement of the attachment area of the temporalis muscle; 5) space-filling to maintain a characteristic head shape (given a relatively small brain); and 6) load resistance. Some of these hypotheses are potentially interrelated, and all of them should be tested in some way.

Hypotheses 1–5—The shock protection hypothesis, which is based on the analog of cranial appendage-bearing ungulates, appears to be dismissable from the start. Published accounts of hyaenid behavior contain no references to head-butting in *Crocuta crocuta* (e.g., Kruuk, 1972), or in the other living hyena species (Nowak and Paradiso, 1983): such behavior is apparently unknown in any living carnivoran.

Any direct role of the elongated frontal sinuses in cooling the brain would be nearly impossible to test directly in live specimens, but the presence of a fully developed orbital rete in hyaenids and other feliform carnivorans (Tandler, 1899; du Boulay and Verity, 1973), which regulates the temperature of the blood supply to the brain (cf. Baker, 1979), renders the potential for a selective brain-cooling function highly unlikely. An olfactory function for the elongated frontal sinuses is dismissable as well. The sense of smell in living hyaenine hyaenids is keen (Kruuk, 1972), but there is no anatomical evidence that the caudal extension of the frontal sinuses in hyaenids could play any active role in olfaction. In Carnivora as a group,

olfactory mucosa appears only in the anterior part of the frontal sinus on the extensions of certain ethmoturbinates (Paulli, 1900c; Read, 1908; Negus, 1958). These ethmoturbinates, however, very clearly do not extend throughout the elongated sinus 2'. Furthermore, explaining the caudad elongation of the frontal sinuses as a pleiotropic effect of some elaboration of the olfactory apparatus would be entirely speculative.

It is also highly unlikely that the elongated frontal sinuses of hyaenids have ever played a direct role in increasing the surface area of temporal muscle attachment on the skull, relative to the norm for carnivorans in general or to feliform carnivorans in particular. The temporal area of the skull (approximate area of attachment of the temporalis muscle) is, proportional to the length of the skull, no larger in the hyaenids measured than it is in the sample of felids measured (Fig. 5), and felids lack hyaenid-like elongated frontal sinuses! Whether a pneumatized skull roof has some broader functional role relative to the jaw musculature, though, must also be considered (see discussion below).

The significance of elongated frontal sinuses in brain:skull or brain:body allometry must be considered, especially in the light of Edinger's interpretation of the frontal sinuses as passive space-filling entities. Gittleman (1986) examined brain weight in living carnivorans relative to body weight and head + body length. It is noteworthy that Gittleman found hyenas to have the second smallest brain sizes relative to head + body length among the living Carnivora; by the same relative measure, viverrids (*sensu lato*) have the very smallest brains, and ursids have the largest (Gittleman, 1986:fig. 2) among the living Carnivora. Visual comparisons between adult hyaenid and felid skulls (Fig. 2A, B, D) also seem to support small relative brain size in hyaenids. Small relative brain size in living hyenas is apparently significant as a family-level pattern, and might be considered as support for the origin of an enlarged frontal sinus as a space-filling device within the skull. By itself, however, this argument could easily be undermined by a single, pointed question: why should the frontal sinus be elongated over the brain cavity to "fill up space" when the ancestral (and indeed more typical) mammalian cranial Bauplan, repeated time and again in taxa with small braincases, merely involves the development of a high plate-like sagittal crest without any extension of the frontal sinuses over the brain? Small relative brain size probably is an important factor in the evolution of the elongated frontal sinuses, but it is unsatisfying as the only explanation.

The Structural Hypothesis (Hypothesis 6)—Using the work of Buckland-Wright (1971, 1978) on force transmission in carnivoran skulls as a starting point, Werdelin (1989) interpreted the vaulted foreheads of presumed bone-cracking fossil canids and bone-cracking living hyaenids as mechanical adaptations for a strong premolar bite. The vaulted forehead that produces the characteristic profile of non-proteline hyaenids and borophagine canids is the direct result of the enlargement of the anterior part of the frontal sinus. Werdelin (1989:395) interpreted the vaulted forehead and enlarged anterior frontal sinus as providing "a single, unbroken, strengthened tract of bone along the force trajectories emanating from the teeth . . . and blending into the top of the skull," which can dissipate the compressive forces produced by premolar bone-cracking.

Increased structural support provided by the elongated frontal sinuses could well be compatible with the Werdelin's (1989) results, but his hypothesis explains only the anterior enlargement ("valuting") of the frontal sinus in bone-crushing hyaenids, and not the elongation of the frontal sinus seen in all hyaenids examined in this study. *Ictitherium viverrinum*, *Hyaenotherium wongii*, and *Palinhyena reperta* show significant caudal extension of sinus 2', but these species lack forehead vaulting of the grade evident in the living hyaenine hyaenids and *Adcrocuta eximia* (see Werdelin and Solounias, 1991:fig. 49), as

well as enlarged, robust premolars. Thus, a sweeping and largely unqualified statement about the specific function of elongated frontal sinuses, relative to specific dietary habits through hyaenid evolution, would be difficult to accept.

Despite the cautions mentioned above, structural engineering principles may illuminate the significance of elongated frontal sinuses relative to cranial mechanics. The theoretical argument is centered around the interpretation of the sagittal crest: the pneumatized skull roof of non-proteline hyaenids is equivalent to the "shell" of the civil engineer (Gould, 1988; Scott, 1993), while the common plate-like sagittal crest of many other carnivorans is simply a cantilever plate (Fig. 10). Shells have clear advantages over other structures with regard to loading (loading in the case of the skull being produced by the masticatory muscles, particularly the temporales) and compressive forces generated by premolar biting (see Werdelin, 1989). In the most simple case of symmetrical compressional loading, a vertical plate subject to compression in the vertical axis (say, by the temporales) concentrates all of that loading along its base, whereas only half of that force would be concentrated on either side of a shell structure of comparable dimensions (Fig. 10).

If loaded on only one side, or bilaterally but asymmetrically, as might be expected of the sagittal crest in unilateral mastication, a vertical plate develops a moment (M) directly proportional to its length (l) and height (d):

$$M = fl(d/2); \text{ where } f = \text{load/length (see Fig. 10)}$$

With further analysis, it is clear that the longer, higher, and thinner the vertical plate (b = plate thickness; see Fig. 10), the greater the bending stress (σ_b):

$$\sigma_b = (MC)/I,$$

where

$$C = b/2 \quad \text{and} \quad I = \text{moment of inertia} = 1/12(lb^3)$$

Analyzing for asymmetrical stress in a shell is exceedingly complex, and the reader is referred to Gould (1988) for a complete discussion. It is an established fact, however, that shells minimize shear as well as bending and twisting moment relative to other structures; instead, shells efficiently resist applied load primarily by producing thrust along their curvature in a fashion very similar to a simple arch (Gould, 1988). Both arches and shells resist load primarily by extension, as opposed to the flexural behavior of beams and plates; but, whereas an arch is a one-dimensional flexural member, a shell is a two-dimensional flexural member capable of "remain(ing) virtually momentless for a variety of loadings" (Gould, 1988:6). Thus, a shell is an extremely resistant, yet very lightweight and material-conservative structure. Presumably, a shell would be an ideal element in cranial architecture under the bounding constraints of brain: body allometry, head:body proportionality, skull weight, and cranial function. The hypothesis that explains the elongated frontal sinuses of non-proteline hyaenids as a load-resisting shell is compatible with other aspects of the hyaenine Bauplan as well as with the interpretations of Werdelin (1989) regarding cranial function. Furthermore, the elongation of the frontal sinus during ontogeny (as seen in neonatal vs. adult *Crocuta crocuta*) indicates a dynamic interaction between growing and reshaping bones, enlarging cranial muscles, and resultant cranial mechanics during life, rather than the development of the elongated frontal sinus as a completely passive, space-filling structure.

In this structural interpretation, the caudal elongation of hyaenid frontal sinuses and the resulting pneumatization of the skull roof provides resistance to various stresses acting on the skull, and not merely masticatory muscle forces. The elongated sinuses can be viewed as a buttress between the braincase and the face, particularly the frontal region, which would resist any

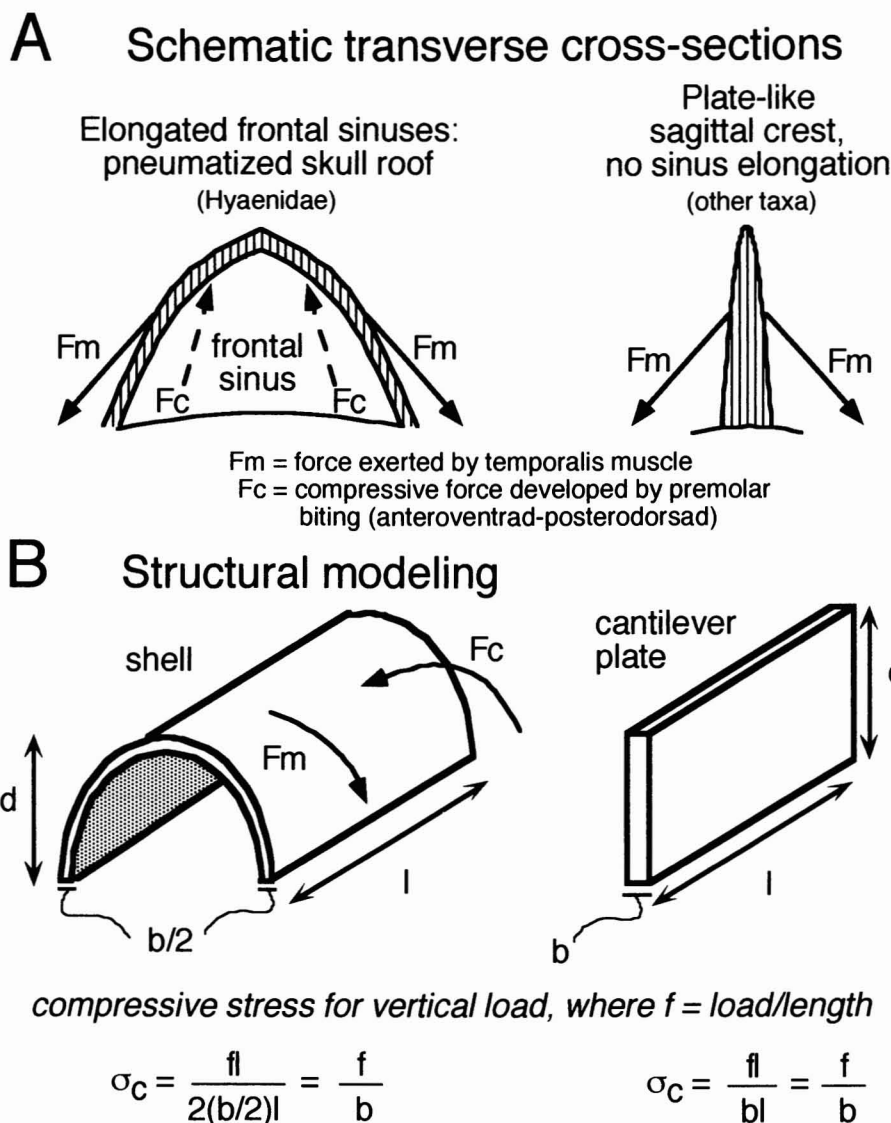


FIGURE 10. A, schematic modeling of caudally-elongated frontal sinuses (pneumatized skull roof) in non-proteline hyaenids discussed in this paper, versus typical mammalian plate-like sagittal crest found in other carnivorans. Compressive force (F_c) generated by premolar biting follows analysis of Werdelin (1989). B, structural modeling of pneumatized skull roof/caudally elongate frontal sinus as shell structure versus cantilever plate of typical plate-like mammalian sagittal crest. Shell structure presented by elongated frontal sinus in hyaenids can resist bending from many directions, particularly any bending imposed by masticatory musculature (F_m) and by premolar biting (F_c).

dorsal torque imposed on the face during biting (see Werdelin, 1989). Enlargement and elongation of the frontal sinuses would seem to be the only effective way of buttressing the skull without adding weight or greatly modifying its external form, particularly in terms of bone-muscle relationships.

CONCLUSIONS

Caudally elongated frontal sinuses are probably a synapomorphy of a large clade within the Hyaenidae. This clade would exclude *Proteles* and possibly *Plioviverrops* and *Tungurictis*, as well. Nonetheless, the absolute verification of elongated frontal sinuses as a synapomorphy awaits the discovery and/or description of more complete crania of several genera that fall in between *Ictitherium*, *Hyaenotherium*, *Palinhyena*, *Parahyaena*, *Hyaena*, *Adcrocuta*, and *Crocota* in a cladistic analysis (see Werdelin and Solounias, 1991:fig. 38). The degree of caudal elongation of these sinuses in the Hyaenidae is apparently unique among the Carnivora. Caudally elongated frontal sinuses

appear in some form in small Miocene hyaenids that lack the typical features (e.g., strongly vaulted forehead/enlarged anterior frontal sinus, out-bowed zygomatic arches/voluminous temporal fossa, robust premolars, robust skull, heavy jaws, etc.) of the larger, modern hyaenine hyaenids. Elongated frontal sinuses (increasing in length to cover the entire brain cavity) are maintained, together with an enlarged anterior frontal sinus (vaulted forehead), in the large "typical" hyaenid genera *Adcrocuta*, *Crocota*, *Hyaena*, and *Parahyaena*. Positive facial flexion is negatively related to frontal sinus extension in fossil hyaenids; therefore, there is no evidence that the frontal sinus grows and enlarges caudad due to some backward displacement or reorganization of cranial compartments prompted by rotation of the face.

The presence of elongated frontal sinuses in all of the hyaenids examined in this study except *Proteles* is a striking pattern that is amplified greatly in the appearance of modern hyaenines. Several possible functional/adaptive scenarios for the evolution

of elongated frontal sinuses, though, are dismissable as far-fetched, trivial, or otherwise unsatisfactory. The work of Gittleman (1986) suggests that hyaenids have relatively small brains, yet the elongated frontal sinuses are unlikely to be simply a passive space-filling phenomenon. Basic engineering principles suggest that the elongated frontal sinus is an architectural improvement over the simple plate-like sagittal crest common in many mammalian taxa. This interpretation, while teleological, is highly compatible with the development of the modern hyaenine cranial Bauplan. In the very least, it has been demonstrated that the caudally elongated frontal sinus was present in small, early hyaenids such as *Ictitherium*, and that it increased in prominence with the development of the vaulted forehead and other characteristic features of the modern hyaenine-like skull form.

Many questions remain unanswered in the assessment of the hyaenid frontal sinus, but two questions are particularly nagging. First, considering that other anatomical features (e.g., saber canines, vaulted foreheads, bone-crushing premolars) evolved in parallel between different groups with no close relationship, why do no other groups of carnivorous mammals, living or extinct, show a caudal extension of the frontal sinus completely over the brain? Second, was the caudally-elongated frontal sinus merely a preadaptation (a phylogenetic constraint on skull morphology established near the base of the hyaenid radiation) to the mechanics of the modern hyaenine hyaenid cranial Bauplan? These questions tempt speculation, but their answers lie outside the currently available data. Regardless of possible functional significance and evolutionary implications, however, the morphology of the frontal sinus in non-proteline hyaenids stands out as a unique feature among Carnivorans, if not non-ungulate eutherian mammals as a whole.

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APPENDIX. In earlier publications, fossil hyaenids discussed in this study are referred to by their original AMNH field numbers. The following table correlates those field numbers with newly assigned permanent AMNH numbers and indicates the publication in which each specimen is assigned to a particular species.

Specimen	Field number	Identification
<i>Adcrocuta eximia</i> (AMNH 129664)	35-B216	Werdelin and Solounias (1990)
<i>Hyaenotherium wongii</i> (AMNH 129666)	94-L779	Werdelin (1988a); Werdelin and Solounias (1991)
<i>Ictitherium viverrinum</i> (AMNH 129665)	57-L549	Werdelin (1988b)
<i>Palinhyena reperta</i> (AMNH 129667)	42-L338	Werdelin (1988a)