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INTERNAL ANATOMY OF THE SNOUT AND PARANASAL SINUSES OF *HYAENODON* (MAMMALIA, CREODONTA)

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The Creodonta (late Paleocene–late Miocene) are cast as the archaic terrestrial carnivores in Tertiary mammalian faunas from Europe, Asia, Africa, and North America. Their evolution was in parallel to that of the Order Carnivora, which are considered to be the more progressive mammalian carnivores of the Tertiary. Carnivorans have, since the early Miocene, usurped niches previously held by creodonts. The long-standing concept of a creodont-carnivoran sister-group relationship was retained, albeit with varying degrees of reluctance, until very recently (e.g., Novacek et al., 1988; Wyss and Flynn, 1993). New analyses (Polly, 1993, 1994, 1995, 1996; Fox and Youzwyshyn, 1994) refute that relationship, and even cast doubt on the monophyly of the Order Creodonta. In this study, computed tomography (CT) scanning supply data that improve our understanding of hyaenodontid creodonts while providing a reference point for future investigations of the relationships of creodonts with other eutherian orders.

The Family Hyaenodontidae includes both the largest creodonts and the last creodonts to go extinct (e.g., *Hemipsalodon*, *Megistotherium*, *Hyaenodon*, *Hyainailouros*, *Dissopsalis*). The family is monophyletic, yet subfamilial systematics of hyaenodontids have been questioned on the basis of dental and other characters (Polly, 1995). *Hyaenodon* is the best-represented creodont in the fossil record of North America, ranging over >10 million years from the late Eocene to the early Miocene (Mellett, 1977; Bryant, 1993). In Eurasia, the genus ranges over a roughly equivalent time range (Mellett, 1977; Savage and Russell, 1983). The several fine crania of *Hyaenodon* collected from the late Eocene–late Oligocene White River Group of Nebraska, Colorado, Wyoming, and South Dakota (Mellett, 1977) constitute the largest sample of well-preserved creodont crania in the world. We examined some of these crania in order to: 1) characterize the internal morphology of the snout; 2) attempt to find preserved fossil maxilloturbinates, which have already proven useful in carnivoran systematics (Anthony and Iliesco, 1926; Ewer, 1973; Hunt et al., 1994); and 3) survey cranial morphology in general.

MATERIALS AND METHODS

We scanned skulls of *Hyaenodon crucians*, *Hyaenodon brevirostris*, and *Hyaenodon horridus* from collections of the American Museum of Natural History (F:AM) and the Museum of Geology, South Dakota School of Mines and Technology (SDSM). Scans were taken at 1.5–3 mm intervals using a General Electric (GE) High-Speed Advantage[®] CT scanner. The resultant 16-bit CT images were manipulated in an Interactive Display Language (Research Systems, Inc.) program called “GEview,” written by Mr. Will Tribbey, a former employee of the Image Processing Laboratory, University of Tennessee-Knoxville Medical Center. “GEview” fits the 16-bit images to an 8-bit space via the user’s selection of particular window level and window width values, from which all pixel values are scaled to fit in an 8-bit space bounded by level $\pm 0.5 \times$ window width. Individual images can then be saved in 8-bit format and converted to PICT, TIFF, and other formats that can be opened in various personal computer programs. In this study, rescaled 8-bit images were converted to PICT files (~20–200K each) for manipulation and

duplication using Adobe Photoshop[™] on a Macintosh[™] personal computer. Images converted in this fashion can be enhanced in a variety of ways using the editing tools available within Adobe Photoshop[™]. For purposes of this study, anatomical details of the snout were enhanced within Adobe Photoshop[™] by inverting white-on-black X-ray images and then manipulating brightness and contrast. The resultant enhanced images were saved as TIFF files (each > 1 M) at 300 pixels per inch, and laser-printed with a 600 dpi printer on Scott SPectraTech[™] (Warren Paper Co.) glossy coated paper, thereby eliminating the need for photographic duplication. The PICT images from which these TIFF files were created are small enough that several key images can be easily loaded onto inexpensive floppy discs for storage. Although this procedure precludes the inclusion of all images in a given study, it has the advantage of being much less expensive and more widely usable than an optical disc storage scheme (note that PICT files can be opened in a variety of other widely available programs, such as Microsoft Word[™] and Canvas[™]).

OBSERVATIONS

Maxillary Sinus

The moderate- to large-sized species of *Hyaenodon* examined in this study have large maxillary sinuses (Figs. 1, 2A–D, 3). In *H. horridus*, these sinuses occupy as much as 25–30% of the transverse cross-sectional area of the skull at the level of M1, and they extend anterior, dorsolateral to the middle part of the nasal cavity, to a point dorsal to P2 (Fig. 3). The approximate length of the maxillary sinuses can be surmised from external examination of skulls (e.g., *Hyaenodon horridus*, SDSM 3017), because there is a discernible bulge extending anterior in the dorsal part of the maxilla to the level of the infraorbital foramen. At any given cross section, the size of the maxillary sinuses

Approximate location of CT scan images (by figure number)

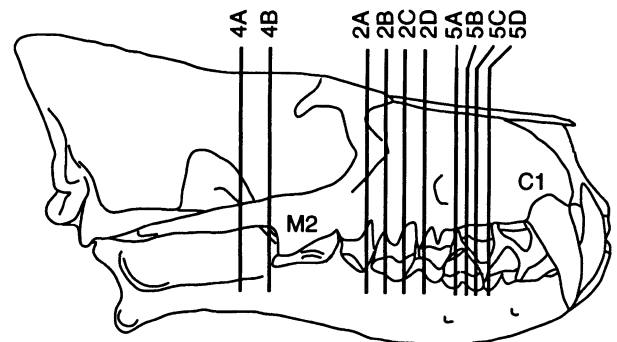


FIGURE 1. Approximate location of CT scan images presented in this study (*Hyaenodon* skull after Scott and Jepsen, 1936).

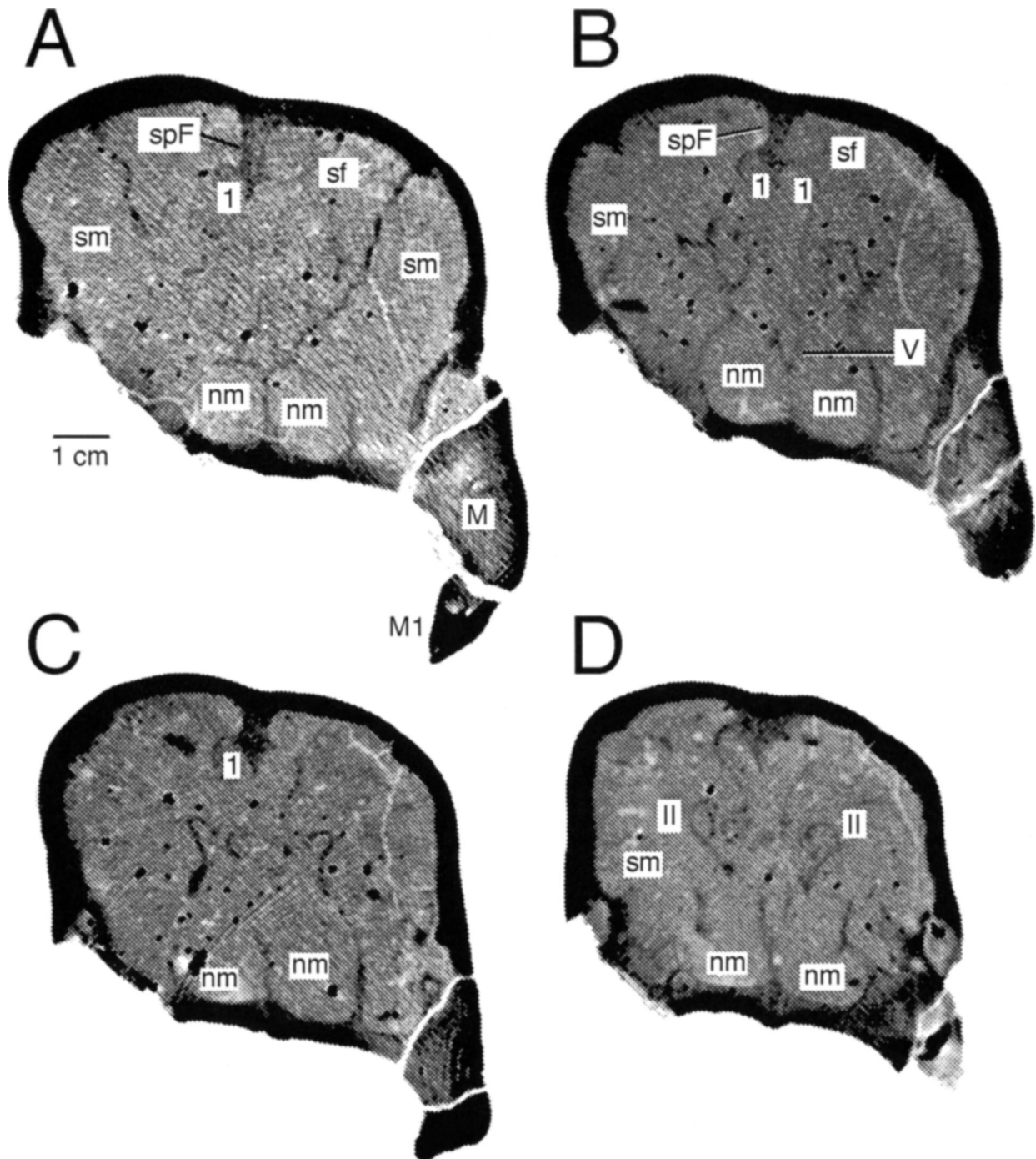


FIGURE 2. CT scans of *Hyaenodon horridus* (SDSM 28142) through ethmoturbinates; rescaled 8-bit image manipulated in Adobe Photoshop[®] (see “Materials and Methods”). **A**, scan at level of anterior end of M1, showing maxillary sinuses (**sm**) bounding roughly triangular cross section of olfactory compartment-anterior frontal sinus (**sf**), remains of ethmoturbinates, nasopharyngeal meatus (**nm**), and maxilla (**M**). Ectoturbinate 1 (**I**) and endoturbinate II (**II**) identified; spF = septal process of the frontal bone. **B**, scan approximately 15 mm anterior to **A** showing vomer (**V**) and remains of ethmoturbinates. **C**, scan approximately 15 mm anterior to **B** (at level of P4) showing remains of ethmoturbinates. **D**, scan approximately 15 mm anterior to **C** (at level of alveolus of P3 alveolus) showing remains of ethmoturbinates, including possible endoturbinate II immediately to left of “**sm**” (maxillary sinus): if properly identified, arrangement of ethmoturbinates and number of ethmoturbinate plates likely differed significantly from that of extant carnivorans (see Evans and Christensen, 1979, figs. 4–25 and 4–26).

is inversely proportional to that of the olfactory compartment (i.e., the space occupied by the ethmoturbinates). The olfactory compartment in *Hyaenodon* does not fill all of the caudal part of the snout, and therefore the maxillary sinuses are proportionately larger than in Carnivora (particularly larger than in extant canids, felids, and ursids of similar size), which have very large olfactory compartments and small maxillary si-

nuses (Negus, 1958; Moore, 1981). In *H. horridus*, negative allometry of the nasal cavity with respect to increasing skull size (cf. Edinger, 1950) results in a particularly large maxillary sinus. *Ursus arctos* has a particularly large maxillary sinus extending partially into the nasal bone (Pauli, 1900), but this sinus is still less extensive than the maxillary sinus in *Hyaenodon horridus*.

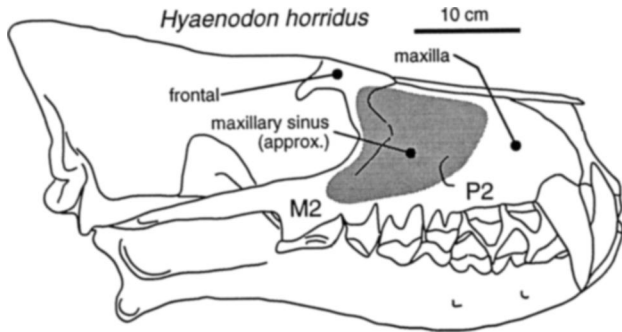


FIGURE 3. Approximate extent of maxillary sinus in *Hyaeonodon horridus* (skull after Scott and Jepsen, 1936).

Sphenoid Sinus

Hyaeonodon has well-developed, paired sphenoid sinuses (Fig. 4A), which appear to contain some extensions of the ethmoturbinates in a few CT images, although these laminae are faint. The olfactory region, and therefore the ethmoid, extends in some manner into the presphenoid in some or all of the extant Lipotyphla, Chiroptera, Carnivora, Rodentia, and Edentata (Moore, 1981), although the Carnivora appear to have the most prominent sphenoid sinuses of these five groups.

Frontal Sinus

The frontal sinus of *Hyaeonodon* is large, producing a prominent forehead and supraorbital processes, yet it is not strikingly disproportionate to the remainder of the skull (Figs. 2A, 4). It does not extend caudally under the sagittal crest, and its shape and position are analogous to those in typical carnivorans (for discussions of variations in carnivoran frontal sinuses, see Joeckel [1995] and Joeckel and Stavas [1996]). Multiple "compartments" or small sinuses (at least four) make up the frontal sinus in one *Hyaeonodon* specimen (Fig. 4A), just as in large carnivorans, particularly ursids (Paulli, 1900; Moore, 1981). This "compartmentalization" of the frontal sinus is compatible with the enlargement of the maxillary sinuses in both extant ursids and *Hyaeonodon horridus* in that it may also be related to negative allometry of the brain and brain cavity relative to the rest of the skull as body size increases. In

many extant carnivorans, some of the ethmoturbinates extend into the frontal sinus (Paulli, 1900; Negus, 1958; Moore, 1981). It cannot be determined, however, whether any of the ethmoturbinates extended into the frontal sinus in *Hyaeonodon*.

Maxilloturbinates

CT scans show a simple maxilloturbinate in *Hyaeonodon*, one consisting of semi-scroll-shaped dorsal and ventral laminae that are spiral in cross section (Fig. 5). In SDSM 28142, the specimen that provided the clearest CT images, the dorsal lamina forms an incomplete spiral, whereas the ventral lamina forms a full spiral (Figs. 5, 6). This grade of maxilloturbinate development approximates that seen in many viverrids and herpestids, as well as in several other eutherian groups (see Negus, 1958).

Nasopharynx

In *Hyaeonodon*, the nasopharyngeal meatus is persistently divided at the midline by the ventral crest of the vomer, thereby forming two circular to oval passages (Fig. 7). In several extant Carnivora, the nasopharyngeal meatus is undivided caudally, or only partially divided, by the vomer. Whereas the divided nasopharyngeal meatuses in *Hyaeonodon* are circular to oval (with a dorsoventral long axis) in cross section, the nasopharyngeal meatuses in extant Carnivora examined, whether confluent or divided by the vomer, are oval (with a mediolateral long axis) to rectangular in cross section (Fig. 7). The floors of the nasopharyngeal meatuses in *Hyaeonodon* are troughs excavated in the dorsal surface of the hard palate, but in extant Carnivora examined, the nasopharyngeal meatus(es) has a nearly flat, horizontal floor (Fig. 7).

Olfactory Compartment and Ethmoturbinates

In *Hyaeonodon*, the olfactory compartment produced by the ethmoid combined with the anterior ends of the frontal sinuses, is roughly triangular in cross section in its caudal part (Fig. 2A). In extant carnivorans, the olfactory compartment is rectangular to squarish in cross section in the same region. The olfactory compartment of *Hyaeonodon* is bounded by maxillary sinuses that are large relative to those in extant carnivorans of comparable body size (see Paulli, 1900; Negus, 1958; Moore, 1981). The ethmoturbinates in examined specimens of *Hyaeonodon* specimens are not optimally preserved, yet CT scans hint that they were much less elaborate than the ethmoturbinates in extant Carnivora. Possibly, they were significantly different in overall architecture (Figs. 2, 4B).

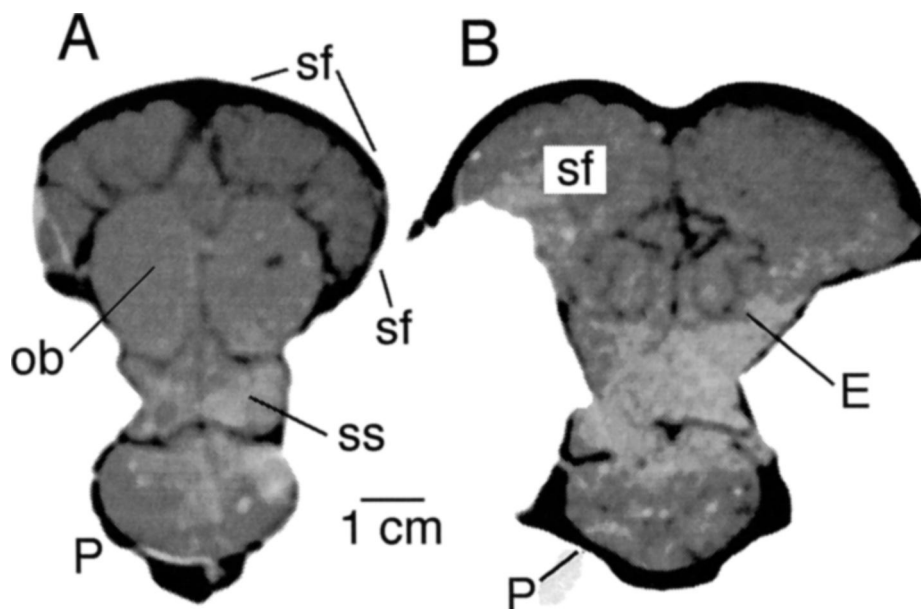


FIGURE 4. CT scans of *Hyaeonodon crucians* (SDSM 3117) on either side of cribriform plate showing frontal (sf) and sphenoidal (ss) sinuses, cavity for olfactory bulb of brain (ob), caudal part of ethmoturbinates or ethmoid labyrinth (E), and ventral contact of pterygoids (P) at midline to form "narial tube" or extended bony posterior nares noted by Scott and Jepsen (1936) and Mellett (1977). A is approximately 24 mm posterior to B.

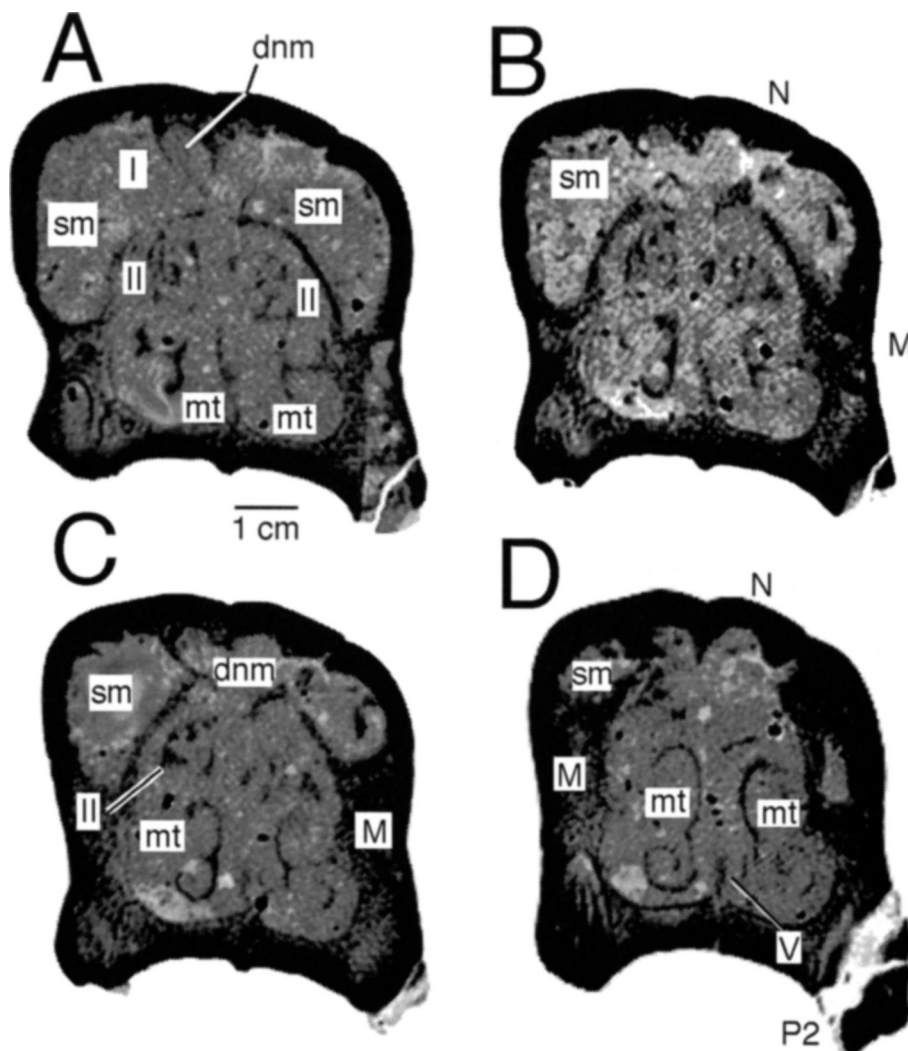


FIGURE 5. CT scans (treated as Fig. 1) of maxilloturbinate in *Hyaeodon horridus* (SDSM 28142). A, scan in vicinity of P2–P3 diastema; note dorsal nasal meatus (dnm), extension of maxillary sinus (sm), maxilloturbinate (mt), ectoturbinate I (I) and endoturbinate II (II). B, scan approximately 6 mm anterior from A, showing nasal (N) and maxilla (M). C, scan approximately 4.5 mm anterior from B, showing nasal bone (N) and simple scrolling of maxilloturbinate (mt); note also anterior extension of maxillary sinuses. D, scan approximately 10.5 mm anterior from C, with vomer (V) and P2 identified.

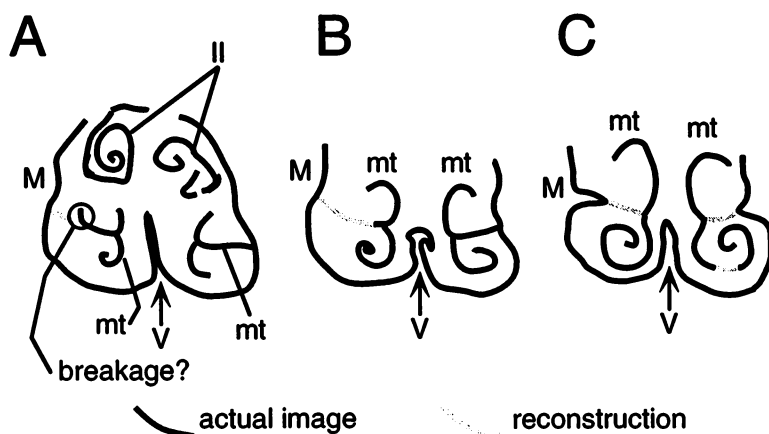


FIGURE 6. Reconstruction of shape of *Hyaeodon* maxilloturbinate (mt) based on scans presented in Figure 5A (A), 5C (B) and 5D (C). See Figure 2 for abbreviations.

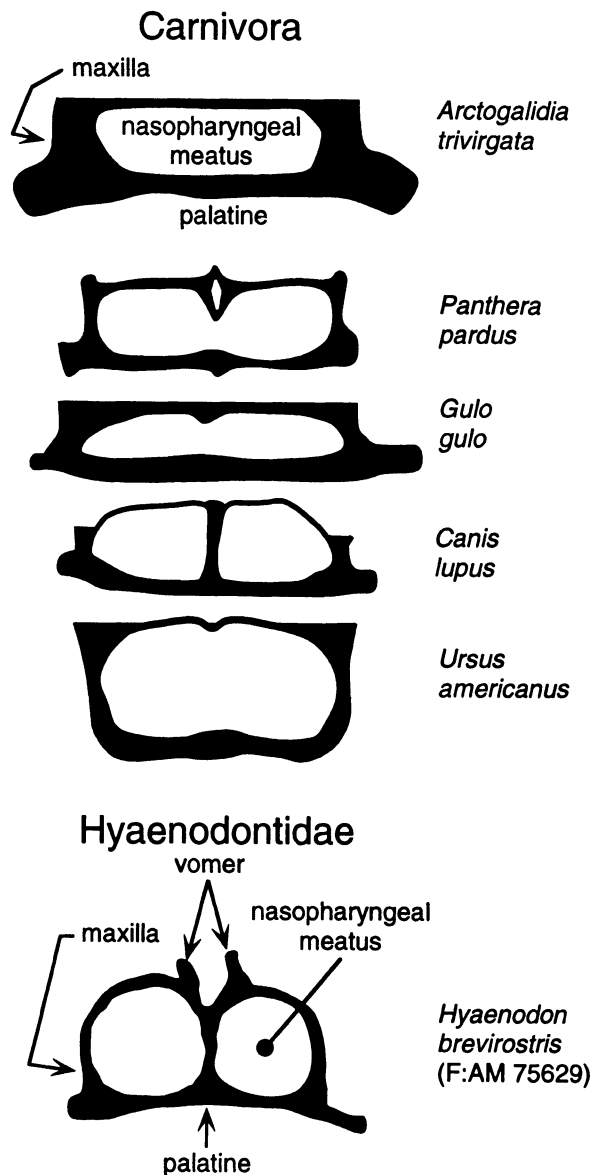


FIGURE 7. Nasopharyngeal meatus in some extant Carnivora and in *Hyaenodon brevirostris* (nearly undeformed specimen) and in representative extant carnivorans, approximately at level of P4 or M1. Drawn from CT scans, but scaled to same size. Note nearly circular cross section of nasopharyngeal meatus in *Hyaenodon*.

The lamina transversalis, a horizontal sheet of bone separating the olfactory compartment from the nasopharynx, is purported to be well developed in extant Carnivora, particularly in canids (Moore, 1981). CT scans of a small sample of canid, ursid, mustelid, and procyonid crania carried out by the first author indicate that this more pronounced separation of the olfactory compartment from the nasopharynx is a general characteristic of the Canifomia, rather than of canids alone. The lamina transversalis in *Hyaenodon* is more like that seen in extant felids; in other words, the lamina is not as prominent as in Canifomia.

SUMMARY AND CONCLUSIONS

Based on observations made in this study, the snout of *Hyaenodon* differs from those of carnivorans in three obvious characters: 1) the circular cross-sectional shape of the nasopharyngeal meatus and the groove it produces on the dorsal surface of the palate; 2) the non-rectangular shape and relatively small volume of the olfactory com-

partment; and 3) the large relative size and anterior extent (in *H. horridus*) of the maxillary sinuses. Character 1) may be an autapomorphy of *Hyaenodon*. Ideally, the polarity of this character would be assayed against the shape of the nasopharyngeal meatus in other Creodonta (which are unlikely to be represented by as well-preserved cranial material as for *Hyaenodon*), fossil and extant Lipotyphla, and any other possible sister-groups of the putative Creodonta, yet details of the internal anatomy of the snouts of many of these taxa are poorly known, unknown, or perhaps even unknowable (e.g., Novacek, 1986). Published figures of the nasopharynxes of extant mammals (e.g., Negus, 1958) support a conclusion that the shape of the nasopharyngeal meatus in *Hyaenodon* is an autapomorphy. The polarity of 2) is surmised to be primitive, because the olfactory compartment is large in extant carnivores. Character 3) is an autapomorphy of *Hyaenodon horridus*, the result of negative brain (brain cavity) allometry relative to the skull as overall body size increases during the evolution of a particular lineage.

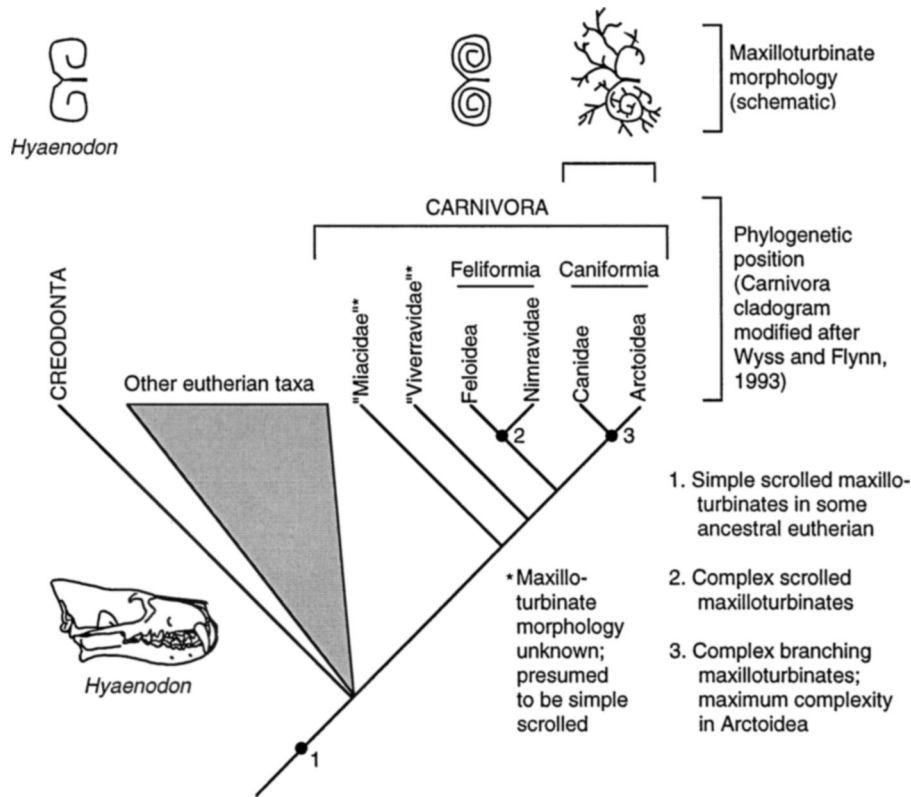
It is highly significant that the snout of *Hyaenodon* provides no compelling support for a Creodonta + Carnivora clade. If, in the future, specimens are secured that better illustrate the morphology of creodont ethmoturbinates, paleontologists may be better able to determine synapomorphic features of the carnivoran ethmoid, particularly if preserved ethmoturbinates of early carnivorans and oxyaenid creodonts can be found. These future observations will, more than likely, also require improved equipment and techniques. The auditory regions of carnivorans, creodonts, and "insectivores" have provided some general clues to phylogeny; perhaps the snout, being another anatomically complex region, will provide even more clues.

Hyaenodon has a simple-scrolled maxilloturbinate of a primitive eutherian grade (see figures of eutherian maxilloturbinates in Negus, 1958). The elaborately branched maxilloturbinates of caniform carnivorans (Arctoidea + Canidae) (Anthony and Iliesco, 1926; Negus, 1958; Ewer, 1973; Hunt et al., 1994) are, by all available observations, unique among carnivorans, yet a credible out-group comparison is ultimately necessary in determining character polarity. If Creodonta are not, in fact, the sister-group of Carnivora, then *Hyaenodon* cannot provide a strict outgroup comparison. Apparently, the nagging question of what is the true sister-group of Carnivora remains, but, in the least, the maxilloturbinates of *Hyaenodon* provide one more important bit of evidence arguing strongly in favor of the derived nature of the elaborate caniform carnivoran maxilloturbinate (Fig. 8) relative to that of other eutherians.

In Eurasia, Africa, and North America, the hyaenodontids *Hyaenodon horridus*, *Megistotherium osteothlastes*, and *Hemipsalodon grandis* (Mellett 1969, 1977; Savage 1973) attain body sizes comparable to (probably exceeding, in the case of *Megistotherium*) the largest caniform carnivorans (amphicyonids and ursids). It is compelling to speculate that the extinction of the terminal lineages of creodonts (hyaenodontids), particularly the large-bodied taxa, might be due in part to a physiological disparity with large carnivorans evolving contemporaneously. The elaborate maxilloturbinates of caniform carnivorans and the carotid retia of feliform carnivorans (e.g., Davis and Story, 1943) are surmised to be efficient solutions to problems of thermoregulation (cf. Baker, 1979, 1980, 1982), although maxilloturbinates may have multiple physiological functions (Negus, 1958). Although it is impossible to determine whether hyaenodontids, or for that matter any creodont, had carotid retia, observations made in this study indicate that they had very simple maxilloturbinates—simpler than either the elaborately branched maxilloturbinates of caniform carnivorans or the multiple-turn scrolled maxilloturbinates of many felids. Furthermore, considering the apparent simplicity of ethmoturbinates in *Hyaenodon* and the smaller size of the olfactory compartment in *Hyaenodon* (relative to carnivorans), it is likely that the olfactory capabilities of hyaenodontids were not as acute as at least those Neogene carnivorans of comparable body size (canids, ursids, felids, and hyaenids), if not carnivorans in general. This hypothesized disparity in olfactory acuity would have imposed significant limitations on prey detection and intraspecific communications, leading to speculation that hyaenodontid behavior, as well as physiology, differed appreciably from the patterns observed in modern carnivorans—their ecological replacements in the last half of the Tertiary.

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"Other eutherian taxa" not likely to include any Ungulata or Edentata.

FIGURE 8. Preliminary cladogram showing distribution of maxilloturbinate types. Long-standing Creodonta + Carnivora clade (e.g., Wyss and Flynn, 1983) is refuted by Polly (1994, 1995, 1996) and Fox and Youzwshyn (1994), rendering a strict outgroup comparison between *Hyaenodon* and Carnivora impossible, but some higher-level eutherian taxon includes both orders and probably excludes ungulates and edentates (cf. Novacek, 1986; Novacek et al., 1988). Lack of resolution in cladogram may eventually be remedied by close examination and comparison of nasal cavities in fossil and extant Lipotyphla and Leptictida, as well as other eutherians.

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