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**THE HUMAN NASAL COMPLEX: A STUDY OF ITS ANATOMY, FUNCTION AND
EVOLUTION BY CT, COMPARATIVE
AND
MORPHOMETRIC METHODS**

**By
SAMUEL MARQUEZ**

VOLUME I

**A dissertation submitted to the Graduate Faculty in Anthropology in partial fulfillment of
the requirements for the degree of Doctor of Philosophy, The City University of New York**

2002

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APPROVAL PAGE

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ABSTRACT

**THE HUMAN NASAL COMPLEX: A STUDY OF ITS ANATOMY, FUNCTION AND
EVOLUTION BY CT, COMPARATIVE
AND
MORPHOMETRIC METHODS**

By

SAMUEL MARQUEZ

Advisor: Professor Jeffrey T. Laitman

This dissertation focused on the comparative study of the human nose and paranasal sinuses (nasal complex) in order to better understand its place among mammals and to assess specific features of the human condition. The research design included a three-phase approach. First, a preliminary investigation focused on the nasal region in terrestrial mammals and extant humans by dissection, endoscopic examination and computer tomography (CT) imaging. Second, a morphometric and CT examination was done of the effects of climate on the nasal complex of closely related macaque species living at high and low altitudes, thus serving as a natural experiment. Third, a quantitative and qualitative study of two extinct hominins – an “archaic *Homo sapiens*” (Kabwe) and a classic Neanderthal (Gibraltar I) - was undertaken in order to compare their nasal regions to a large sample of regionally distinct modern populations.

Results from phase 1 showed considerable inter-species variation with regard to the size of the bony elements surrounding the nasal cavity and paranasal sinuses and in the specific configurations of its boundaries. Assessment of the nasal complex in humans revealed that the advent of new imaging modalities is providing a more detailed and precise understanding of specific aspects of the region than previously available. Results from phase 2 showed that the use of internal nasal features greatly enhanced our appreciation of nasal complex anatomy. Results also showed specific effects of climate on different components of the nasal complex. Lastly, results on the nasal complex in fossil hominins and extant humans showed that Neanderthals were distinct from both archaic and modern *Homo sapiens* having external and internal nasal features consistently and significantly falling outside the ranges of these groups. These data suggest that the nasal complex in particular, the entire respiratory tract in general, in Neanderthals may have been considerably different from that found in archaic and modern *Homo sapiens*. The results of this study support a species level distinction for *Homo neanderthalensis*.

The three-phase approach permitted the utilization and integration of different methodologies which allowed both external and internal parameters of the nasal region to be examined for the first time. This approach has provided a more complete perspective upon the function and evolution of a major component of the upper respiratory tract.

DEDICATION

**To the homeland and people of my parents' place of birth –
Colombia, South America**

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CHAPTER 1

SCOPE AND OVERVIEW OF STUDY

1.1. SCOPE OF STUDY

This dissertation examined aspects of variation in the nasal complex of mammals which may be diagnostic for providing functional and phylogenetic inferences about human evolution. This study integrated three different approaches in an effort to better understand the morphological design and adaptive nature of the human nasal region. First, a comparative macrosmatic and microsmatic study of the mammalian nasal complex was undertaken utilizing computer tomography (CT) imaging, endoscopic examination techniques, and gross anatomical dissection. Second, an animal model was employed to explore the climatic effects of the nasal region in macaques living in high and low altitudes implementing traditional morphometrics of external craniofacial landmarks and internal parametric dimensions (e.g., maxillary sinus volumes). Third, a qualitative and quantitative study examined a multiregional sample of modern humans in order to compare and contrast its nasal complex morphology to the fossil human record. Finally, the synthesis of all three phases of the study permitted a discussion on the evolutionary implication to modern human origins and avenues of future research.

1.2. THE IMPORTANT ROLE OF THE NASAL COMPLEX

As the nasal complex will be discussed in considerably more detail in the coming chapters, only a brief discussion is offered here. The term nasal complex represents the morphophysiologic concept incorporating components of the upper respiratory system,

including the external nose, nasal cavity proper, paranasal sinuses, its osseous construction, vasculature, innervation, mucociliary transport system, glandular distribution, epithelial profile and gas composition, which together operates as a well-integrated functional unit during respiration.

1.3. BACKGROUND

The nose is a prominently placed “organ” that participates in a variety of important physiologic activities including being the entry portal of the upper respiratory system. The nose with its sinus cavities the paranasal sinuses, which communicate with the nasal cavity proper, have their ostia well protected by the protruding folds of the turbinate bones. The nose itself, apart from its function as an olfactory organ, prepares inspired air for the lungs by modifying its temperature and providing humidification. It further protects the body and the lower respiratory passages against invasion by noxious agents.

The work of Goodale (1896) demonstrated experimentally the efficiency of the nose in heat exchange. Proetz (1922) and Negus (1952) found the humidification of inspired air by the nose for preservation of the physical “water film” at the alveolar membrane for the proper diffusion of respiratory gases to be highly efficient. However, others diminished the importance of this physiologic mechanism, citing that this occurred even in tracheotomized patients (Proetz, 1941) in which the nasal passages were bypassed. The nose was then thought not to be essential in respiratory physiology. However, in tracheotomized patients, the humidity of the inspired air is less than optimum from the absence of water supplied by the mucosa of the middle turbinate and

middle meatus which results in a pathologic increase in the viscosity of the mucous blanket covering the respiratory mucosa, even with forced hydration of the organism. In this regard, Hilding (1932) has demonstrated the lethal effect of dryness on mucociliary activity and reemphasized the critical important function the nose provides during respiration.

1.3.1. Climate –A Critical Determinant of Change in Morphological Design

Climate effects ecological conditions which, in turn, affect the diversity of fauna and flora. Natural selection can act through dietary requirements by the selection of morphological regimes that accommodate the available food staples. Although dental morphology has been used to closely track environmental shifts in food hardness and texture encountered in various feeding strategies (Szalay et al., 1987, pg. 80) what has been often overlooked is the respiratory adaptive response of the organism to climatic change. Survival occurs when the pace of climatic change equals the pace of evolutionary adaptive change, or when the adaptive capability of a particular biological system is sufficient to adequately respond to the climatic challenge. Accordingly, respiration must be assigned the highest value and accorded primacy in the organism's struggle for survival, even before the mode of acquisition of food can be considered.

1.3.2. Regional traits

Clinal patterns in nasal form among modern humans and their strong association with climatic variables are widely viewed as evolutionary adaptations optimizing

respiratory heat and moisture exchange in the nasal mucosa (Thomson and Buxton, 1923; Davies, 1932; Weiner, 1954; Negus, 1958; Wolpoff, 1968). An adaptive response to climatic variability probably underlies most global variations in nose form.

The regional patterns seen in nasal form have been affected by natural selection (through climate on respiratory function), over relatively long periods of time. Stringer (1990) contended that the determination of modern human origins will “center on the pattern of evolution of geographic variants – commonly called races – of *Homo sapiens*.” In this regard, modern skeletal regional variation is manifested more clearly and consistently in the splanchnocranium rather than in the neurocranium. Consequently, regional morphological stability is the expected result in the absence of migration from other global climatic zones, which can provide important evidence for phylogenetic interpretations.

1.3.3. Developmental stability of cranial regions

The oral cavity volume is primarily responsible for the growth of the midfacial skeleton (Moss et al., 1968) with vertical growth being unique in primates (Bromage, 1986). Periods of rapid vertical growth in humans are related predominantly to increasing respiratory need, and not to tooth development (Enlow, 1968). A proposed close association between the maxillary sinuses (a component of the upper respiratory system) and final dental eruption has been shown to be unfounded (Libersa et al., 1981, Márquez et al., 1997, Koppe et al., 1999, Lewis et al., 1999). These results support previous studies which demonstrated that the nasal region is much more stable developmentally than the neurocranial and masticatory components (Antón, 1989).

Although a variety of dietary differences and paramasticatory behaviors potentially influence facial form (e.g., Hylander and Johnson 1997) their effects on nasal form appear to be minimal and secondary to the primacy of selection for an effective respiratory functional system (Glanville, 1969).

1.3.4. Development of nasal form

Population differences in nasal form are often manifested very early during ontogeny. Significant differences in nasal morphology exist, for example, between African-Americans and Euroamericans as early as the second trimester of prenatal development. These features include the form of the inferior border of the piriform aperture, the size of the anterior nasal spine, the breadth of the nasal aperture, and the morphology of the cartilage and integumental structures of the external nose (Franciscus, 1995). Accordingly, authors have proposed that most features of the nose are strongly genetically encoded (e.g., Koppe et al., 1999). Consequently, the well-documented geographic regional patterns of variation, the developmental stability, the primacy in facial growth and development, and the strong genetic encoding, make the nose an ideal region for phylogenetic analysis (Franciscus, 1995). While previous studies have largely focused on the external parameters of the nasal region few have investigated the internal aspect of the nose. This includes the nasal cavity proper with its internal structures and particularly the paranasal sinuses.

1.3.5. Proposed functions of the paranasal sinuses

The paranasal sinuses are an integral part of the nasal complex as these cavities all developed from, and remain in communication with, the nasal cavity. A general consensus is lacking as to their functional role although many investigators *a priori* have taken a position. Proposed functional roles for the paranasal sinuses can be categorized in three components: 1) structural role; 2) physiological role; and 3) as evolutionary residuals. In an effort to identify the exact role of the paranasal sinuses investigators have examined factors involved in the evolution of the primate crania. Brain enlargement, facial and orbital orientation, basicranial flexion, tooth size and masticatory loads were among those considered, and the conclusion reached was that the observed differences in sinus morphology in various taxonomic groups cannot be explained by a single factor. These authors believe that the widely assumed structural role for the paranasal sinuses is incorrect: instead, the real function of these spaces may be related to the upper respiratory tract, playing a physiological rather than a structural role (Koppe et al., 1999). Recent molecular biological studies of the paranasal sinuses have reaffirmed a non-structural explanation of sinus function (Lundberg et al., 1994). The discovery within the paranasal sinuses of the production of nitric oxide, a potent neurotransmitter with profound effects on pulmonary vasculature and tissue oxygenation has altered the traditional explanations of sinus physiology (Gerlach et al., 1994). Recent experimental evidence on mucosal blood flow also has shown that the paranasal sinuses, a component of the nasal complex, function as an interactive mosaic of otherwise anatomic distinct units (Gannon et al., 1997). Accordingly, any human evolutionary study on the nose

must include components of the nasal complex in order to assess the critical role they may have played during natural selection.

1.4. OVERVIEW OF CHAPTERS

1.4.1. Chapter 2

Chapter 2 surveys a variety of macrosmatic mammals to track their sinus diversity in order to better appreciate variations in the upper respiratory system. The chapter provides insight into the modifications of sinonasal morphology by the organisms to solve the challenges posed by their environment. A critical modification of this region is how olfaction is subserved in these mammals. Utilizing computer tomography it was found that the mammalian respiratory system is an apparently efficient and adaptable design uniquely constructed for their environments and mode of life.

1.4.2. Chapter 3

Chapter 3 focuses primarily upon the structure and development of the human nasal complex. Gross anatomical dissection, CT and endoscopic examination of cadavers was performed to illustrate the intricate and sometimes confusing anatomy of the nasal complex. This chapter addresses issues regarding inconsistencies and vagaries in terminology, as these have often been a major source of confusion among those studying the sinuses. An overview of the proposed functions attributed to the sinuses is presented with an accompanying explanation and/or critical commentary from a modern

perspective. In addition, an exhaustive historical review of publications on sinus morphology was undertaken to record the earliest known descriptions of each sinus to help explain the basis for persisting errors in nomenclature.

1.4.3. Chapter 4

Chapter 4 investigates the climatic effects on the nasal complex of *Macaca mulatta* and *Macaca fascicularis*. As previous studies examining the effects of climate on the nasal region have been usually limited to external craniofacial landmarks this chapter approached the issue by assessing data from both internal dimensions and volumes, in conjunction with the more traditional external measurements. During formulation of this approach it became clear that inclusion of the internal nasal complex parameters was a critical factor in providing a more meaningful analysis.

1.4.4. Chapter 5

Chapter 5 examines the nasal complex of two extinct hominins – an African archaic *Homo sapiens* (Kabwe) and a classic European Neanderthal (Gibraltar). A qualitative and quantitative study was undertaken on a large sample of regionally distinct human populations in order to compare these two human fossils. New to such previous studies was the morphometric incorporation of internal nasal structures (i.e., maxillary sinus volume) which may add to our understanding the systematic position of these two fossil humans.

CHAPTER 2

EXAMINATION OF THE NOSE AND PARANASAL SINUSES

IN A

VARIETY OF MAMMALS

The focus of this chapter is the examination of the components of the nasal complex in a variety of mammals. In contradistinction to earlier studies employing gross anatomic dissection this study utilized CT imaging which permitted non-invasive visualization of the various structures and permitted calculation of their dimensions. This provided the background for interspecies comparison.

2.1. INTRODUCTION

The paranasal air sinuses have long been a source of great interest to anatomists who have studied a considerable number of vertebrate species within the Class Mammalia (e.g., Pauli, 1900a,b, c; Dieulaufé, 1906; Nemours, 1931; Negus, 1958), and especially in the Order Primates, which have received particular attention (e.g., Wood Jones, 1936; Wegner, 1936; Cave and Haines, 1940; DuBrul, 1965; Hershkovitz, 1977; Maier, 1980; Koppe, 1995). Clinically oriented human studies, however, represent the largest proportion of the morphological literature relating to paranasal sinus investigations. Some of the well known contributors to our knowledge of the human paranasal sinuses during the late 19th century include such

legendary clinicians as Zuckerkandl (1882), Bosworth (1888), Mouret (1898), Killian (1900), Onodi (1903), Sieur and Jacob (1901), and Grünwald (1925), to name a few. However, these authors of human clinical studies gave different names to the same anatomical structures, and sometimes the same name was applied to different structures. This generated considerable confusion for those interested in studying nonhuman mammalian paranasal sinuses. Since no universally accepted terminology was available, these investigators were free to choose anatomic terms they favored rather than adhering to strict nomenclatural guidelines. Investigators studying nonhuman mammalian sinuses utilized terms in some of these landmark human studies as a guide for their anatomical descriptions, which only served to perpetuate and compound the current state of confusion. This lack of consensus persists today, although impressive efforts have been made to address this problem (see for example Stammberger et al., 1995).

Paranasal pneumatization is not restricted to mammals, with numerous other vertebrates exhibiting air-filled epithelial diverticula of the nasal cavity region (e.g., birds, crocodiles). Although the paranasal sinuses in non-mammalian vertebrates have often been given the names of their presumed mammalian counterparts, the homologies of some of these sinuses have only recently become the subject of scrutiny (Witmar, 1995a).

Progress in interpreting the morphologic diversity of vertebrate sinuses has been hampered historically by the application of typological approaches that have sought to homologize mammalian (primarily human) sinuses with those of other vertebrates, under the often unstated belief that all organisms will display

manifestations of the archetype (Witmar, 1995a). The problem is further compounded by the lack of a universally accepted terminology to describe these pneumatic spaces and their contiguous structures, even within such restricted mammalian groups as Old World monkeys. As an example, Rae and Koppe (2000) have cited the interchangeable use of the terms *lateral recess* and *maxillary sinus*, whereas in fact each term represents a distinct and different morphological entity. Moreover, agreement on the anatomical nomenclature for the *nasal complex*, generally defined as the nose, nasal cavity and paranasal sinuses, is lacking even in the single species *Homo sapiens* (see for example Stammberger et al., 1995). Ultimately, it is hoped that by taking a broad phylogenetic perspective, the significance of sinus diversity will be correctly interpreted and yield insight into which structures are truly homologous, in order to establish the appropriate functional and evolutionary conclusions. Undertaking such a broad phylogenetic approach to document sinus diversity among vertebrates is beyond the scope of this dissertation. Rather, this chapter will be limited to the examination of the nasal complex in a representative sample of terrestrial mammals in order to accomplish the following aims.

2.2. DEFINITIONS, THE MAMMALIAN NASAL COMPLEX, AND NASAL CAVITY EPITHELIAL COVERING

2.2.1. Definitions

Some anatomical definitions and concepts must be clarified before the distribution of pneumatic structures throughout the chosen mammalian sample can be examined. The first is the distinction between a soft tissue pneumatic diverticulum and the bony recess that often houses it. While some investigators insist that making this distinction is not important, I believe it is critical in drawing comparisons across broad taxonomic groups. As an example, an epithelial diverticulum is present in numerous taxa but the actual pneumatization of bone occurs only in a subset of these taxa. In the archosaurs, a monophyletic group whose extant members include birds and crocodiles, a suborbital diverticulum is present that later forms the *antorbital* sinus, a key morphological character that unites this group (Witmar, 1997). An important contribution to our understanding of the pneumatization process was Witmar's (1995b) report that superficial bony recesses occupying the same anatomic area in different taxa may arise from pneumatization via different diverticula (see below). Consequently, errors in homology will arise if differences in the ontogenetic pattern are not recognized. Although a full understanding of the ontogenetic patterns and processes of pneumatization is currently lacking, some of the physiological mechanisms by which pneumatization takes place are known.

The structure and maintenance of the operational framework of bone involves three primary cell types: osteoblasts; osteocytes; and osteoclasts. Osteoblasts are

bone-forming cells responsible for synthesizing and depositing bone material known as osteoid, or pre-bone tissue, which is an uncalcified organic matrix rich in collagen. Calcification of bone takes place as crystals of hydroxyapatite, the inorganic component of bone, are deposited into the osteoid matrix. Once surrounded by bony matrix, the osteoblastic cells are now called osteocytes, cells that are responsible for maintaining bony tissue. In turn, osteoclasts are cells responsible for the resorption or removal of bone tissue. The reshaping or remodeling of bone is a dynamic process which takes place at the cellular level, as osteoclasts remove bony tissue and osteoblasts rebuild it. The opposing processes of bone formation and resorption allow bones to maintain or change their shape and size during ontogeny.

The action of osteoclasts in the resorption of bone is an important factor in the process of pneumatization. The onset of this interaction is intimately related to the formation and presence of a respiratory epithelial diverticulum; however, precise details of the initiation at the molecular, cellular and even gross levels are still unknown. Nevertheless, diverticula and bony recesses can be considered causally related from a morphogenetic viewpoint. In the majority of cases, the bony recesses are actually produced by pneumatization through the epithelial diverticulum and its osteoclastic front (Witmar, 1990, 1995a, 1997).

Another distinction should be made between intracapsular and extracapsular recesses with regard to their diverticula. *Intracapsular recesses* are those internal to the cartilaginous nasal capsule. Only epithelial diverticula that have escaped the bounds of the cartilaginous capsule are competent to pneumatize bone (Witmar, 1995a). This distinction may be difficult to make in many clades of vertebrates as the

nasal capsule is not a complete cartilaginous box. In addition to the nares and choanae it has various openings that may transmit evaginations of nasal epithelium, allowing intracapsular epithelium to become extracapsular. As will be discussed later in this chapter, some of these outpocketings bear some histologic resemblance to pneumatic diverticula, but only a few actually pneumatize bone. Investigators failing to draw this distinction have incorrectly applied names to nasal anatomical structures suggesting “true” pneumatic recesses which are inappropriate by their ontogeny (e.g., Mihalkovics’ [1898] identification of a “sinus maxillaris” in the lizard *Lacerta*).

Another point requiring clarification relates to the site of origination of the pneumatic diverticulum within the nasal cavity that invades and pneumatizes contiguous bony structures (Witmar, 1995a). Since the precise point of origin is an important factor in describing and classifying the pneumatic spaces of the skull correctly, a clearly defined knowledge of the organizational framework of the nasal region is essential to track the ontogenetic pathways of these diverticula (see discussion pg. 25). In primates, as in all mammals (Paulli, 1900a, b, c; Moore, 1981), all of the paranasal sinuses originate as diverticula from the nasal cavity proper. However, in nonmammalian vertebrates exhibiting paranasal pneumaticity, diverticula arise not only from the nasal cavity proper, but also from the other portions of the *cavitas nasalis*. Consequently, although mammals generally have more extensive paranasal sinuses relative to other vertebrates, the morphogenetic diversity of sinuses in mammals is certainly less than in some other vertebrate clades.

Concerning the Class Mammalia, guidelines for the proper identification of a paranasal sinus must be established. The definition of a “true” paranasal sinus is

based purely on its ontogenetic pattern given by Cave (1967). A “true” paranasal sinus must have its respiratory diverticulum originate from, and remain in communication with, the nasal cavity. Its growth must be from a given meatus of the nasal cavity and have a patent communication via an ostium which remains permanently associated with that meatus. The sole guide to its morphological identity is provided not by the bone or bones it may ultimately pneumatize, but by the bone or bones circumscribing its ostium, or point of origin (Cave, 1967). Cave (1967) further explains that neglect of this basic consideration has resulted all too frequently in the misinterpretation of analogous cavities as homologues, to the great confusion of the subject. An example of this misclassification can be drawn from my CT examination of the Orangutan which have been traditionally reported as exhibiting only one paranasal sinus – the maxillary sinus (see Figure 2-1).

A number of investigators in their anatomical descriptions of certain specimens have incorrectly identified and assigned paranasal sinus status to a number of structures. For example, in a study of the skull morphology of Anthropodea, Du Brul (1965) reported the presence of a “peculiar pair of deep fossae” on the exocranial surface of the sphenoid bone in the lion marmoset *Leontideus rosalia* - a platyrrhine monkey. According to Du Brul, the only other mention of these unique morphological structures was in a study by Hershkovitz (1949) which called attention to these ‘sphenoidal pits and vacuities.’ Although Du Brul accurately described and considered these sphenoidal depressions in establishing their taxonomic valence in

Figure 2-1. a: An axial scan of a subadult orangutan (*Pongo pygmaeus*) showing what appears to be a sphenoid sinus but is actually the maxillary sinus invading the sphenoid bone (*red arrow*). **b:** In an adult orangutan, the communication (*yellow arrows*) between the left maxillary sinus and the evacuated sphenoid bone is clearly shown; the right maxillary sinus (*red arrows*) is seen to encroach upon the sphenoid bone.



Figure 2-1

platyrrhine phylogeny, he assigned them paranasal sinus status without investigation of their mode of genesis. Du Brul further reported on the paranasal sinuses of two other New World monkeys (*Lagothrix* and *Aloutta* claiming the existence of a sphenoid sinus in the former and maxillary, frontal and sphenoidal sinuses in the latter, all of which have been proven to be incorrect. He based his conclusions on sagittally sectioned crania from museum collections, and it is the use of this limited material that explains his error in according these spaces paranasal sinus status. A figure of *Lagothrix* reveals a cavitation of the anterior portion of the sphenoid body which might pass superficially for a genuine sphenoidal sinus (Du Brul, 1965, pg. 268). The cavity described by Du Brul is incomplete and open anteriorly, without an ostium, and is essentially a topographical invasion of the body of the sphenoid bone by the posterior portion of the nasal cavity. According to Cave (1967), this intrasphenoidal cavity may function as a paranasal sinus in lightening the skull (if one subscribes to this suggested sinus function), but anatomically it is not a true sinus.

The figure of *Aloutta* reported by Du Brul (1965, pg. 268) demonstrates the pitfall of solely using dry adult cranial specimens in paranasal sinus identification. The specimen appears to manifest frontal and sphenoidal sinuses, the latter of which “extends laterally.” However, the complete anatomical dissection of a wet specimen (Cave, 1967) offers an entirely different interpretation. It demonstrated that only a single paranasal sinus, the maxillary sinus, was present in this species. Although the frontal and sphenoid sinuses may appear as independent sinuses in sagittally sectioned dry crania, they are actually intrafrontal and intrasphenoidal extensions of this single but enormous maxillary sinus.

Many other investigators have made similar errors. The great anatomist Emil Zuckerkandl (1887a) also mistakenly believed that the ethmoidal and sphenoidal extensions of the *Aloutta* maxillary sinus were true paranasal sinuses which had become secondarily confluent. However, the absence of ostia between these cavities and the main nasal cavity renders such an interpretation untenable (Cave, 1967). The concept that the enormous maxillary sinus of *Aloutta* is not constrained within the body of the maxilla but can invade adjacent bones such the frontal, and even a relatively distant bone such as the sphenoid, is not restricted to this New World monkey. This phenomenon is also seen in the great apes where the maxillary sinus of orangutans is capable of invading the frontal, the sphenoid, and even the palatine (Schwartz, 1988). This phenomenon is also seen in another ape, the chimpanzee, and in non-primate mammals such as the mountain goat and North American deer.

2.2.2. The Mammalian Nasal Complex

The nasal complex has been considered an organ of respiration for more than a century (Bosworth, 1888; Harkema, 1991; Cole, 1993; Márquez et al., 2001), and yet, the detailed morphology of the mammalian nasal region has not been completely defined (Maier, 1993a). The morphological components that comprise the region and the physiological processes subserved are both intricate and oftentimes elaborate. The osteocartilaginous framework and its topographical orientation (e.g., Killian, 1903; Schaeffer, 1920; Naumann, 1991, Patra et al., 1986), the fluctuating intranasal pressures and gaseous composition (e.g., Suarez, 1952; Scharf, 1994; Mikula et al., 1995), the intricate morphology of the internal bony structures (Hillienius, 1992,

1994), and the different mucosal linings (e.g., stratified, respiratory, transitional, and olfactory epithelium, see Harkema, 1991; Busuttil et al., 1977) are all components that contribute to the region's complexity. In its totality the nasal complex comprises a vital functional unit during respiration. The physiologic needs of the lower respiratory tract which are carried out by the nasal mucosa's highly evolved morphologic specializations reflect a successful evolutionary adaptation to meet these various demands. Ultimately, it functions to protect the pulmonary airway over a wide range of ambient conditions that may be harmful to the delicate epithelial linings of the terminal bronchi and alveoli where the exchange of oxygen and carbon dioxide takes place (Negus, 1952; Proctor et al., 1978).

The activities of the mucosal coverings that subserves the respiratory system are collectively known as the *air conditioning function* of the aerodigestive tract (Guyton and Hall, 1996), and can be arranged under four broad categories: 1) temperature modification and humidification (e.g., Negus, 1952); 2) regulation of the flow of inspired air (e.g., McCaffrey, 1993); 3) control of the rate of respiration (e.g., Lundberg et al., 1996); and 4) resistance to invasion by pathogenic microorganisms and filtering and cleansing (e.g., Brain, 1970). The upper respiratory defenses provided by the nasal mucosa operate by three mechanisms: 1) absorption of water-soluble gases and vapors (Aharonson et al., 1974); 2) metabolism of inhaled xenobiotics (i.e., biologically active compounds not endogenous to the organism - Dahl et al., 1982), and 3) trapping and clearing inhaled particulate matter (Proctor et al., 1978). Billions of molecules of noxious gases and particulate matter (e.g., dust, asbestos) that are potentially infectious, allergenic, irritative, or toxic in nature are

present in breathable air, of which 10,000 to 20,000 liters are inspired daily by the average human (McCaffrey, 1993). Animals of larger body mass undoubtedly require significantly larger volumetric air consumption to meet their respiratory needs. This air is required to be filtered, neutralized, and eliminated by the mucociliary system of the respiratory epithelial lining, and then temperature/moisture modified, rendering it in an ideal condition for the bronchial and alveolar regions (Negus, 1952). Humidification and temperature regulation is managed by the extensive sinusoidal network of large capacitance vessels within the nasal “erectile tissue” primarily present in the mucosa on the inferior turbinate and anterior nasal septum (Widdicombe, 1986). This “erectile tissue,” is technically not true erectile tissue as is found in the genitalia (corpora cavernosa of the penis and clitoris), as the location is deeper and the mechanism by which blood enters the sinusoidal spaces and the underlying biochemistry regulating its flow is different (Bosworth, 1888, pg 121).

2.2.3. Nasal Cavity Epithelial Covering

A brief comment on the histological composition of the nasal cavity is required. In a typical nonhuman mammal the nasal cavity can be divided into three parts: the anterior respiratory chamber; the nasopharyngeal canal; and the olfactory cul-de-sac (Scott, 1954). Within these regions, four histologically distinct types of epithelium are present: stratified squamous; olfactory; respiratory; and transitional epithelium. There is considerable variation in the distribution of the four types among different species but as a rule the anterior segment of the cavity is lined by stratified squamous epithelium, the superoposterior portion by olfactory epithelium,

with the remainder of the region covered by respiratory epithelium, except for a thin layer of transitional epithelium at the boundary between the olfactory and respiratory epithelium (Harkema, 1991). According to Moore (1981), the area of mucous membrane is increased in reptiles and birds, with an even greater increase in mammals by the formation of turbinals from the lateral walls of the nasal cavity. The comparative study by Harkema (1991) demonstrated the complexity and diversity of the nasal cavity region found in different animal species. Harkema (1991) reported that rats, rabbits and dogs have more complex turbinate systems than monkeys and humans, with considerably more olfactory epithelium found in the former group of taxa. The osteological protrusion of the turbinals in macrosmatic mammals provides additional surface area for olfactory epithelial coverage a contradiction to microsmatic species which have a smaller reliance on olfaction and accordingly have a much simpler turbinate system. A consequence of turbinate complexity in mammals is the enhancement of temperature modification, humidification and cleansing of inspired air. However, the principal effect of an increased mucosal surface area in most mammals is an increase in olfactory perception.

Of the four histological lining types, the two principal ones are respiratory and olfactory epithelium. The difference in surface areas between these two types has enabled the classification of most mammals into two major groups - macrosmatic and microsmatic species based on their degree of dependence on olfaction. Although a number of workers have claimed that the nose has evolved for the purpose of olfaction (e.g., Negus, 1957,1958), the primary function is generally accepted to be respiration, as the first mammalian act after birth is breathing. Nevertheless, olfaction

plays an important function in the great majority of mammals. Macrosmatic species require large bony surface areas for the accommodation of olfactory epithelium necessary in their search for food, detection of predators, and mediation of sexual behavior. A prognathic facial morphology accommodates this need for olfaction, the extreme of which is seen in the form of a snout. The hard tissue anatomy that serves as the substrate for the mucosal epithelial lining is afforded by the bony walls of the nasal cavity proper and by the nasal septum. The latter consists of an anterior cartilaginous and a posterior bony portion that compartmentalizes the nose into two nasal cavities and permits a near doubling of surface area (Marshall and Attia, 1987). The overlying mucosal surface area is further augmented by the presence of maxilloturbinate and ethmoturbinate bony elements within the nasal cavity (see below).

2.3. THE MAMMALIAN NASAL CAVITY

All terrestrial mammals possess a nasal chamber termed the nasal cavity proper, however, marked differences exist in the hard tissue anatomy that comprises the opening into it. The lateral and inferior border of its anterior opening in humans, referred to as the piriform aperture, is composed of the nasal and frontal processes of the maxilla, with the nasal bones enclosing the aperture superiorly. In other mammals, (e.g., other primates, artiodactyls), the lateral borders are the incisive, or premaxillary bones, while the nasal bones continue to be the superior border of the aperture. Another difference observed in the bony configuration in humans is the presence of a thin projection of bone in the midline, at the inferior margin of the nasal

aperture, called the anterior nasal spine (Mooney and Siegel, 1991). This structure is unique to humans, with the chimpanzee the only other primate having even a rudimentary bony tubercle in this region. The functional role of this projection of bone in humans is currently unknown. Despite these differences in the external borders, all terrestrial mammals have an anatomical region that can be called a nasal cavity. Although the internal configuration of the nasal cavity varies in the great majority of mammalian groups, the existence of a spatial region that is the nasal cavity proper appears to be present across terrestrial mammals. The consistent presence of this region in the skull appears to be unrelated to such factors as total body size and diet, which have profound effects upon the morphology of other cranial regions (Albrecht, 1978). The principal influence must relate to the organism's respiratory and olfactory demands and be dictated by its genetic blueprint.

2.3.1. Nasal cavity proper

Conceptualizing the nasal cavity as a four-sided box, the outer walls would represent its lateral margins, the superior and inferior walls would represent the superior and inferior margins, with the anterior and posterior walls absent and represented by the anterior and posterior nares. Placing a partition through its median plane divides the box internally into two halves. This analogy approximates the general bauplan of the nasal cavity in most mammalian groups. Assembling the osteological elements of each wall of the nasal cavity is the next constructive step.

2.3.2. Osteological components of the nasal cavity

The principle skeletal elements in the lateral wall of the nasal cavity are the premaxilla, maxilla, palatine, frontal, ethmoid, nasoturbinal, maxilloturbinal, and lacrimal bones. The median wall of the nasal cavity, referred as the nasal septum, is composed of the perpendicular plate of the ethmoid, vomer, maxilla, and palatine bones, and also has a cartilaginous component. The superior wall, or roof, is the anterior extension of the cranial base and includes the cribriform plate of the ethmoid and a portion of the frontal and nasal bones. The inferior wall, or floor, is formed by the hard palate (maxilla and palatine bones). In addition to the above structures, there are present scroll-like bony plates, the turbinals, which project into the lumen of the nasal cavity from its lateral walls (see below under nomenclature of the subdivisions of the ethmoid bone).

2.3.2.1. *Controversy regarding the maxilla*

It should be noted that the term maxilla, as generally used in human anatomy, corresponds to the premaxilla and the maxilla of most mammals. All mammals, with the exception of the Chiroptera (i.e., bats) and Xenarthra (i.e., armadillo, anteater and sloths), possess premaxillary bones which generally remain distinctly separated from the maxilla both on the facial and endofacial aspect (Romer and Parsons, 1977). Ever since the publication of Vesalius (1543) there has been controversy over the presence of the premaxilla in humans. It is generally accepted that before Vesalius, Galen based the classical teaching of anatomy on the anatomy of monkeys. As a result, Galen erroneously described the existence of a premaxillary suture on the facial

aspect of humans, but did correctly report the presence of the palatine portion of the premaxillary suture intraorally, as it is seen in monkeys. Based on human dissection, Vesalius corrected Galen's assertion that a premaxillary suture is seen on the facial aspect of the skull which was subsequently corroborated by Camper (1778). Many investigators including Colombo (1559), Fallopius (1561), Kölliker (1882), Fawcett (1911) have all confirmed the observation of a palatine suture. Albinus (1746) also made a description of this endofacial portion of the premaxillary suture, as did Goethe (1786) and Rosenmueller and Hassius (1804). Johann Friedrich Blumenbach earned the distinction of being considered the father of anthropology (*sensu lato*) by his efforts to document the suite of soft- and hard-tissue morphological characters that distinguished *Homo sapiens*. He named the premaxilla the intermaxillary bone because it was topographically orientated between the two maxillae (Blumenbach, 1775).

In the older literature, the premaxillary bone had been identified as the incisive bone, or *os incisivum*, because the upper incisors are rooted in it. With Blumenbach's new designation the bone was now referred to as the *os intermaxillare*. Blumenbach's objective was to demonstrate that humans are the same as other animals in having two bones that comprise their upper jaw. In his studies of human fetuses, Blumenbach observed sutures that may correspond to the separation of an intermaxillary bone and the surrounding maxillary bones, but found no evidence of an intermaxillary bone postnatally. He then used an Old World monkey and an Asian ape (the orangutan) for his anatomical dissection studies and mistakenly concluded that there was no evidence for an intermaxillary bone, which has been recently shown

to exist in both of these species (Schwartz, 1999). This led him to conclude erroneously that the *absence* of an intermaxillary bone was not unique to *Homo sapiens* and could not be used osteologically to distinguish humans from other animals.

Two other important figures entered into this morphological controversy, Johann Wolfgang von Goethe and Pieter Camper. Goethe seemed preoccupied with proving that the only distinguishing attribute of humans from all other animals was centered around their mental capacity for reason. He believed that humans were otherwise the same morphologically as all other animals. His anatomical studies led him to mistakenly identify an intermaxillary bone in *Homo sapiens*. In contradiction, Camper (1778) failed to find an intermaxillary bone in humans and declared that this characteristic essentially distinguished humans from the other animals possessing it.

George W. Callender, in 1869, was the first to provide a detailed developmental account of the intermaxillary bone in humans (Woo, 1949). Based on the examination of 20 human embryos and fetuses ranging in age from two to seven months, Callender (1869) concluded that the intermaxillary bone did exist in humans. Callender (1869) documented the intermaxillary bone as fully formed in a 4.3 inch crown-rump length specimen, which corresponds to a 112 to 140 day old fetus. He further reported that the intermaxillary bone was formed in membrane similar to many other mammals including the fetal pig and fetal kangaroo. He described fusion of the greater part of the intermaxillary bone with the maxilla in a nine-inch long fetus. He noted that the anterior edge of its nasal process had already fused to the nasal process of the maxilla and that its horizontal portion was inseparably attached to

the upper surface of the incisor process. The outline of the bone was preserved by a fissure which could be traced along its posterior margin, from the middle of the nasal process of the maxilla to the palate. He offered the following explanation for the lack of a suture delineating the intermaxillary and maxillary bones on the anterior facial surface. While the suture can be observed in a four month old fetus, by the fifth or early sixth month, the nasal and incisive processes of the superior maxilla begin to develop and cover over, or “bury,” the intermaxillary bone on the facial surface of the skull, leaving a permanent visible fissure only on the hard palate (Callender, 1869, p.168). Support for this 1869 study comes from Aiello and Dean (1990) who confirmed that prenatally the *os incisivum*, or intermaxillary bone, becomes completely overgrown by bone anteriorly leaving little evidence postnatally of a separate bone. They further stated that the incisive sutures that run from the incisive canal behind the incisor teeth to fade out between the lateral incisors and canines were the only remnants of a premaxillary ossification center in humans. In a more recent study of maxillary ossification in human embryos and fetuses, Vacher et al. (1999) concluded that in humans the term “premaxilla” does not conform to any anatomic reality, thus fueling and continuing the controversy.

23.2.2. Controversy regarding the vomer

The controversy regarding the vomer bone relates to its embryologic development. Studies on the vomer have reported that the mode of ossification is endochondral (e.g., Loty et al., 2000) while others have reported development to occur by intramembranous ossification in the membrane covering the cartilaginous

nasal capsule (e.g., Sandikcioglu et al., 1994). The term vomer is derived from the Latin meaning ploughshare and because of its morphological similarity to the farmer's irrigating tool was given its name. This bone is often overlooked as one of the key morphological components that comprises the skeletal portion of the nasal cavity. In humans, the vomer is a flat bone of trapezoidal shape forming the inferior and posterior portion of the nasal septum; it articulates with the sphenoid, ethmoid, two maxillae, and two palatine bones. In mammals, it articulates with all the bones mentioned above including the intermaxillary bone. Its base in mammals is anchored by the articulation of the nasal processes of the intermaxillary, maxillary and palatine bones. The dorsal border of the bone projects freely toward the nasopharynx and separates the choanae. The superior border, the thickest part of the bone, is divided into two spreading alae which articulate posteriorly with the rostrum of the body of the sphenoid. In humans, the anterior superior border is grooved for the reception of the septal cartilage and the dorsocephalic portion is ankylosed on one or both sides to the perpendicular plate of the ethmoid bone. The septal cartilage of young mammals extends posteriorly to the presphenoid bone, with the vomer embracing its inferior edge (Cleland, 1862). The development of the vomer is from two centers of ossification and therefore consists fundamentally of two alae. Between these wings a groove runs along its whole length which is occupied by the septal cartilage. Additionally, the edge of each alae becomes confluent with a horizontal shelf of bone – the transverse lamina of the ethmoid in those mammals that possess such a structure (see discussion below). The anterior extremity of the vomer forms a short vertical border which abuts the nasal crest of the intermaxillary bone dorsally and is

extends variably at its upper end in the groove of the crest. Cleland (1862) noted that this articulation sometimes does not occur because the intermaxillaries have no nasal processes, or very short ones. When they are present, however, there is a vomerine groove that continues forward between the intermaxillae.

2.4. ANATOMICAL TERMINOLOGY AND APPLICATION OF ANATOMICAL TERMS TO THE ETHMOID BONE

2.4.1. Anatomical Terminology

It has been estimated that toward the end of the 19th century, about 50,000 anatomical names were in use to describe 5,500 structures in the human body (Woerdeman, 1957). With 50,000 anatomical names in use throughout Europe and with medical dictionaries sometimes listing as many as 20 synonyms for one structure, the multiplicity of terms served only to generate intense confusion. In 1887 the German Anatomical Society undertook the task of standardizing the nomenclature and with the assistance of other national anatomical societies reduced the 50,000 names to 5,528. This was accomplished in 1895, in Basle. This system of nomenclature is known as the Basle Nomina Anatomica (abbreviated B.N.A.) has subsequently been expanded. In 1950, a major revision of the BNA was started in Oxford, England and finally adopted by the Sixth International Congress of Anatomists at Paris, in 1955. The revised system of nomenclature is currently known as the Nomina Anatomica. Anatomical terms found in medical dictionaries with the abbreviation "NA" following them mean that the terms have been approved and

recognized by the International Congress of Anatomists. There are two other nomina committees: the Nomina Anatomica Veterinaria (NAV) for domesticated mammals; and Nomina Anatomica Avium (NAA) for extant dinosaurs. These two nomina follow the same principles and guidelines as the NA, with the common purpose of providing a universal system of anatomical terms. In 1998 a new compendium known as the Terminologia Anatomica (TA) was issued by the Federative Committee on Anatomical Terminology (FCAT) and the 56 Member Associations of the International Federation of Anatomists (IFAA). Having been adopted by the IFAA the TA list of anatomical terminology supersedes all previous lists.

For example, Peter's (1902) term "*plica semilunaris*," which referred only to the mucosal ridge covering of the uncinate process of the ethmoid is inappropriate in NA terminology (see also TA) as it signifies the curved fold connecting the arcus palatoglossus and arcus palatopharyngeus above the fossa supratonsillaris (Stedman, 1982). Presently, the mucosal covering of the uncinate process and the bone itself do not have separate designations. Similarly, the *concha nasalis inferior* is defined in the NA as the inferior turbinate bone with its thick mucoperiosteum covering (Stedman, 1982), with no distinction made between the bony substrate and the mucosal covering.

Precise definition of the clefts, furrows, and spaces of the ethmoid was of limited importance in the past because surgical procedures were more radical, with all components of the ethmoid complex removed, leaving the maxillary, frontal, and ethmoid sinuses all widely exposed. With the advent of endoscopy and microsurgery precise description and definition of these clefts has become critical. The selective

nature of sinus surgery currently requires accurate description of the lateral wall of the nasal cavity and the ethmoid complex along with a standard nomenclature based on the developmental history of this area. Physiologic considerations brought a new appreciation of the role of ciliary clearance of the sinonasal mucosal blanket and the need for an intimate knowledge of its hard tissue base and the ostia within it.

Concerns with providing physiologically sound ventilation and drainage to the sinuses have led to a reappraisal of the fine anatomy of this region and new standardized terminology. As an example, enlargement of the natural ostium of the maxillary sinus must be made in the membranous portion of the middle meatus as this is the drainage pathway for the sinus. Creating an opening at another site would be ineffective in providing mucociliary clearance of the cavity. This is done by opening what Zuckerkandl (1882) called the anterior and posterior nasal fontanelles, so named because they lack a bony base and are situated in what is termed the *membranous area* of the lateral nasal wall (Stammberger and Hawke, 1993). These structures are not recognized in the NA which defines the 'anterior fontanelle' as the membranous interval at the junction of the coronal, sagittal, and metopic sutures where the frontal angles of the parietal bones meet the two ununited halves of the frontal bone (Stedman, 1982). Accordingly, emphasis will be placed on these narrow spaces and complicated clefts, or prechambers of the nasal cavity in the human anatomy chapter. The health of all the paranasal sinuses is dependent on the function of their prechambers in the lateral nasal wall of the nasal cavity (Stammberger, 1991). The mucosal lining of the paranasal sinuses and the nasal cavity is also of paramount importance in their function.

Taken together, the respiratory mucosal covering and its osteologic substrate comprise a functional unit and individual components of it should be recognized by the TA. There are other nasal anatomical terms that also require consideration by NA and TA. For example, the distinction between the terms naris, internal naris, external naris, choana, has not been fully addressed by NA. The osteological terms naris and choana have been applied to the rostral and caudal apertures of the nasal cavity, respectively. According to NA, 'naris' is defined as the anterior opening on either side of the nasal cavity (Stedman, 1982). This anatomical term collectively includes the soft-tissue structures (skin, cartilage, glands, neurovasculature, and musculature elements, etc.) immediately surrounding the external opening of the nasal cavity. All of the Nomina use the term 'naris' in this sense; however, this is inconsistent with its usage by paleontologists where it designates solely the bony opening (e.g., Witmar, 1995a). The Nomina all apply the terms "bony nasal aperture" (NAV, NAA) or "piriform aperture" (NA) for the bony hole. The posterior naris, or choana is derived from the Greek 'choane', or funnel. All of the Nomina use the term choana for the opening between the nasal cavity and pharynx for both dry skulls and wet specimens without consideration whether the margins are osseous or mucosal. In human anatomy reference is made to the 'nasopharyngeal meatus' for the osseous and mucous membrane rim enclosing the choana. None of the Nomina use "internal naris" or "external naris," which correspond to the choana (NA) and naris (NA), respectively. The "external naris" is of considerable importance in paleoanthropology, especially in regard to Neanderthals. This group of extinct humans has puzzled paleoanthropologists because of their sudden disappearance and

some have implicated their upper respiratory system as the possible anatomic and physiologic weakpoint leading to their demise (Reidenberg and Laitman, 1986). Accordingly, investigators for many years have focused on the wide and large bony entry portal of their upper respiratory tract, *apertura nasi ossea*, or piriform aperture. Recent studies have been directed at the reconstruction of their narial soft tissues in an attempt to understand the physiological implications of the regional morphology (e.g., Churchill et al., 1999). The above cited examples indicate that the Nomina Societies' guidelines should be dynamic and adaptive to demands made by technological advancements and detailed scholarship on the nasal complex.

2.4.2. Application of Anatomical Terms To The Ethmoid Bone

2.4.2.1. Nomenclature of the Subdivisions of the Ethmoid bone

The ethmoid bone serves as the conduit for the passage of odors, allowing detection, perception and interpretation by the brain. Structurally, it is the anterior segment of the cranial base, provides partial bony covering of the orbital region, and contributes to the division of the nasal cavity into two halves. As a full anatomical description of the human ethmoid bone appears in the following chapter, a general description highlighting certain features of the nonhuman mammalian ethmoid bone and its relationship to the remainder of the cranium will be presented.

In humans, the ethmoid bone is positioned strategically to serve as an interface between the brain and the face. The latter, particularly in primates, consists of two components: the endocranial nasal capsule and the exocranial membranous

bones (Maier, 1993b). The cartilaginous nasal capsule of the fetal period constitutes the early framework for the future adult nasal cavity as well as functioning as the structural basis for the developing facial skull. In adults, its ossified parts form the fragile ethmoid bone. The structure of the nasal capsule is determined by the spatial requirements of the orbits and nasal cavity and by the biomechanical properties of the masticatory apparatus. The interaction of these heterogenous factors results in complex, species-specific modifications.

The morphology of the ethmoid bone is best understood by conceptualizing it as a series of bony plates, or lamellae. The horizontal plate possesses multiple perforations through which the olfactory filaments pass from the olfactory cranial nerves of the brain into the nasal cavity and is called the cribriform plate, or the lamina cribrosa. Immediately inferior and attached perpendicular to the cribriform plate is a portion of the bony nasal septum termed the perpendicular plate of the ethmoid. Superior to the cribriform plate in the midline rises another bony plate that is thick anteriorly and tapers to an apex which projects into the anterior cranial fossa and is called the crista galli (Allen, 1882). Both the crista galli and the perpendicular plate of the ethmoid serve to divide the cribriform plate into two components, the right and left cribriform plates. Lateral to the cribriform plate is the orbital plate, or lamina papyracea, which forms a thin bony partition separating the orbit from the nasal cavity. Between the crista galli and lamina papyracea arises another bony plate called the lamina lateralis of the cribriform plate. In humans, this plate serves to divide the multiple perforated region on one side while the other side (between the lamina lateralis of the lamina cribriform plate and the lamina papyracea) is where the

numerous ethmoidal air cells are housed. It is in this region of the ethmoid bone proper where a proliferation of ethmoid air cells occurs that anatomists have described in the human as the labyrinths. In mammals that lack ethmoid air cells, multiple thin bony plates in the form of turbinates occupy this region instead of delicate air filled cavities.

2.4.2.2. Lamina transversalis of the ethmoid bone

In certain keen-scented mammals such as some carnivores, a new ethmoidal structure appears. The transverse lamina is a horizontal shelf of bone constructed of two plates, which ossify along the midline. These plates project medially from the lateral ethmoidal plates of each side to articulate with the wings projecting laterally from the vomer. The transverse lamina is positioned superiorly parallel to the hard palate, and divides the nasal cavity posteriorly into an upper and lower compartment. The upper compartment houses the nasoturbinal and ethmoturbinal structures along with the cribriform plate, while the lower compartment is simply a continuation of the conduit between the external environmental air and the nasopharyngeal space. The lower compartment, or nasopharyngeal meatus, is therefore respiratory in function, being continuous anteriorly with the inferior meatus and terminating posteriorly at the choanae. The presence of the transverse lamina excludes the greater part of the olfactory region from respiratory air currents. Olfaction must then be dependent upon diffusion from the scent-laden inspired air, or by actively sniffing to propel puffs of air into the upper compartment, or olfactory region. A possible advantage of

separating the olfactory apparatus from the main airstream may be that air is not immediately washed out during exhalation and will be retained longer for olfactory analysis.

2.4.2.3. Turbinate Anatomy of the Ethmoid Bone

One of the most distinctive feature in the mammalian nasal cavity is the presence of a series of thin, often highly convoluted sheets of bone, the turbinates, or turbinals (Hillenius, 1992). The nasal cavities of most mammals possess three different types of turbinals based on their embryology, which are named after the bones on which they insert. Most mammals possess on each side of the nasal cavity several ethmoturbinates, a nasoturbinate and maxilloturbinate. The ethmoturbinates are so named because their bony scroll-like plates originate solely from, and are part of, the ethmoid bone. The nasoturbinate is derived from the ethmoid bone but shares its insertion with both the ethmoid and nasal bones. The nasoturbinate and ethmoturbinates are located in the dorsal and posterior portions of the nasal passages, respectively, dividing this region into a series of blind recesses. As stated previously, these structures are often partially protected from respiratory air-currents by the transverse lamina in those mammals that possess this horizontal shelf of bone. These turbinates bear primarily olfactory epithelium and serve to greatly increase the surface area for this tissue (see Allen, 1882; Negus, 1958 and Harkema, 1991). The maxilloturbinate has its own center of ossification and accordingly is considered a separate bone. It is covered with respiratory rather than olfactory epithelium and is

situated in the anteroventral portion of the nasal cavity directly in the line of respiratory airflow. Maxilloturbinates are complex structures, consisting of elaborately scrolled, folded, or finely branched lamellae (e.g., Takahashi, 1981). Their principle function is the air-conditioning of respired air which must be defensively filtered, either warmed or cooled to core body temperature, and humidified by evaporation of water from the mucosa of the turbinate body before reaching the trachea.

2.4.2.4. Structural Organization of the Ethmoid Bone

The ethmoid bone can be structurally divided into a meso-ethmoid (the body) and the ethmoturbinals (the appendages). The meso-ethmoid consists of the perpendicular plate, the crista galli, and the lateral masses of the ethmoid. Allen (1882, pg.135) also described a pair of symmetrical ossicles appended posteriorly to the lateral masses known as the “cones of Wistar.” Allen’s “cones of Wistar” are synonymous with Bertini’s ossicles of the sphenoid, which gives rise to the sphenoidal concha of humans. The arrangement of the ethmoid bone in humans is so different from most other mammals that a detailed anatomical description is necessary and will be discussed in the human nasal anatomy section. As stated previously, in most mammals the ethmoturbinals are largely olfactory in nature. However, in higher primates such as apes and humans, the middle conchae share both respiratory and olfactory epithelial coverings. Each ethmoturbinal element is anchored by a lamella, or olfactory plate, the terms being interchangeable, with the

former term used more contemporaneously (Moore, 1981) and the latter found in the older literature (see for example Paulli, 1900). These terms are used to describe the medial projections into the nasal cavity from the lateral ethmoidal and cribriform plates. Each lamella is extensively plicated and covered by olfactory mucosa and forming an olfactory fold. The free projecting ends of the olfactory plates constitute the olfactory lobes. The lamella may undergo repeated branching, especially in keen-scented species, with the free extremities undergoing inrolling to form olfactory lobes. Some investigators use separate anatomical terms to distinguish the bone from the mucosa that covers them (e.g., Peter, 1902 and Aiello and Dean, 1990). For example, the uncinat process is an anatomical term referring to both the thin projecting ethmoidal bony process and the ridge of mucosa, which covers it (Cave and Haines, 1940). In humans, this anatomical landmark serves as the anterior inferior border of the hiatus semilunaris, a key structure which is the anterior drainage pathway of several sinuses into the nasal cavity proper. The term “plica semilunaris” refers to the mucosal ridge alone (Peter, 1902) and describes the shape of the region. Aiello and Dean (1990) applied similar distinctions with regard to the maxilloturbinates and ethmoturbinates. The term “turbinate” was used to refer only to the bony substrate, while the term “concha” includes both the bone and the overlying mucous membrane. However, the Nomina Anatomica considers inferior turbinate and inferior concha as interchangeable terms and recognizes no such distinction. Nevertheless, the distinction is important and the subject requires clarification.

2.4.2.5. Confusion of Ethmoturbinal Terminology

The existence of confusion in the terminology of the ethmoid was already identified more than a hundred years ago (Allen, 1882). It began with the publication of Richard Owen – “Archetype and Homologies of the Vertebrate Skeleton”, in 1848, who named the meso-ethmoid the prefrontal and gave the ethmoturbinals their current name. His study of many terrestrial mammals formed the basis of the ethmoid and ethmoturbinal nomenclature. As an example, he applied the term ‘labyrinth’ to describe the mesh-like convoluted mass of thin bony plates that congregate into their elaborate branching system present in the internal nasal cavity of the hog. He distinguished between the labyrinth and the ethmoturbinals, but restricted the term ethmoturbinal to the lower plates of the ethmoid mass which corresponds to the present designation of the endoturbinals. Allen (1882) cites the work of Coues who considered the ethmoturbinals as synonymous with the lateral mass and considered that the perpendicular plates as being homologous with a pair of coalesced prefrontals. Encountering the “spongy convolutions” which correspond to the elaborate branching of the ethmoturbinals, he commented that it would be “extremely difficult in describing the details of the spongy convolutions (Allen, 1882, pg. 139).

Another source of confusion of ethmoturbinal nomenclature, according to Allen (1882) was Chatin’s 1880 work in which he described each olfactory plate as it appeared upon the median surface and named it a “cornet.” He named the nasoturbinal the “superior cornet,” while the ethmoidal cornet corresponded to the endoturbinals. In a kangaroo specimen, the maxilloturbinal was named the “volute

ethmoidal.” Allen (1882, pg. 137) also reported that Gurlt 1843 described the mammalian ethmoid using the structure of the human ethmoid bone as his guide. Consequently, he incorrectly identified the nasoturbinal as the superior concha and the endoturbinal as the middle concha. All parts not appearing on the median surface he grouped under the heading of the “Labyrinth.”

Finally, the study by Parker (1874) of the structure and development of the pig skull reported the first plate of the ectoturbinals as the “upper turbinal,” the first endoturbinal as the “middle turbinal,” and the maxilloturbinal forms the “lower turbinal.” He linked the maxilloturbinal and an “alinasal turbinal” to an olfactory function. This “alinasal turbinal” was described as a ledge-like point within the nostril continuous with the ledge supporting the maxilloturbinal (Parker, 1874, pg. 298).

2.4.2.6. Organization of Ethmoturbinals

The ethmoturbinal plates have been traditionally divided into two groups: the endoturbinals and the ectoturbinals (Paulli, 1900a,b,c). As stated previously, each ethmoturbinal consists of a lamella, or olfactory plate that projects medially into the nasal cavity from the lateral ethmoid and cribriform plates. Paulli (1900a) noted that not only does the olfactory plate have the potential to undergo repeated branching but their free extremities could inroll to form elaborate olfactory folds. Depending on the distance that the olfactory folds project medially into the nasal cavity determines to which group they are assigned. A major source of confusion regarding the

classification of ethmoturbinal morphology is the conflicting systems of numbering offered by many authors. According to the scheme devised by Paulli (1900a,b,c) all ethmoturbinals were arranged into two rows, or two groups of rows, with those elements forming the more medial rows termed endoturbinals (represented by Roman numerals), and those more lateral classified as ectoturbinals (represented by Arabic numbers). The nasoturbinal is considered an ethmoturbinal plate but because its projection runs along the dorsal but median aspect of the nasal cavity it is considered to be the first endoturbinal.

Most authors include the nasoturbinal as the first endoturbinal based on the fact that its posterior portion partially ossifies at least in part from the ethmoid (e.g., Cave and Haines, 1940). Others contend that to be classified as an endoturbinal each lamella must articulate solely with the ethmoid bone. Since the anterodorsal aspect of the nasoturbinal can sometimes articulate with the nasal bones, this nullifies its status as a “true” endoturbinal. Rejecting the nasoturbinate as both an endoturbinal and ectoturbinal topographically has led some authors to designate it independent status. Also, there is no consensus to whether the numbering system should be applied to all olfactory plates or only to those with origin from the lateral plate of the ethmoid. The situation is complicated by the tendency of the lamella to divide close to its origin to give rise to more than one olfactory plate that projects into the median aspect of the nasal cavity. Presently, most authors follow the numbering system proposed by Paulli (1900a,b,c) in which the nasoturbinal is considered to be the first endoturbinal. Ultimately, it is the extent by which the basal lamella will project its branch into the nasal cavity that will determine its name. However, without invasive techniques,

which destroy the specimen, the task of identifying the basal lamella remains extremely difficult.

2.5. EARLY METHODS OF STUDY

Previous studies examining the nasal complex have employed traditional anatomical dissection (see Hartman, 1900; Killian, 1903), or plain film radiographic techniques (e.g., Shapiro and Schorr, 1980; Lund, 1988). However, both of these approaches have their limitations and disadvantages. Dissection being a destructive process limits the visualization of the inter-connected structures and spaces present in their entirety. Plain X-rays cannot satisfactorily delineate the intricate bony borders of the sinuses (see Márquez et al., 1996). In 1896, Alan Swinton, an electrician and photographer, used Röntgen's "new rays" to produce the earliest known radiographic image of the paranasal sinuses (Chavda et al., 1996). Other early investigators employing this technique include Scheier, in 1896, Killian, in 1903, and Caldwell and Coakley, in 1906. Studies investigating maxillary sinus morphology were based upon linear measurements derived from plain radiographic films from which volumes were mathematically derived. However, plain film radiography does not permit precise determination of landmarks because of superimposition of structures and magnification errors. Accordingly, dimensional measurements are by necessity estimates and volumetric measures based upon these are imprecise. Our ongoing research has confirmed that the results obtained with conventional X-rays lack both accuracy and reproducibility (Márquez et al., 1996).

Studies that have employed water, mercury, or seed-filling techniques (Mündnich, 1937; Bezold, 1943; Márquez, 1997) may yield quantitative data (e.g., sinus volumes) but do not reveal the form and structure of the cavity. Plaster (Loeb, 1912) or rubber cast filling techniques (e.g., Schreider and Raabe, 1981) result in destruction of specimens. New technological advances in CT imaging offers a number of advantages over previous methods, and provides a unique opportunity for examining the nasal region (see chapter 4). Accordingly, the following investigation employed CT imaging, which provided the abilities to delineate and spatially reconstruct the nasal complex of mammals inhabiting different ecogeographic localities.

2.6. MATERIALS

Different terrestrial mammalian species were chosen in order to assess varying degrees of dietary, olfactory and climatic affects upon the structure of the nasal complex. As the methodology employed is extremely time and labor intensive it was decided to have an in-depth examination of a relatively small number of animals as oppose to using a larger sample in a less comprehensive manner. Future studies will build upon this sample adding different groups to further the hypotheses tested here.

Species chosen for study include domestic pig, white tailed deer, domestic dog, North American black bear, wild boar, and red fox (Table 1). All specimens were adult, as determined by molar dental eruption pattern, except for the pig whose third molar was just beginning to erupt. As noted above, due to the labor intensive

time, cost and manipulation, an *N* of 1 was used for each species. Specimens were dry crania from the collections of the Departments of Anthropology Lehman College, City University of New York (i.e., boar, fox, and bear) and the Center for Anatomy and Functional Morphology at the Mount Sinai School of Medicine (i.e., pig, deer, and dog). Specimens were chosen based upon the intact nature of the facial skeleton and complete and identifiable borders of foramina and fissures. In addition, transillumination of internal nasal morphology and examination of external appearance of the specimens were undertaken.

Table 2-1 List of mammals examined via CT imaging

<u>Common name</u>	<u>Scientific name</u>	<u>Dietary Classification</u>
North American black bear	<i>Ursus americanus</i>	carnivore
Domestic dog	<i>Canis familiaris</i>	carnivore
Red Fox	<i>Vulpes vulpes</i>	carnivore
Wild boar	<i>Sus scrofa</i>	omnivore
White-tailed deer	<i>Odocoileus virginianus</i>	herbivore
Domestic pig	<i>Sus scrofa domestica</i>	omnivore

2.7. METHODS

The morphology of the maxillary sinus of dry crania was analyzed using two-dimensional and three-dimensional reconstructions derived from computer tomography (CT) scans. Two dimensional reconstructions were particularly valuable in supplying linear dimensions of such measures as anteroposterior length, maximum width and height of the maxillary sinus. Three dimensional reconstructions added another dimension by allowing contiguous structures to be graphically represented in conjunction with the sinuses adding an appreciation of their size and shape dimension. CT imaging affords a non-destructive way of visualizing the space of the sinuses and contiguous bony structures that cannot be accomplished through sequential destructive dissection.

All specimens were dry crania scanned with the same model scanner (i.e., GE HiSpeed Advantage CT scanner machine) at the Department of Radiology, Mount Sinai School of Medicine. Coronal scans of 1.0 mm slice thickness were taken for all specimens. Use of the smallest thickness minimizes partial volume averaging affords the best possible spatial resolution perpendicular to the scan plane (Spoor et al., 2000). In CT reconstructions a major source of segmentation artifact is partial volume averaging. For example, when contrasting materials occupy a voxel (a unit representing 3-dimensional space) the CT signal becomes a mixture of those materials. The bone and air both occupy a voxel its CT signal may be below the range that is representative for bone. During scanning of crania this effect results in artificial low CT signal of thin bony structures, such as parts of the temporal and

ethmoid bone. To minimize such digital data errors the slice thickness should be set as the smallest the machine can allow. The minimum slice thickness that the GE scanner can scan at is 1.0 mm which was the preferred choice selected in this study. FDOV (Field Depth Of View) pertains to the area covered by the image. Using FDOV parameters larger than the specimen would result in loss of resolution. All specimens were positioned in the supine position with some anchored by foam blocks, cloth tape and cotton sheets while other specimens requiring only foam blocks. The position of the specimens allowed using the minimum FDOV parameters. Before actual scanning, scout beams insured the position of the specimen to be aligned centered and perpendicular to the X-ray beam geometry. The CT digital capture intensity specifications of the scanning machine will be reported for each specimen in the following section.

Two different methods of analysis were employed: 1) a Silicon Graphics Indigo (SGI) 2-XZ Workstation using VoxelView 2.5 High-Performance 3D Imaging for Biomedicine software and 2) GE scanner console utilizing the NT Windows Scanning CT digital 3.11 software. The UNIX- based computer environment that the SGI 2-XZ Workstation provides is housed in the Center for Anatomy and Functional Morphology. Using VoxelView required a number of intermediate steps to be performed before analysis of the CT digital data could be undertaken. First, the digital data of the CT scans were transferred to a Digitized Audio Tape (DAT). The translation of the tape into a universal format DICOM (Digital Imaging and Communications in Medicine) was required and took place at the American Museum of Natural History. It was now possible to perform manipulation and analysis of the

CT digital data using VoxelView software. This volume and surface rendering program allows for 2- and 3-dimensional reconstructions of digital data. The program can generate reconstructions of varying size perspectives, enabling the skull to be viewed in any plane (e.g., coronal, sagittal, axial). Metrical analyses made possible with this software include 2-D measures (length, width, height, perimeter, and area) and 3-D measures (surface area and volume). The perimeter outline of the maxillary sinus was traced with the cursor on each CT scan image in the coronal plane by using one of the tracing programs that VoxelView provides (i.e. contour trace). The surface contours of the maxillary sinus cavities were generated from the summed perimeters and graphically displayed both *in situ* and isolated.

As we progressed in our studies we were afforded the opportunity to use the extremely high level in house CT scanner console in the Department of Radiology at Mount Sinai School of Medicine. One particular benefit for this particular method was that the intermediate step of translating the digital data into DICOM format was bypassed. Thus the second method of manipulation and analysis of digital data utilized the NT Windows Scanning 3.11 software permitted the above morphometrics to be obtained. It should be noted that dedicated use of this expensive and time precious equipment in an active Radiology department is subject to availability. However, both of these methods, VoxelView and direct console analysis, proved to produce identical quality visualization and quantitative results.

2.8. RESULTS FOR THE PIG (*SUS SCROFA DOMESTICUS*)

2.8.1. CT scanner specifications and method of analysis

Intensity specifications for CT digital capture scanning were as follows:

DFOV – 31.6 cm, Bone resolution, 140 kV, 60 mA, 1 mm slice thickness/1.0 sp.

VoxelView 2.5 High-Performance 3D Imaging for Biomedicine software was utilized for inspectional and quantitative analysis. All reference window scout images will correspond to specified areas on the multiplanar CT figures.

2.8.2. General remarks

This specimen exhibited three paranasal sinuses: (1) maxillary, (2) frontal, and (3) sphenoid sinuses. No ethmoid sinuses were observed.

2.8.3. Maxillary sinus – General observations

The maxillary sinus was present in this specimen. The most anterior projection of the sinuses occurred in the coronal plane at the mesial border of M².

The maxillary sinus floor covered the last two molars, extending posteriorly beyond M³ into the maxillary tuberosity territory. The lateral walls at the point of their maximum width formed a horizontally disposed apex. Partitions, or septae, were not observed within the sinuses. The maxillary sinus of adult specimens has been reported in the literature to have an anteroposterior length covering the entire six

molar dental roots from PM^2 to M^3 and into the maxillary tuberosity. The age of the specimen studied is clearly a subadult based on the absence of some of the permanent dental eruption which must be considered in interpreting the morphometric data presented.

2.8.4. Right maxillary sinus

The following observations were made from a coronal planar perspective with the orientation specified by the corresponding sagittal and transverse planar views in a reference window. The greatest width was measured in the coronal plane at the anterior one-third border of M^3 where the lateral extension enters the zygoma, with the medial extension bordered by the lateral wall of the nasal cavity. No medial extension into the hard palate was observed. The distance from the lateral to the medial point was 42.9 mm (Figure 2-2). The greatest height was recorded in the coronal plane at the distal border of M^2 , measuring 23.7 mm from the most superior point to the most inferior point (Figure 2-3). The greatest length from the most anterior to the most posterior point in the sagittal plane was 35.2 mm (Figure 2-4). The floor of the sinus was relatively flat, with the roof of the infraorbital canal occupying a significant portion of the sinus floor. Tracing of the outline of the maxillary sinus (shown in red in Figure 2-5) in the coronal plane of M^2 yielded a perimeter reading of 48.93 mm. The area for that same slice was 103.13 mm^2 (Figure 2-6) and the derived volume was 0.103 mm^3 (Figure 2-7). Perimeter, area and volume measures of a selected region of the pig's

maxillary sinus were derived from each coronal CT slice (see table 2). The maxillary sinus 3-dimensional space was digitized and graphically represented both *in situ* and extracted yielding an appreciation of the sinus topographical relationship to its contiguous structures when viewed in the coronal and sagittal perspective (Figure 2- 8).

2.8.5. Left maxillary sinus

The greatest width was recorded at the protocone – paracone coronal plane of M^3 and measured 40.5 mm. The greatest height occurred in the coronal plane at the distal border of M^2 , measuring 27.8 mm from the most superior point to the most inferior point. The sinus greatest length measured 33.9 mm from a sagittal perspective. The floor of the sinus is highly convex due to the superior bulging of the infraorbital roof causing restriction of its height.

Table 2-2 Perimeter, area, and volume measures of a selected region of the pig's maxillary sinus (slices 1 to 160 correspond to the rostrum of the nasal region anterior to the sinus)

Slice number	Perimeter (mm)	Area (mm ²)	Volume (mL)
161	48.93	1033.13	0.103
162	54.745	125.00	0.125
163	58.225	203.34	0.202
164	61.964	239.06	0.239
165	62.934	256.25	0.256
166	67.131	290.62	0.291
167	68.001	294.53	0.295
168	68.97	309.37	0.309
169	69.211	320.31	0.320
170	72.025	349.22	0.349
171	77.785	413.485	0.414
172	78.898	432.81	0.433
173	79.117	429.69	0.430
174	81.527	453.91	0.454
175	83.492	481.25	0.481
176	85.765	488.59	0.486
177	87.729	521.09	0.521
178	85.751	528.12	0.528
179	89.007	537.5	0.538
180	91.267	564.71	0.565
		Total	7.339

2.8.6. Ethmoid sinus

This specimen exhibited no ethmoid air cells.

2.8.7 Frontal sinus

The frontal bone appeared heavily excavated by a sinus cavity. Following Loeffler's (1959) nomenclature, the specimen had right sinus frontalis rostralis lateralis (SFRL), a sinus frontalis rostralis medialis (SFRM), and a right sinus frontalis caudalis (SFC) (Figure 2- 9). The right SFRL was further subdivided into two sinuses, which appeared to have separate origins as they do not intercommunicate. The left SFRL was similarly also subdivided into two sinuses. The left SFC was larger than the right.

2.8.8. Sphenoid sinus

The specimen exhibited two symmetrical sinuses which excavated the entire body of sphenoid except for the median septum that divides them. No pneumatization of the pterygoid plates, occipital bone or parietal bones are observed.

Figure 2-2. Frontal view illustrating the greatest width shown in green within the right maxillary sinus (MS) of the domestic pig. Above is the reference window showing the corresponding coronal slice in sagittal view along with the morphometric tool box window indicating the measurement length of the MS height.



Figure 2-2

Figure 2-3. Frontal view of the domestic pig illustrating the greatest height as indicated by the green line within the right maxillary sinus (MS). Above is the reference window showing the corresponding coronal slice in sagittal view along with the morphometric tool box window indicating the measurement length of the MS height.

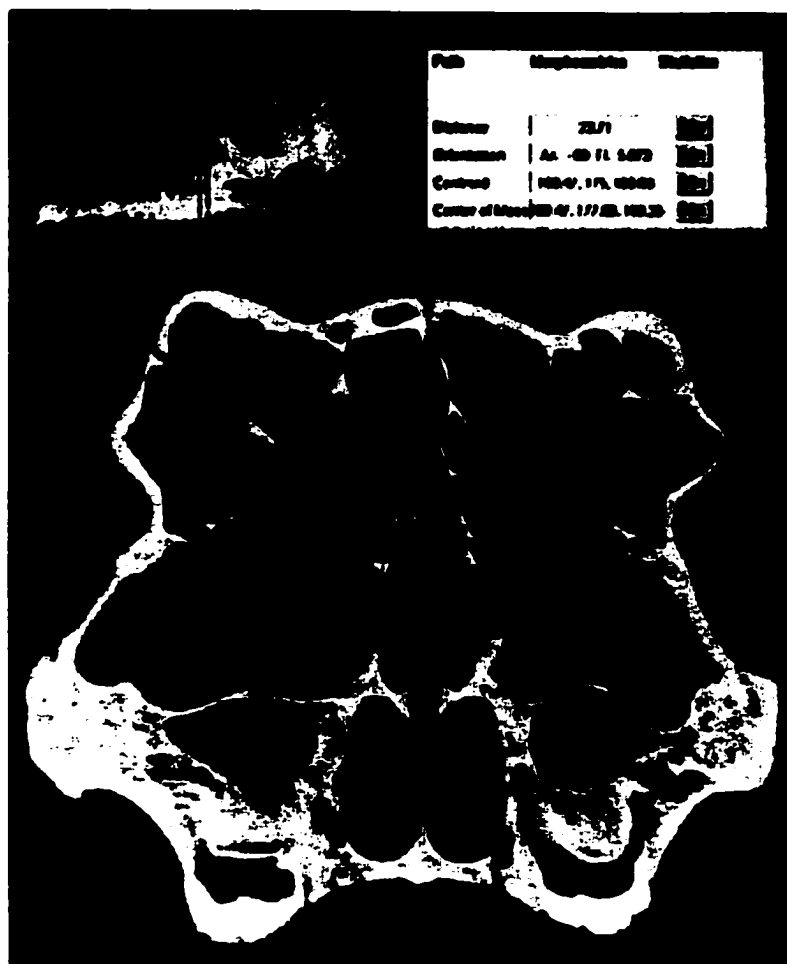


Figure 2-3

Figure 2-4. A sagittal view of the domestic pig showing the anteroposterior length as indicated by the green line with morphometric tool box window above displaying derived measurement.

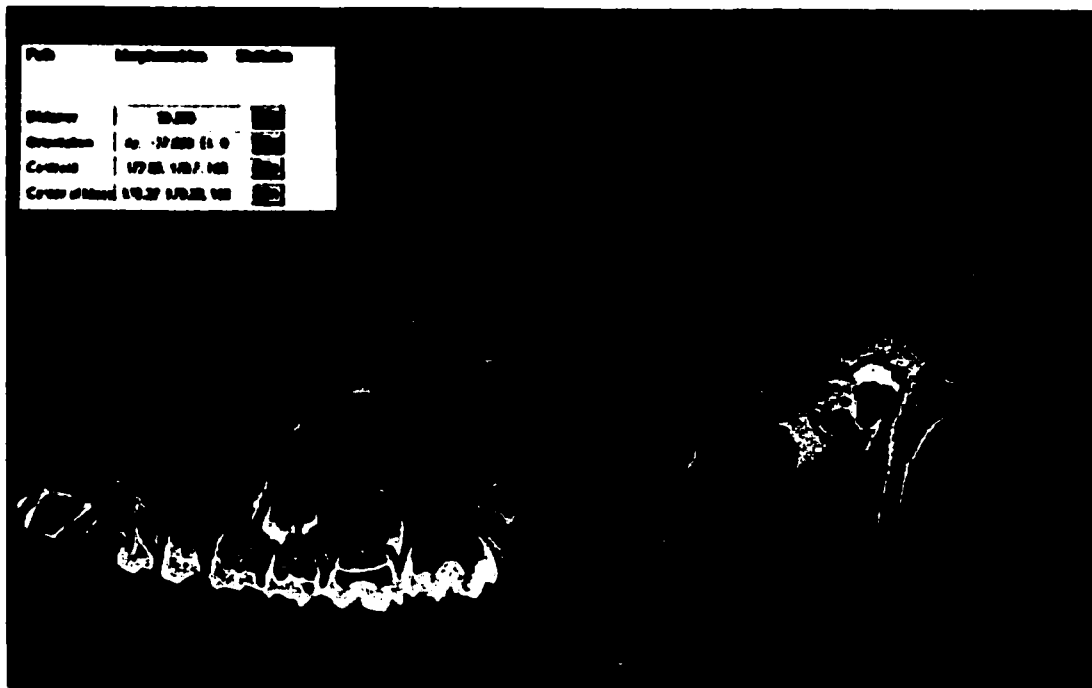


Figure 2-4

Figure 2-5. Frontal view of the domestic pig showing the trace outline of a selected coronal slice of the right maxillary sinus with the perimeter boundary shown in red.

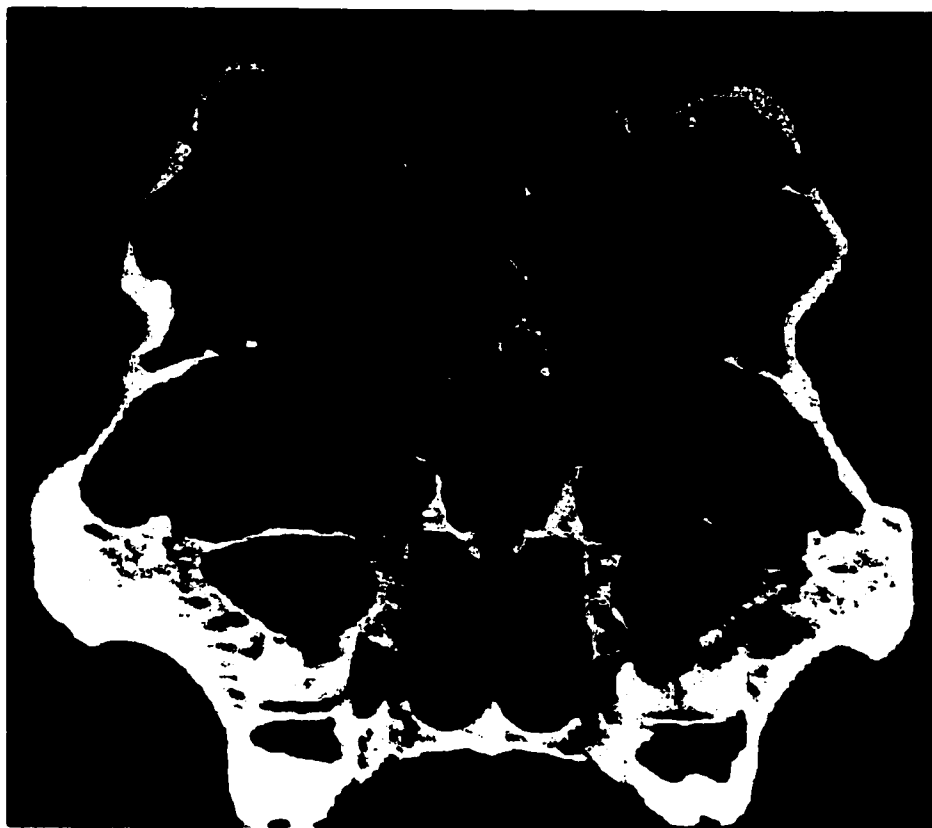


Figure 2-5

Figure 2-6. The area for that same slice as seen in Figure 2-5 showing the enclosed area filled in red.

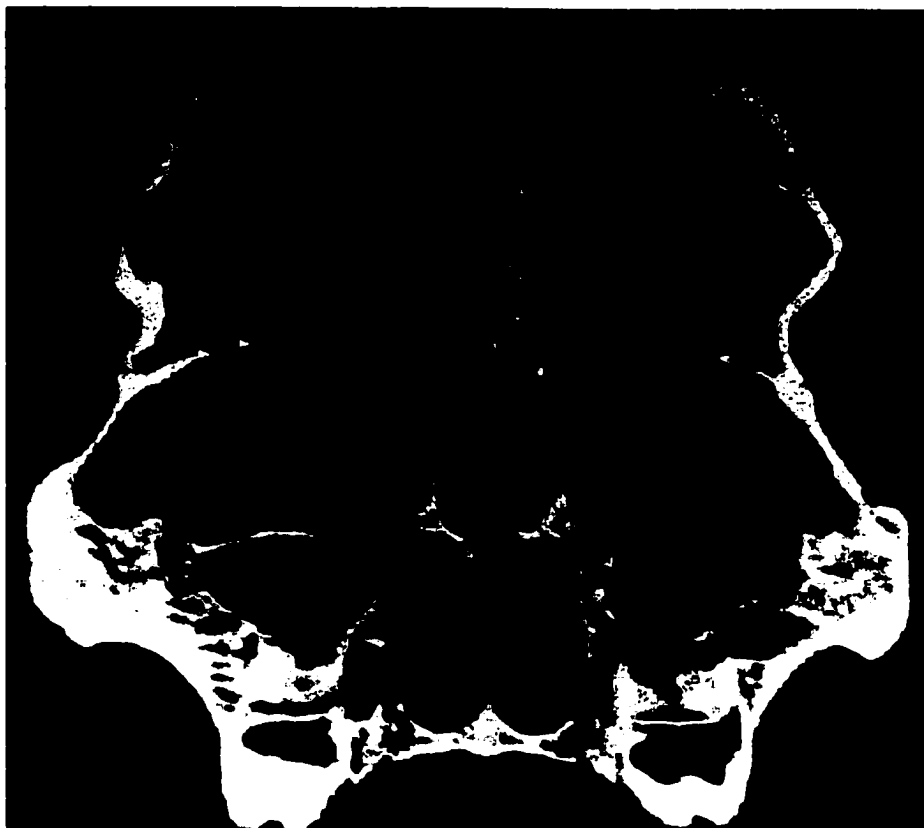


Figure 2-6

Figure 2-7. A composite showing both the trace perimeter outline (left) and its corresponding area filled in red (right) of the domestic pig. Above are the reference orientation windows indicating the corresponding sagittal cuts for the coronal views.

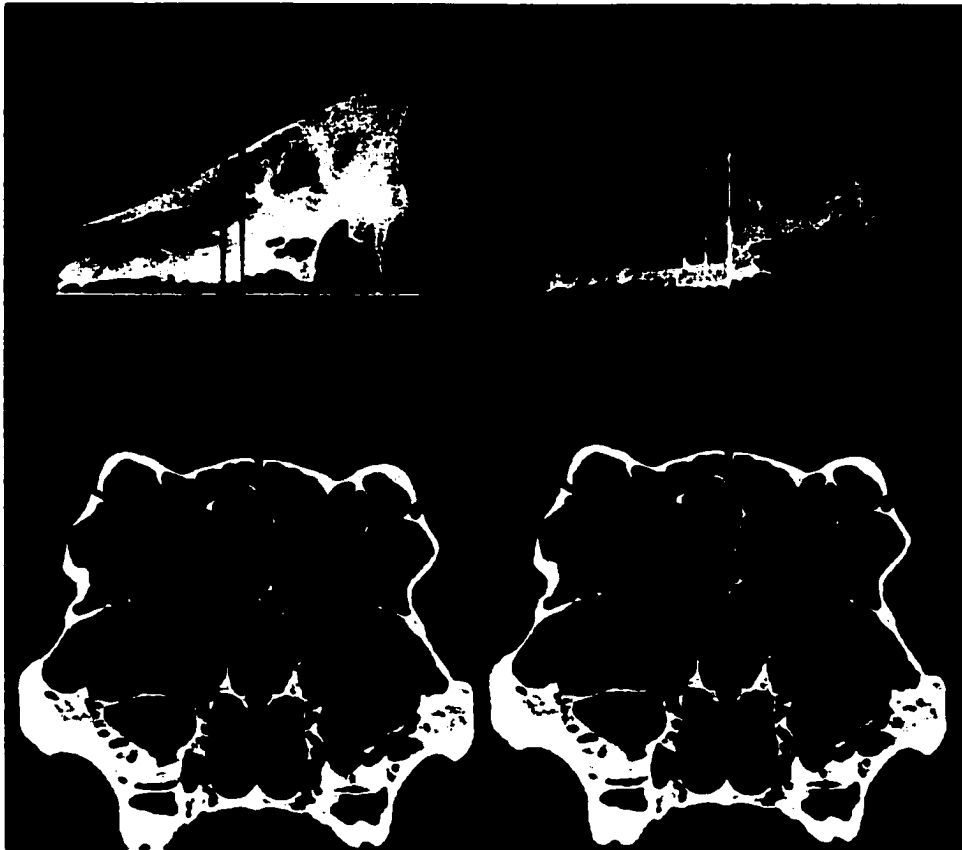


Figure 2-7

Figure 2-8. The 3-dimensional space of the right maxillary sinus of the domestic pig was digitized and graphically represented in frontal view both *in situ* (a) and extracted (a1). Similarly, the left maxillary sinus was digitized and shown in lateral view both *insitu* (b) and extracted (b1). An appreciation of the sinus topographical relationship to its contiguous structures is revealed when the maxillary sinus space is digitized both *insitu* and extracted as viewed in the coronal and sagittal perspective.

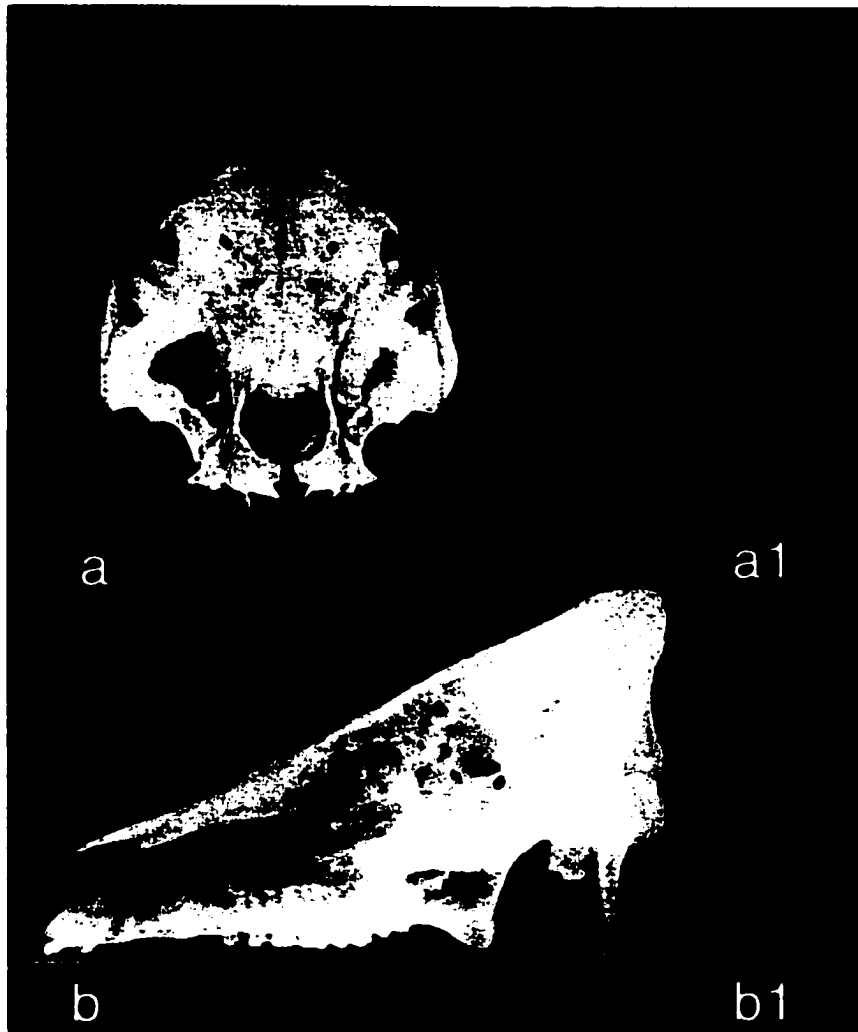


Figure 2-8

Figure 2-9. This high contrast resolution figure shows the outline of the pig's frontal sinus system in parasagittal view. SFRL (Sinus frontalis rostrales lateralis), and SFC (Sinus frontalis cuadalis). Nomenclature of paranasal sinus system follows Loeffler (1959).



Figure 2-9

2.9. Results for the Boar (*Sus scrofa*)

2.9.1. CT scanner specifications and method of analysis

Intensity specifications for CT digital capture scanning were as follows:

DFOV – 31.6 cm, Bone resolution, 150 kV, 80 mA, 1 mm slice thickness/1.0 sp.

Specimen was placed in an axial position anchored by foam blocks, cotton cloths and cloth tape. The scout, or orientation beams were aligned to ensure specimen was in the Frankfort horizontal position. Analyses of all measurements and observations were derived through the use of multiplanar CT imaging by using the Microsoft Morphometric tool software program for CT digital data at the NT computer workstation at the CT scanning facility.

2.9.2. General remarks

Specimen was placed in an axial position anchored by foam blocks and cotton cloths. The scout beams were aligned in order to position the specimen in the Frankfort horizontal alignment. All measurements were obtained by using the Microsoft Morphometric tool software program for CT digital data performed at the NT computer workstation of the CT scanning facility.

The specimen exhibited full dental morphology and was considered an adult based on molar eruption patterns. The superior orientation of the incisors which hook around the snout region to meet at the midline is a hallmark boar characteristic (see Figure 2-10). The specimen exhibited all four paranasal sinuses: (1) maxillary; (2) ethmoid; (3) frontal; and (4) sphenoid sinuses.

2.9.3. Maxillary sinus – general observations

The maxillary sinuses of this adult specimen were well demarcated. The most anterior projection of the maxillary sinuses occurred in the coronal plane at the distal border of PM³, with the most posterior excavation observed in the coronal plane of the maxillary tuberosity. The maxillary sinus floor covered most of the premolar and molar dentition, extending posteriorly beyond M³. A series of partitions in the form of complete and incomplete septa were observed in both maxillary sinuses.

2.9.4. Right maxillary sinus

The following observations were made from a coronal planar perspective with the reference window in the sagittal view demonstrating the position of the coronal slice. The greatest width occurred at the midpoint of M³ where the lateral extension of the sinus invaded the zygoma and the medial extension bordered on the lateral wall of the nasal cavity (Figure 2-11). No medial extension into the hard palate was observed. A distance of 37.5 mm was recorded as the greatest width. The coronal view of figure 1 demonstrated a vertically orientated septal wall causing a portion of the maxillary sinus to be closed off in a medial compartment (Figure 2-12). The greatest height in the coronal plane occurred at the distal border of M³, with a recorded length of 36.0 mm (Figure 2-13). From an axial view, the greatest anteroposterior length was 56.2 mm. A series of septations were observed in this sinus the visualization of which was dependent on the planar slice orientation of the

specimen was in (e.g., coronal, sagittal or axial). Of the several septal partitions present, of the three main ones two were complete and one was partial. From a parasagittal perspective as seen in Figure 2-14, the anterior septum had an inferior-anterior insertion onto the sinus floor at the level of the posterior roots of PM⁴ in the coronal plane and a superior-posterior insertion in the coronal plane at the distal border of M¹. The most posterior septum was also a complete partition occurring in the coronal plane near the juncture of the mesial border of M³. The middle partition was incomplete and does not compartmentalize a portion of the sinus but rather rises from the sinus floor at the juncture between the distal and mesial surface of M¹ and M² respectively, to about 11.3 mm in height. From anterior to posterior direction the wall follows an oblique posterior path resulting in the enclosure of only a posterior portion of the sinus, which occurs at the mesial plane of M³ (see Figure 2-14).

2.9.5. Left maxillary sinus

Greatest width occurred at the protocone – paracone coronal plane of M³, with a chord length of 33.6 mm (Figure 2-15). The greatest height occurred at the distal coronal plane of M³ with a chord length of 38.5 mm (Figure 2-16). The sinus greatest length was recorded at 58.7 mm taken from an axial perspective (Figure 2-17 and see Table 3 for summary of maxillary sinus dimensions). A number of septations

septations were observed in this sinus that required different planar views to fully delineate their morphology. Four septa were observed from study of axial and coronal views (Figures 2-18 and 2-19). In a sagittal view, two bony wall septa were observed. The most anterior one appeared in the coronal plane which inserted onto the sinus floor at the level of the distal roots of PM⁴ after traversing an oblique course posteriorly to insert superiorly at the level of the distal portion of M¹. In a coronal plane, the most anterior insertion of the second septum inserts on the sinus floor at the coronal plane of the anterior roots of M², then arose superiorly in an almost vertical angle terminating in the midporiton of the sinus, and measured 3.3 mm in thickness (Figure 2-20).

Table 2-3 Linear measures of the wild boar's maxillary sinus dimensions

	Right Maxillary Sinus	Left Maxillary Sinus
Greatest Width	37.5 mm	33.6 mm
Greatest Height	36.0 mm	38.5 mm
Greatest Length	56.2 mm	58.7 mm

2.9.6. Ethmoid sinus

This specimen exhibited clear and distinct ethmoid air cells bilaterally. Based on a multiplanar reformatting 2-D reconstructions in the axial plane, five ethmoid air sinuses were present on the right side and six on left side (Figure 2-21). The

relatively large air cells were symmetrical, clearly demarcated, and occupied a considerable portion of the cranial base. Complete enclosure of these cells was determined by visualization in different views of CT slice scans (see for example Figure 2-22).

2.9.7. Frontal sinus

A series of bony septa appears in the coronal level at the mesial border of M², extending into the parietal and temporal regions (Figure 2-23). Application of Loeffler's nomenclature was difficult due to the numerous septa present. Only the right and left sinus frontalis caudalis (SFC) could be confidently identified.

2.9.8. Sphenoid sinus

Large sphenoid sinuses were exhibited in this specimen (Figure 2-24). Pneumatization occupied the body of the sphenoid and extended to portions of the pterygoid plates.



Figure 2-10

Figure 2-10 The boar in parasagittal view showing the orientation of its canine.

Figure 2-11 Frontal view of the boar illustrating the greatest width (white line) within the right maxillary sinus (MS). The Microsoft Morphometric tool software program at the NT computer workstation of the CT scanning facility automatically calculated the measurement, which was recorded as 37.5 mm.



Figure 2-11

Figure 2-12 Frontal view of the boar showing the presence of a bony septum causing the medial compartmentalization of the right maxillary sinus (shown in red).

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Figure 2-12

Figure 2-13 A frontal view of the boar showing the greatest height of the right maxillary sinus with a measured of 36.0 mm (white line).

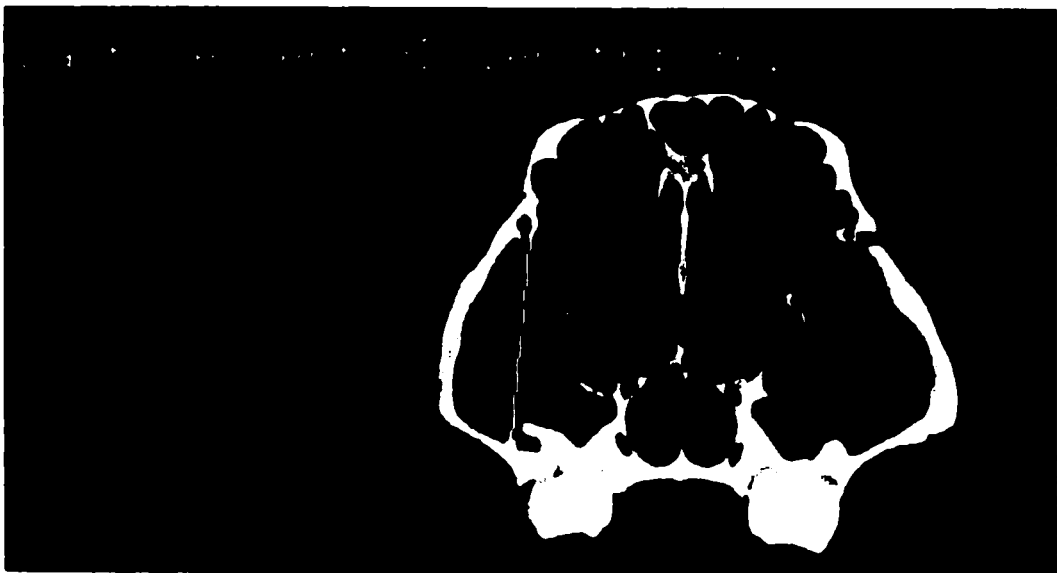


Figure 2-13

Figure 2-14 Two complete (yellow arrows) and one incomplete (red arrow) bony septa are shown in parasagittal view of the boar. The length of the incomplete septa rises 11.3 mm in height.



Figure 2-14

Figure 2-15 Frontal view of the boar illustrating the greatest width (white line) of the left maxillary sinus (MS), measuring 33.6 mm.



Figure 2-15

Figure 2-16 Frontal view of the boar illustrating greatest height of the left maxillary sinus, with a measuring 38.5 mm.



Figure 2-16

Figure 2-17 Axial view of the left maxillary sinus of the boar demonstrating a maximum length of 58.7 mm.

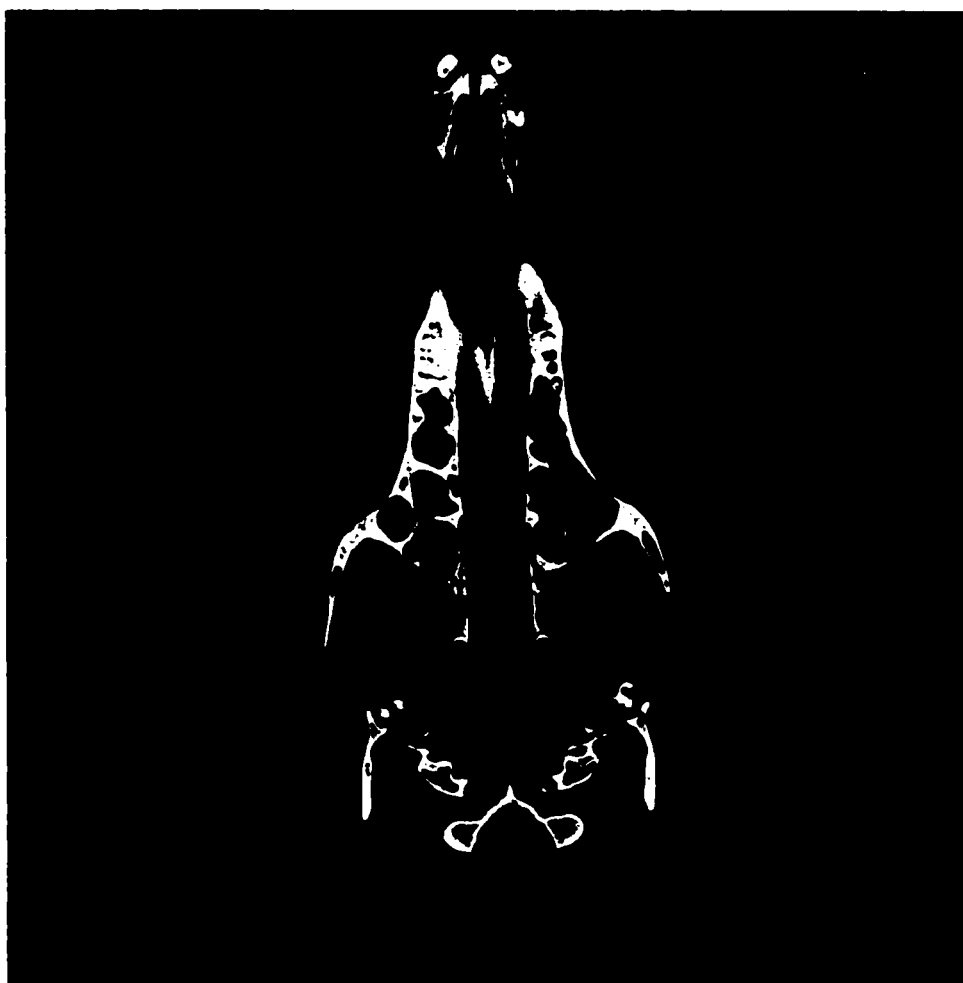


Figure 2-17

Figure 2-18 From an axial perspective several septations within the left maxillary sinus of the boar are observed (yellow arrows).

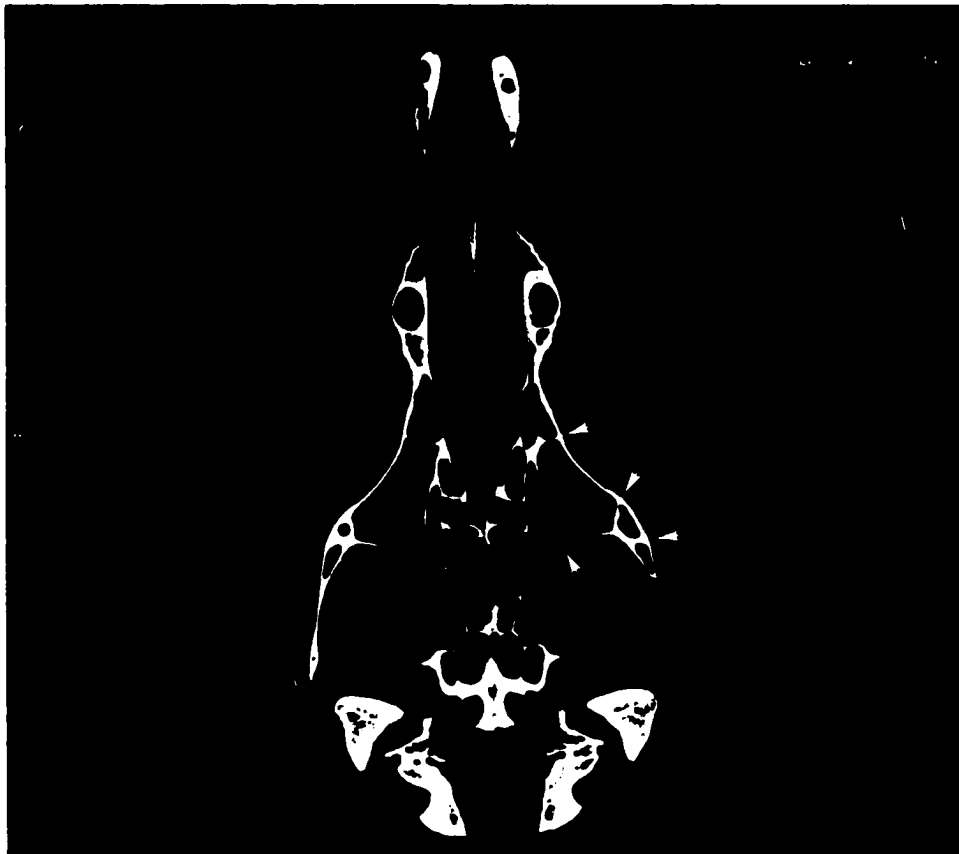


Figure 2-18

Figure 2-19 A coronal view reveals four septa within the left maxillary sinus (green arrows) of the boar.



Figure 2-19

Figure 2-20 Parasagittal view of the boar showing various septa within the left maxillary sinus. Note the thickness of the second septa (3.3 mm).



Figure 2-20

Figure 2-21 In this axial view of the boar the specimen exhibited distinct and bilateral ethmoid air cells. Based on a multiplanar reformatted 2-D reconstruction in the axial plane, six ethmoid air sinuses were identified on the right side and five on the left side.

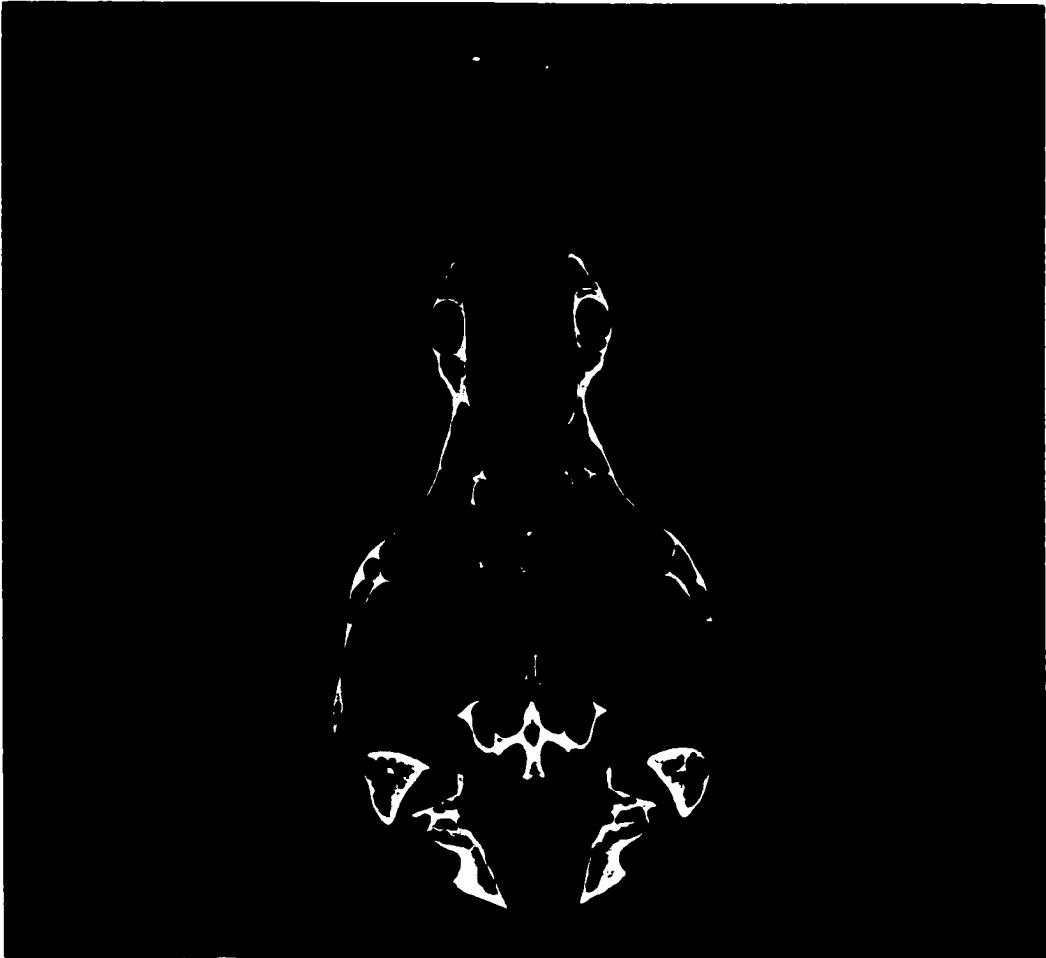


Figure 2-21

Figure 2-22 Confirmation of the complete enclosure of these cells was accomplished by the visualization of different views utilizing a series of multiple CT slices. In parasagittal view the inferior, superior, anterior, and posterior bony walls are seen. Medial and lateral wall enclosure was confirmed from the coronal perspective.



Figure 2-22

Figure 2-23 A series of bony septa in the frontal sinus are observed of the boar extending into the parietal and occipital regions in a coronal view at the level of the mesial border of M² (white arrows).

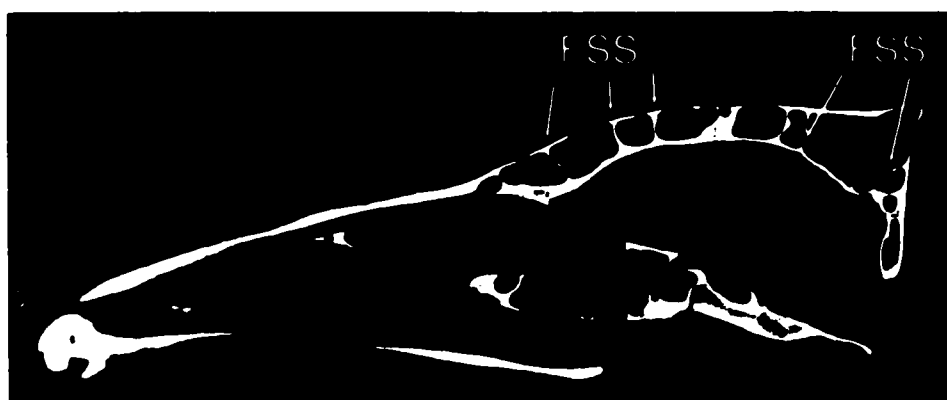


Figure 2-23

Figure 2-24 Pneumatization of the sphenoid body (yellow arrow) and of the pterygoid plates (white arrow) are observed of the boar from an axial planar view.

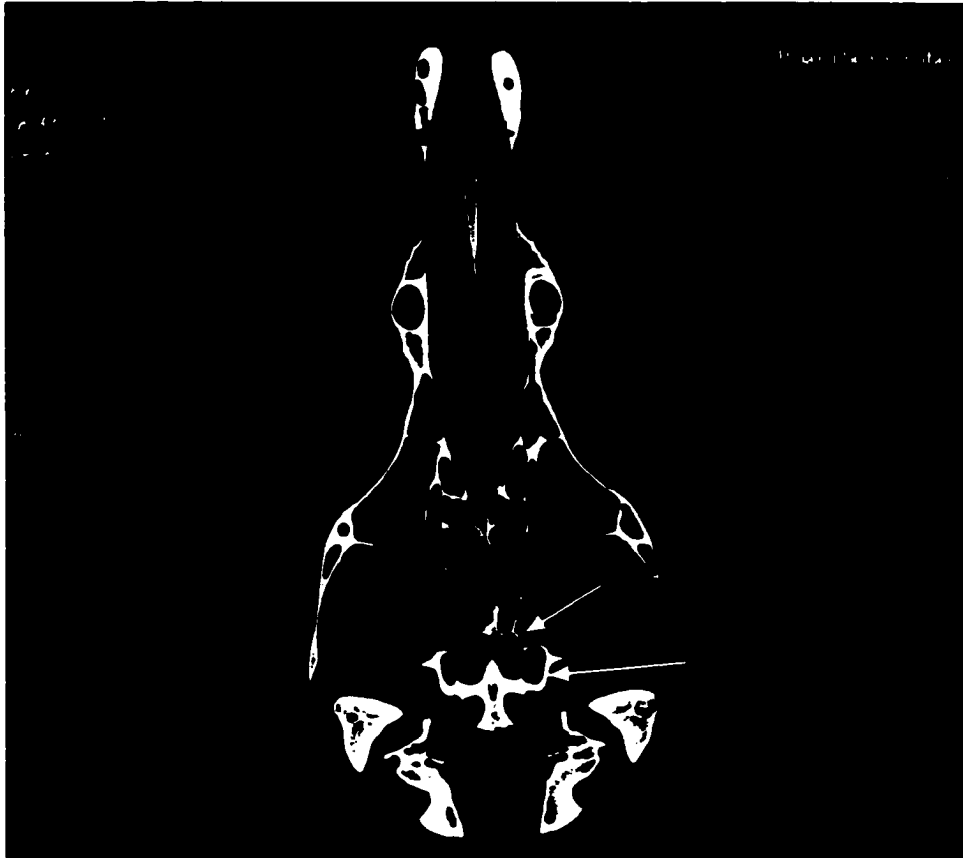


Figure 2-24

2.10. RESULTS FOR THE BEAR (*URSUS AMERICANUS*)

2.10.1. CT scanner specifications and method of analysis

Intensity specifications for CT digital capture scanning were as follows:

DFOV – 30.5 cm, Bone resolution, 120 kV, 150 mA, 1 mm slice thickness/1.0 sp.

The specimen was placed in an axial position anchored by foam blocks, cotton cloths and cloth tape. The scout, or orientation beams were aligned to ensure that the specimen was in the Frankfort horizontal position. All measurements and observations were obtained by the use of multiplanar CT imaging in conjunction with the Microsoft Morphometric tool software program of the NT computer workstation at the CT scanning facility. All reference window scout images correspond with specified areas designated on the multiplanar CT figures.

2.10.2. General remarks

The specimen exhibited three paranasal sinuses: (1) maxillary; (2) frontal; and (3) sphenoid sinuses. The inferior turbinates were well developed and were positioned at the front of the nasal cavity (anteroventral), with the maxillary sinus positioned topographically posterior to the turbinate. The ethmoturbinates were present and exhibited elaborate branching. In parasagittal view, the specimen exhibited a distinct transverse lamina which enclosed the olfactory ethmoturbinates above (see Figure 2-25). The transverse lamina was confluent with the nasal septum superiorly (see Figure 2-26).

Multiplanar CT imaging from anterior to posterior direction viewed in coronal, sagittal, and axial perspective showed the following characteristics of the skull of *Ursus americanus*.

- 1) The most anterior cut showed the inferior turbinate and ethmoturbinate morphology. The anterior portion of the frontal sinus was also observed (see Figure 2-27).**
- 2) The following sequential cut showed evidence of a maxillary sinus with pneumatization extending up to the frontal bone (see Figure 2-28).**
- 3) The third cut, which was a slice through the midportion of the ethmoid bone, showed the transverse lamina which divided the nasal cavity into olfactory and respiratory regions (Figure 2-29). The ethmoturbinals were assembled superior to this plate and were elaborately scrolled, with numerous branches projecting into the frontal sinus region (see Figure 2-30). Posteriorly, in coronal perspective, the extensive branching of the ethmoturbinals coalesced into as a mass of bony spicules surrounding the cribriform plate (see Figure 2-31).**
- 4) CT coronal views showed a series of septations in the frontal sinus (see Figure 2-32); and in parasagittal views, extensive pneumatization of frontal sinus into the parietal and occipital territories was observed (Figure 2-25).**
- 5) The most posterior cut demonstrated the anterior extent of the sphenoid sinus as well as temporal pneumatization by the frontal sinus superiorly to it (see Figure 2-33).**

2.10.3. Maxillary sinus

Extensive pneumatization by this sinus produced invasion into the frontal bone territory with patent communications among the compartments. The floor of the maxillary sinus approached the nasal cavity floor but did not proceed below it. The lateral walls of the sinuses were vertically orientated (Figure 2-28). The sinus was confined to the maxillary bone with no evidence of palatal or zygoma pneumatization.

2.10.4. Frontal sinus

Frontal sinus pneumatization was quite extensive with the pockets of air extending into several bones, including temporal, parietal and occipital bones. A series of complete and incomplete bony septal divisions were seen sagittally, with an extreme and elaborate spider web-like branching apparent in coronal view (Figure 2-32).

2.10.5. Sphenoid sinus

A large sphenoid sinus was present in this specimen. In a midsagittal view, the sinus was expansive and appeared to be compartmentalized by coronal septal barriers (Figure 2-33). However, in a parasagittal perspective the septal divisions appeared to be incomplete falsely giving the impression of multiple sphenoid sinuses. The intrusive nature of the ethmoturbinates was observed at the anterior aspect of the sphenoid sinus inferiorly and frontal sinus territory superiorly (see Figure 2-34).

2.10.6. Ethmoid sinus

No ethmoid air cells were identified.

2.10.7. Turbinate morphology

The actual configuration and dimensions of a structure can be misinterpreted when represented 2-dimensionally, viewed in one perspective or through only one particular plane. In order to safeguard from such errors it is important to view these structures three dimensionally and from different planar views for proper topographical mapping. For example, in coronal view (Figure 2-27) the inferior turbinates and ethmoturbinates appear to intermingle where as in an axial cut above the transverse lamina their independent nature is apparent (see Figure 2-35). When an axial cut is positioned below the transverse lamina only the inferior turbinate is detected (see Figure 2-36).

Figure 2-25. The following structures are illustrated in this parasagittal view of the bear. NC: nasal cavity; HP: hard palate; TL: transverse lamina; and NPS: nasopharyngeal space.

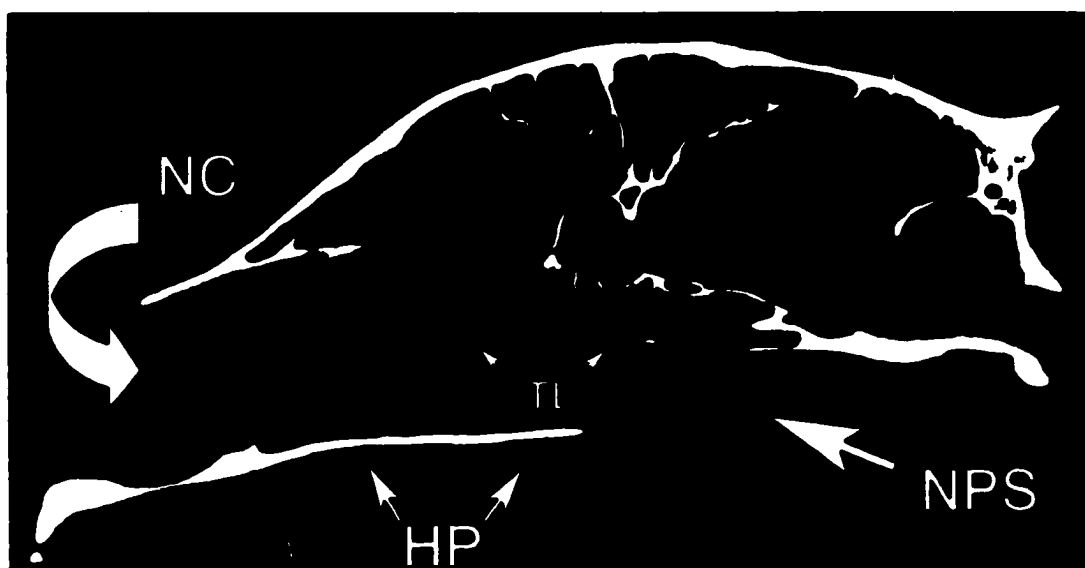


Figure 2-25

Figure 2-26. A midsagittal view (see reference window) of the bear showing the transverse lamina (TL) articulating with the nasal septum (NS) above.

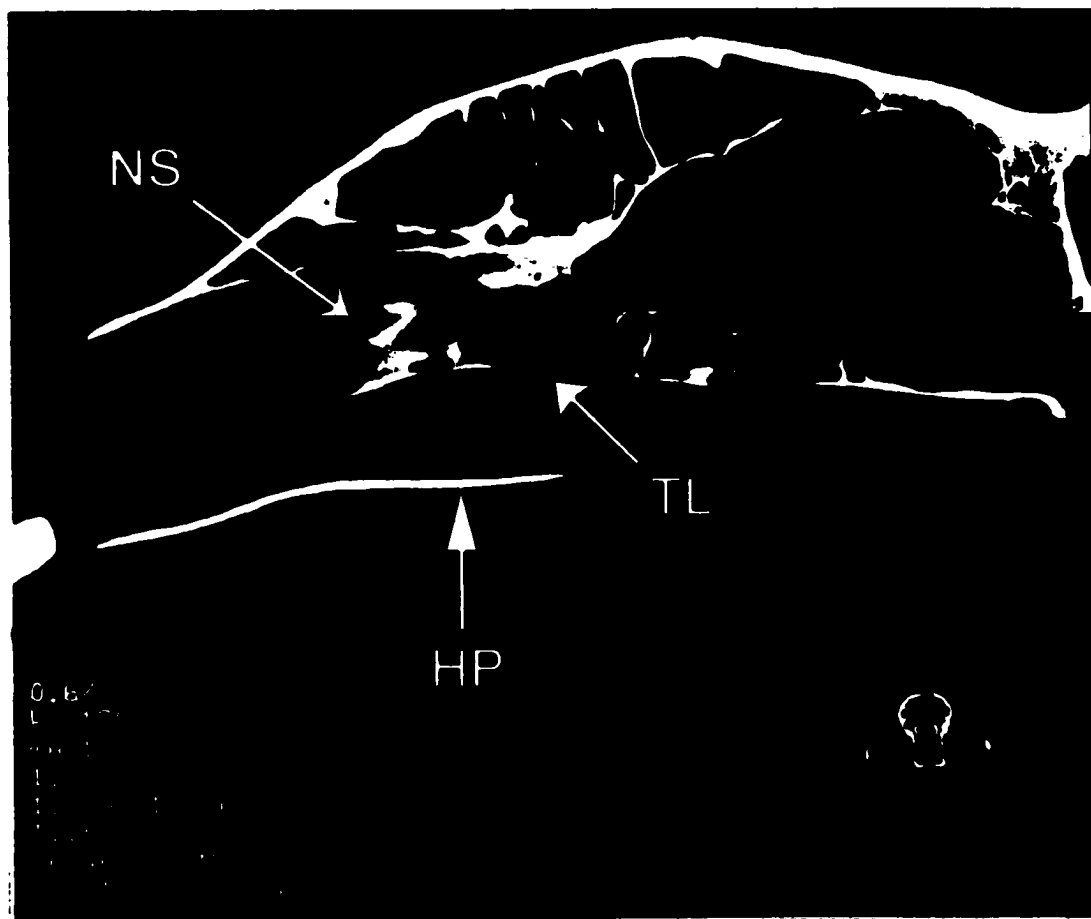


Figure 2-26

Figure 2-27. Frontal view of the bear showing the inferior turbinate (IT) and ethmoturbinate (ET) morphology. The anterior portion of the frontal sinus is also observed (shown by white asterisk).

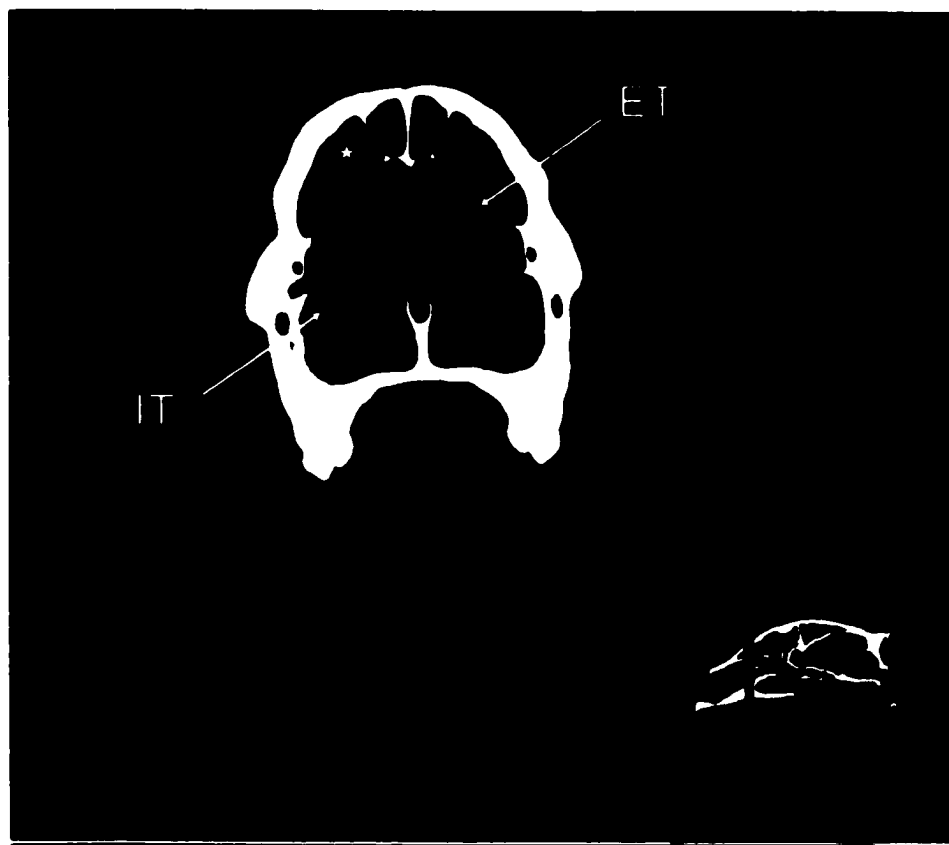


Figure 2-27

Figure 2-28. A frontal view of the bear showing maxillary sinus pneumatization extending up to the frontal bone as indicated by white arrows. Note the floor of sinus does not extend below the level of the nasal cavity floor.

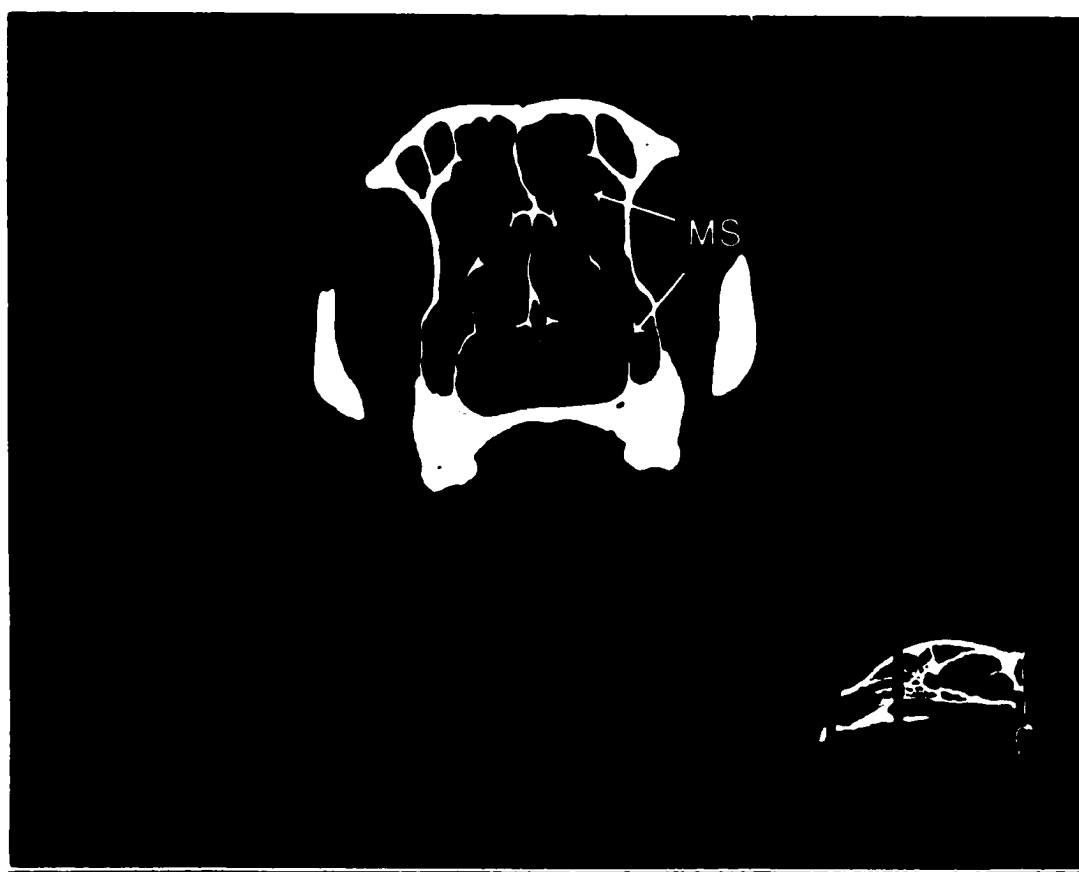


Figure 2-28

Figure 2-29. Parasagittal view of the bear through the midportion of the ethmoid bone, shows the transverse lamina, which divides the nasal cavity into an olfactory (OR) and respiratory region (RR). Refer to figure 1 for description of other abbreviations. The series of radiating white arrows indicate the assembly of ethmoturbinals surrounding the cribriform plate.

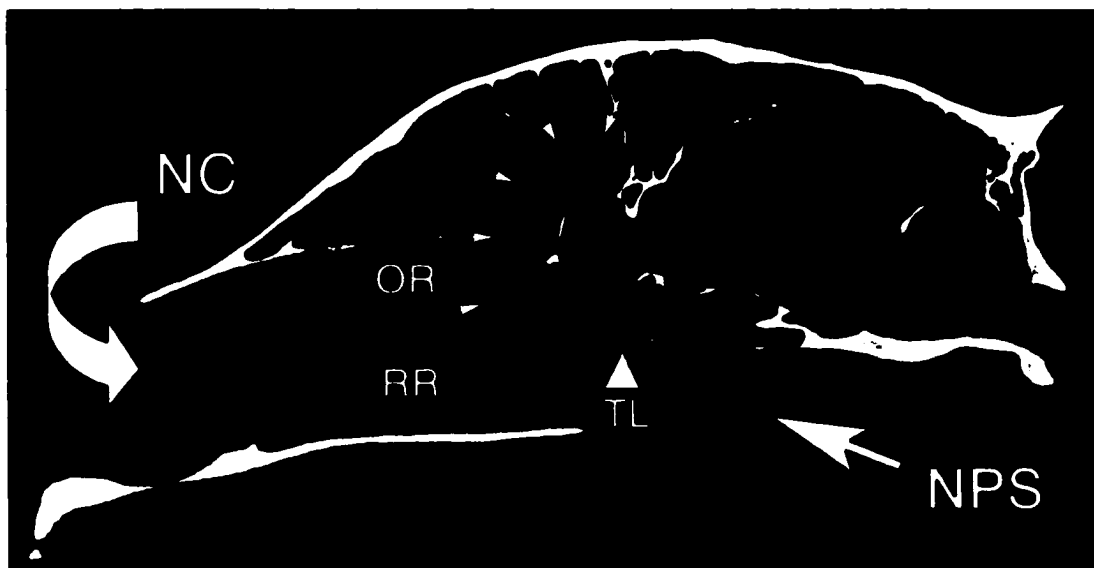


Figure 2-29

Figure 2-30. The ethmoturbinals (ET) superior to the transverse lamina (TL) are scrolled with extensive branching projecting into the frontal sinus region (RR = respiratory region of the bear.

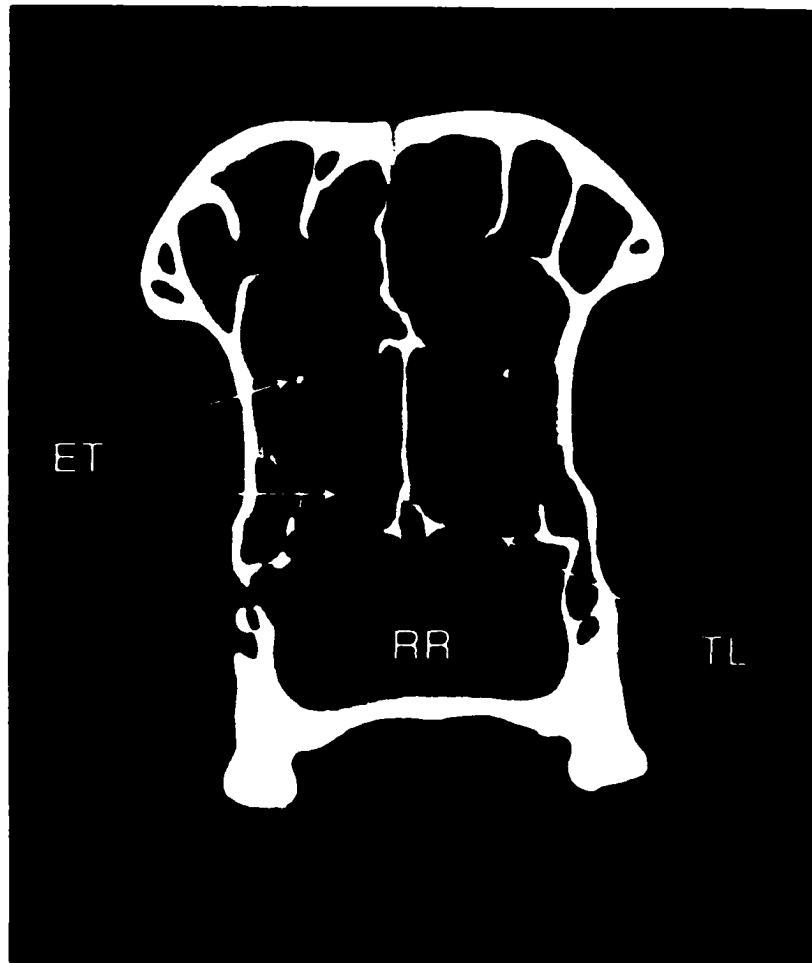


Figure 2-30

Figure 2-31. Moving posteriorly in coronal perspective from figure 48, the numerous branching of the ethmoturbinals (ET) coalesce appearing as a bony mass of spicules. Note frontal sinus septations (FSS).

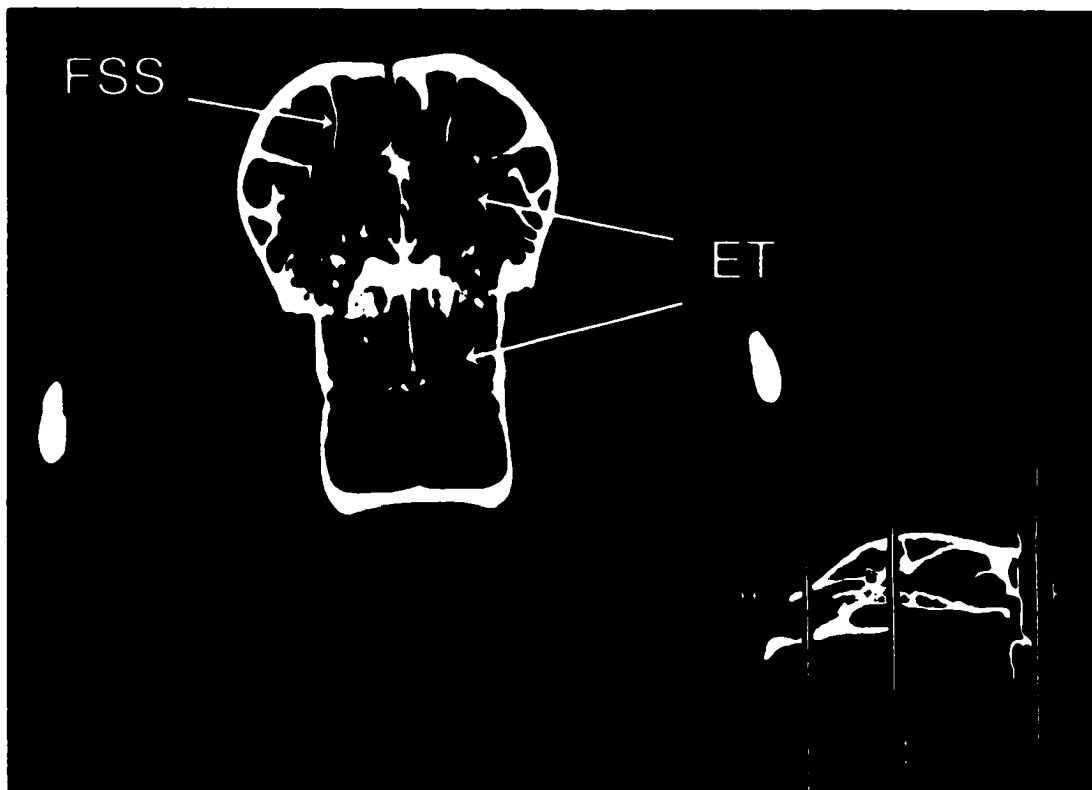


Figure 2-31

Figure 2-32. An axial slice high on the skull vault region shown in coronal view of the bear illustrates an impressive number of bony septations with numerous amount of branching within the frontal sinus.



Figure 2-32

Figure 2-33. A midsagittal view of the bear showing sphenoid sinus morphology (SS). Single arrow shows a septal division giving the appearance of multiple sinuses. Arrow head is pointing to the anterior wall of the sphenoid sinus.



Figure 2-33

Figure 2-34. A parasagittal view of the bear demonstrating no coronal septal division within the sphenoid sinus (white asterisk). Note the intrusive nature of the ethmoturbinates invading both sphenoid sinuses below and frontal sinuses above.

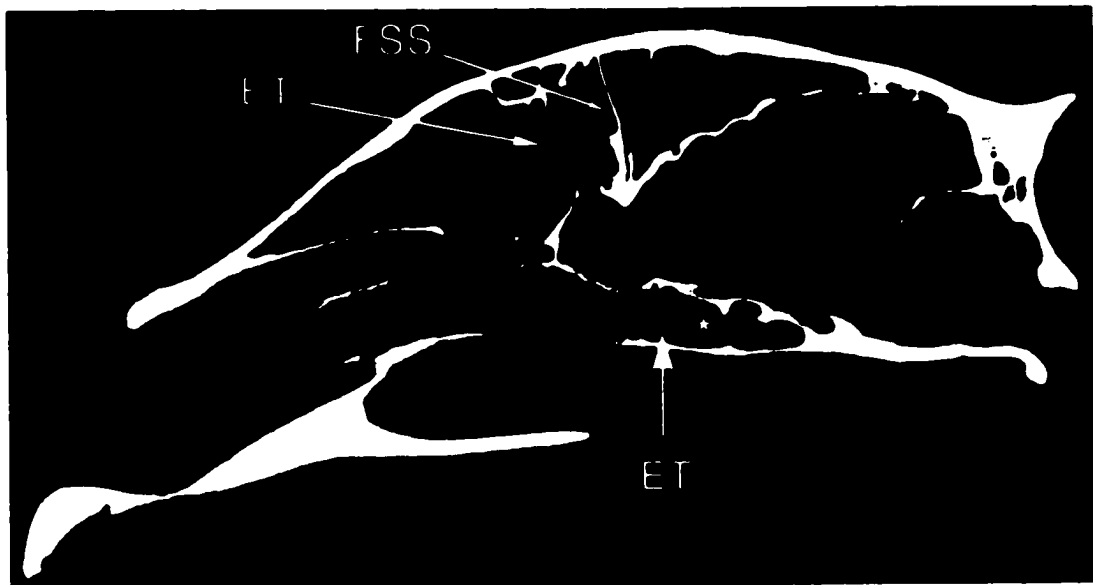


Figure 2-34

Figure 2-35. An axial view of the bear above the level of the transverse lamina (see reference window) showing independent nature of inferior turbinates and ethmoturbinates.

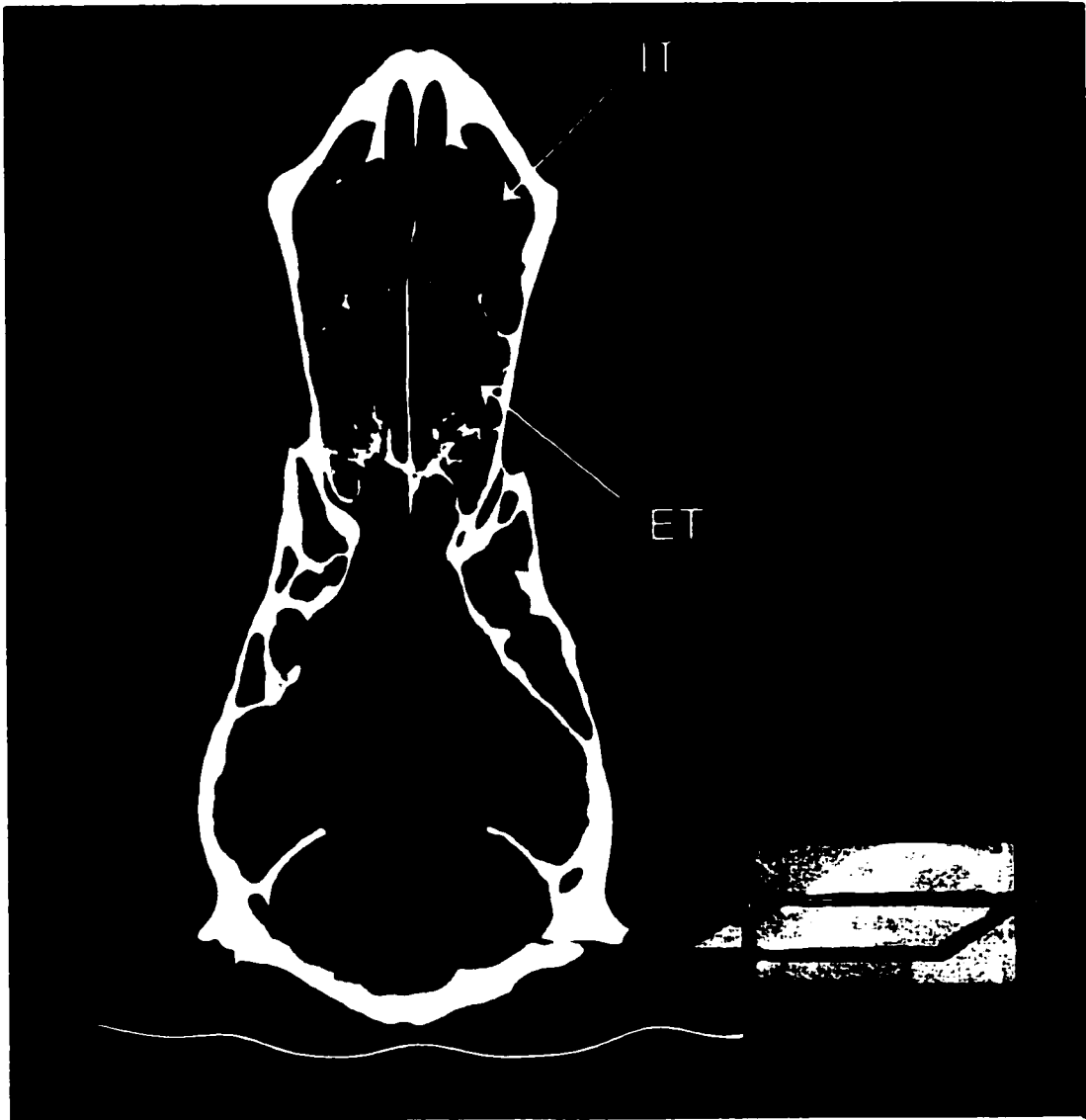


Figure 2-35

Figure 2-36. An axial view of the ear below the level of the transverse lamina (see reference window) showing only the inferior turbinate.

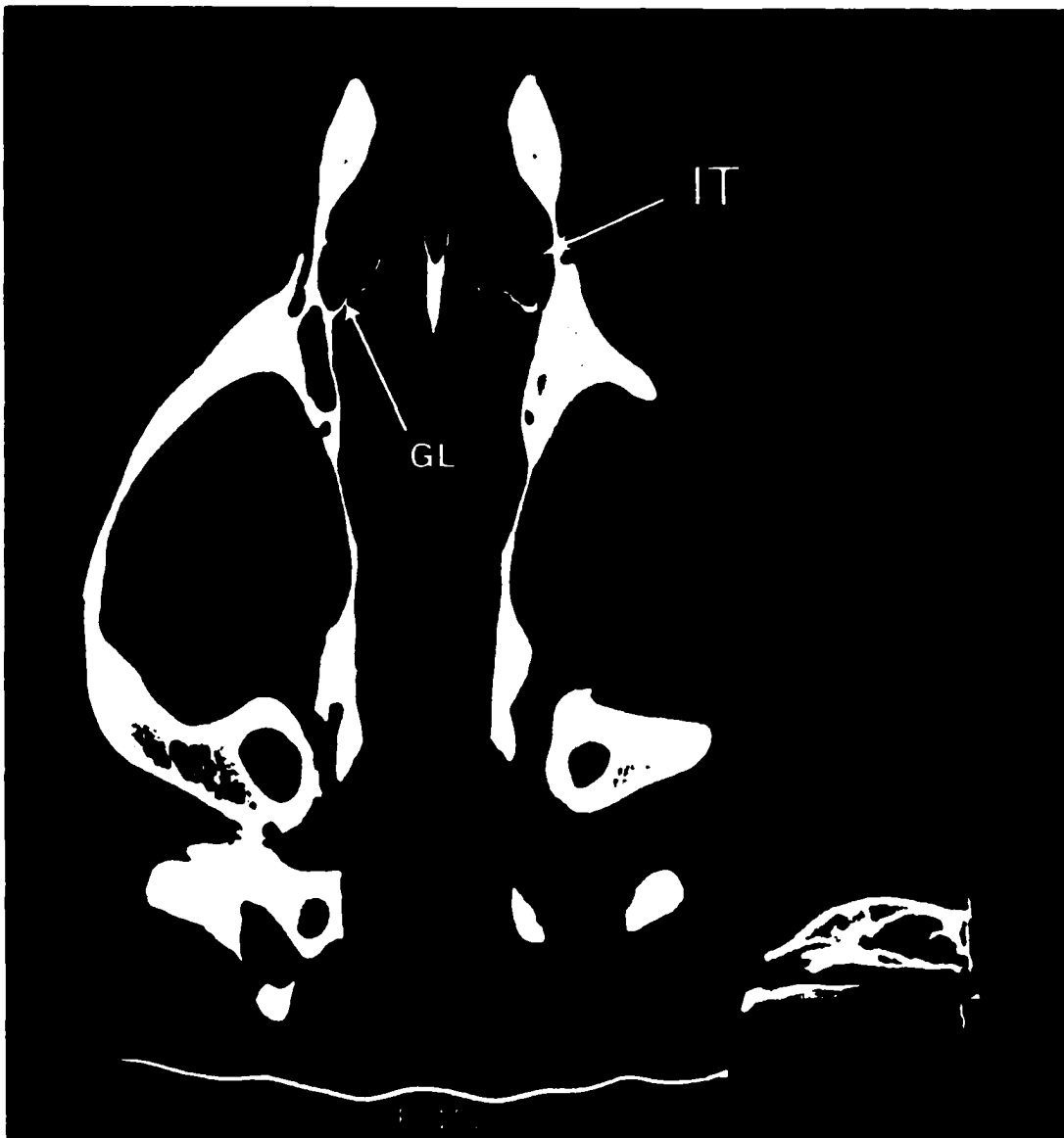


Figure 2-36

2.11. RESULTS FOR THE DEER (*ODOCOILEUS VIRGINIANUS*)

2.11.1 CT scanner specifications and method of analysis

Intensity specifications for CT digital capture scanning were as follows:
DFOV – 31.6 cm, Bone resolution, 140 kV, 60 mA, 1 mm slice thickness/1.0 sp.
Specimen was placed in an axial position and anchored by foam blocks, cotton cloths and cloth tape. The scout, or orientation beams were aligned to ensure that the specimen was in the Frankfort horizontal position. All measurements and observations were obtained through the use of multiplanar CT imaging using VoxelView 2.5 High-Performance 3D Imaging for Biomedicine software. All reference window scout images correspond to specified areas on the multiplanar CT figures.

2.11.2. General remarks

The specimen was an adult based on molar eruption pattern and on size of antler morphology. This particular species, *Odocoileus virginianus*, lacks upper incisor dentition. The specimen exhibited only one pair of sinuses, the maxillary.

2.11.3. Maxillary sinus – general observations

The most anterior projection of the maxillary sinuses occurred in the coronal plane at the juncture of PM², with the most posterior excavation observed in the coronal plane of the maxillary tuberosity. The floor of the maxillary sinus extended over the premolar and molar dentition and slightly posteriorly beyond M³. The

lateral walls of the sinuses at the point of their maximum width were vertically disposed making these cavities appear narrow. Partitions, or septae, were not observed within the sinuses.

2.11.4. Right maxillary sinus

The following observations were made from coronal views with a reference window indicating the corresponding sagittal slice view. The greatest width occurred in the coronal plane at the distal border of M^2 where the zygomaticomaxillary suture marks the laterally extension and the medial border by the lateral wall of the nasal cavity. A transverse distance of 23.6 mm was recorded (Figure 2-37). The greatest height was in coronal plane at the juncture between M^2 and M^3 , with a length of 37.1 mm from the most superior to the most inferior point (Figure 2-38). From an axial perspective, the greatest anteroposterior length was 83.5 mm (Figure 2-39). The floor of the sinus did not approach the level of the nasal cavity floor.

The maxillary sinus was found to extend medially into the hard palate. This extension made contact but did not communicate with the contralateral sinus in the midline of the hard palate (Figure 2-40). Visualization of the sinus was facilitated by digitizing the 3-D space of the entire sinus region and graphically representing its morphology both *insitu* and extracted (Figure 2-41). In the coronal plane, palatal pneumatization is observed anteriorly at the juncture of PM^2 and terminates posteriorly at the midportion of M^2 . The floor of the maxillary sinus proper covers

over the dental roots from PM³ and extends well into the maxillary tuberosity territory.

2.11.5. Left maxillary sinus

The lateral and medial bony walls were similar to the right side. The greatest width (25.1 mm) occurred in the coronal plane at the distal border of M². The greatest height (36.3 mm) in the coronal plane was measured at the juncture between M² and M³. From an axial view, the greatest anteroposterior length was 79.2 mm (see Table 2-4 for summary of maxillary sinus dimensions). The floor of the sinus did not approach the level of the nasal cavity floor.

A medial extension into the hard palate was similarly observed. A thin bony partition at the midline of the hard palate prevented communication the two sinuses. Palatal pneumatization in the coronal plane begin anteriorly at the juncture of PM² and terminated at the midportion of M².

Table 2-4 Linear measures of Deer's maxillary sinus dimensions

	Right Maxillary Sinus	Left Maxillary Sinus
Greatest Width	23.6mm	25.1 mm
Greatest Height	37.1 mm	36.3 mm
Greatest Length	83.5 mm	79.2 mm

2.11.6. Ethmoid sinus

No ethmoid sinus cells were identified.

2.11.7. Sphenoid sinus

No sphenoid sinuses were detected.

2.11.8. Turbinate morphology

The inferior turbinate begins anteriorly to the premolar dentition exhibiting a simple double scrolled arrangement (Figure 2-42a and 2-42a1). The upper scroll had inrolled more than two full revolutions, with the lower scroll making two revolutions (Figure 2-42b). From the coronal perspective and proceeding posteriorly, the upper scroll continued to inroll and enlarges while the lower scroll became diminutive (Figure 2-43). At the level of the mesial border of M^1 the lower scroll was rudimentary with the upper scroll having only one full revolution present (Figure 2-44a and 2-44a1). The basal lamella and the upper and lower scroll remnant of the inferior turbinate are observed in the coronal plane at the mesial border of M^2 (Figure 2-44b and 2-44b1).

Coincident with the posterior ending of the inferior turbinate, an elaborate branching of the ethmoturbinates appeared (Figure 2-45a). The superior extensions of the ethmoturbinate plates perforated the roofing leaving these plates exposed dorsally. The next sequential coronal cut posteriorly showed condensation of these plates to form thick and bony spicules which converged medially. These bony masses were housed in the olfactory region which was separated from the respiratory air-currents by the

transverse lamina (Figure 2-45b). A coronal cut through the maxillary tuberosity still showed evidence of ethmoturbinates well into but below the anterior cranial fossa (Figure 2-46).

Figure 2-37. Coronal view of the deer showing the largest width shown in red within the right maxillary sinus. Above is the reference window showing the corresponding coronal cut.

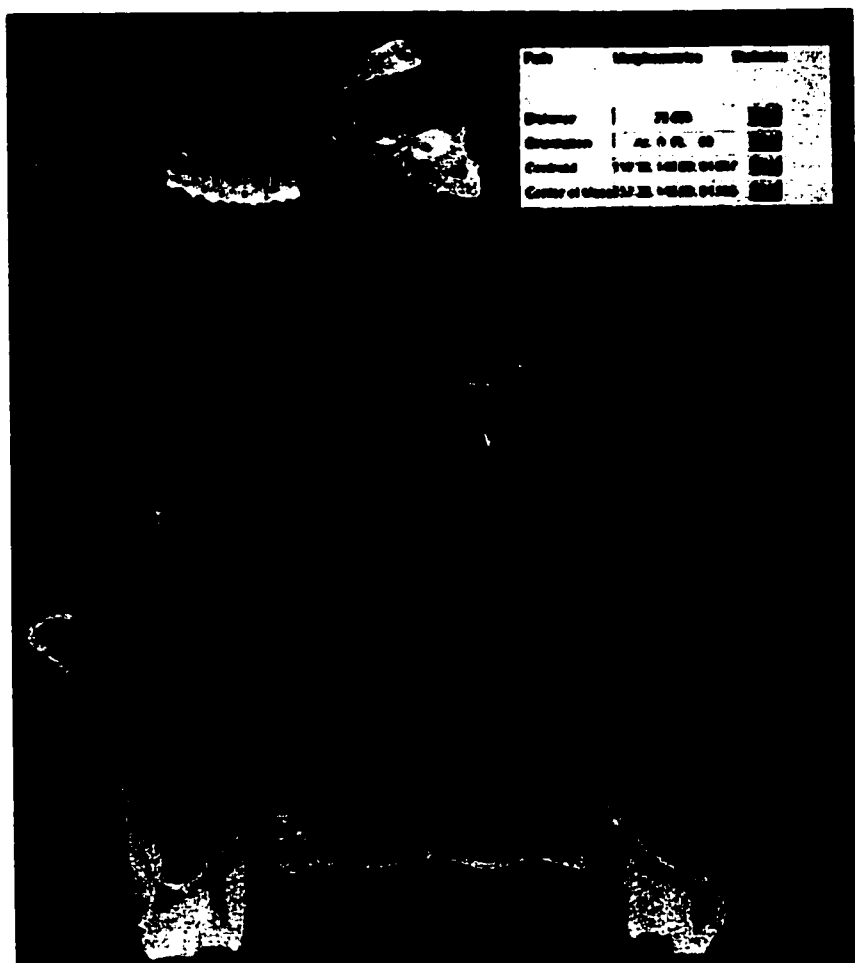


Figure 2-37

Figure 2-38. Coronal view of the deer illustrating the greatest height as indicated by the red line within the right maxillary sinus.

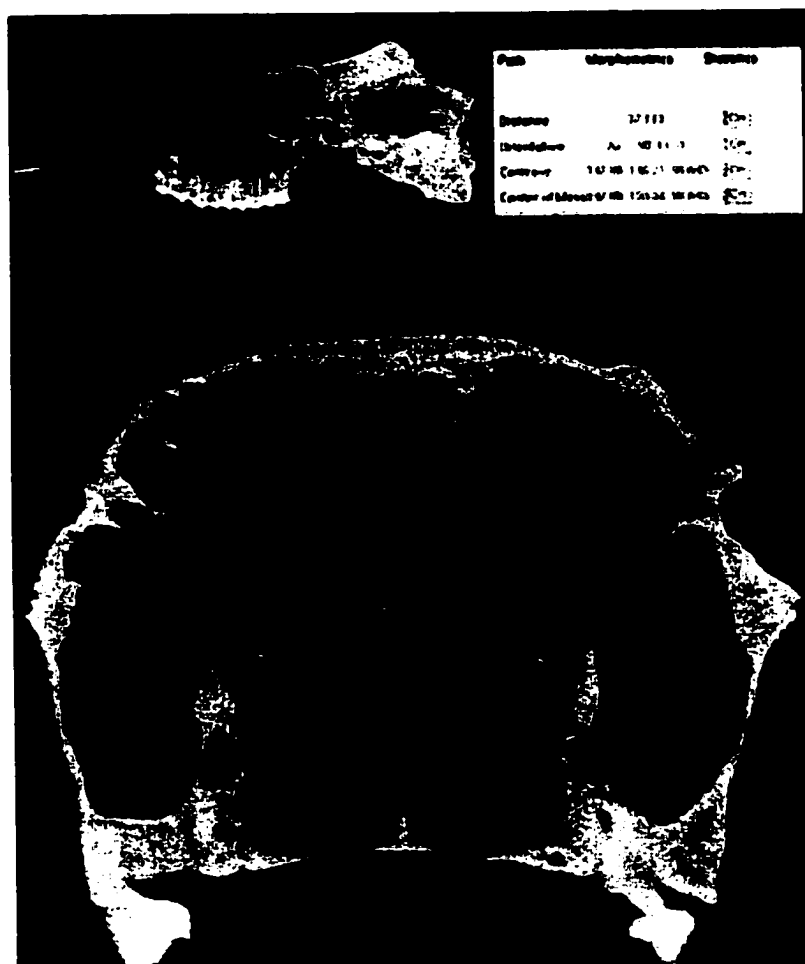


Figure 2-38

Figure 2-39. An axial view of the deer showing the anteroposterior length of the right maxillary sinus.

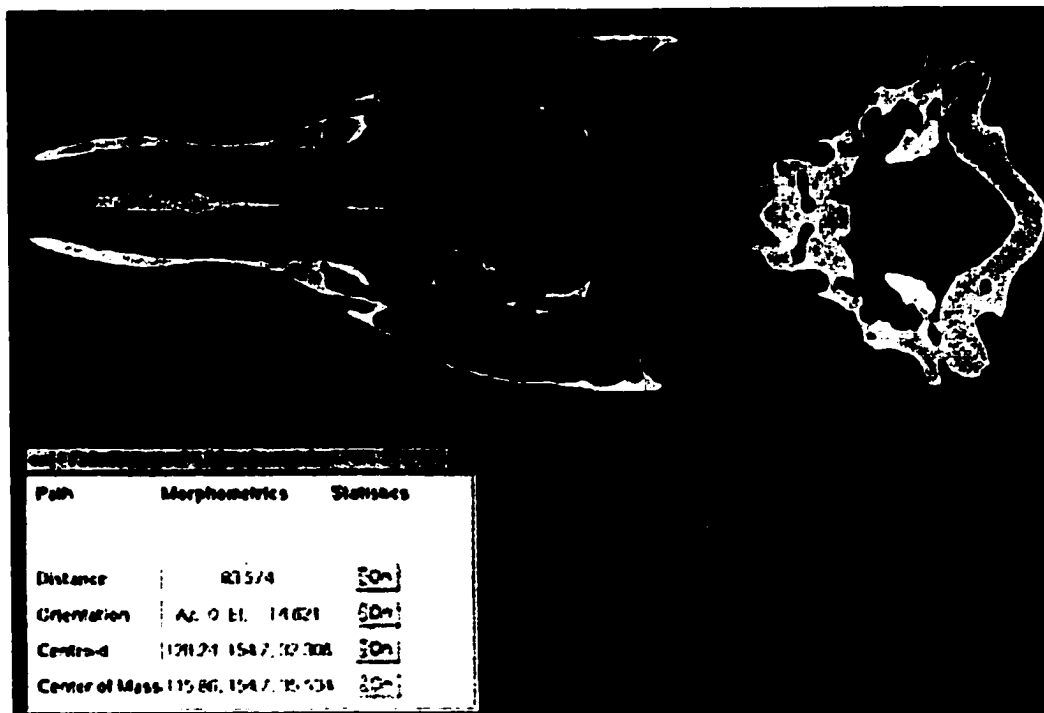


Figure 2-39

Figure 2-40. A coronal cut through the distal border of PM² shows the medial invasion of the maxillary sinus into the hard palate extending to the midline (MSPN: maxillary sinus palatal pneumatization) of the deer.

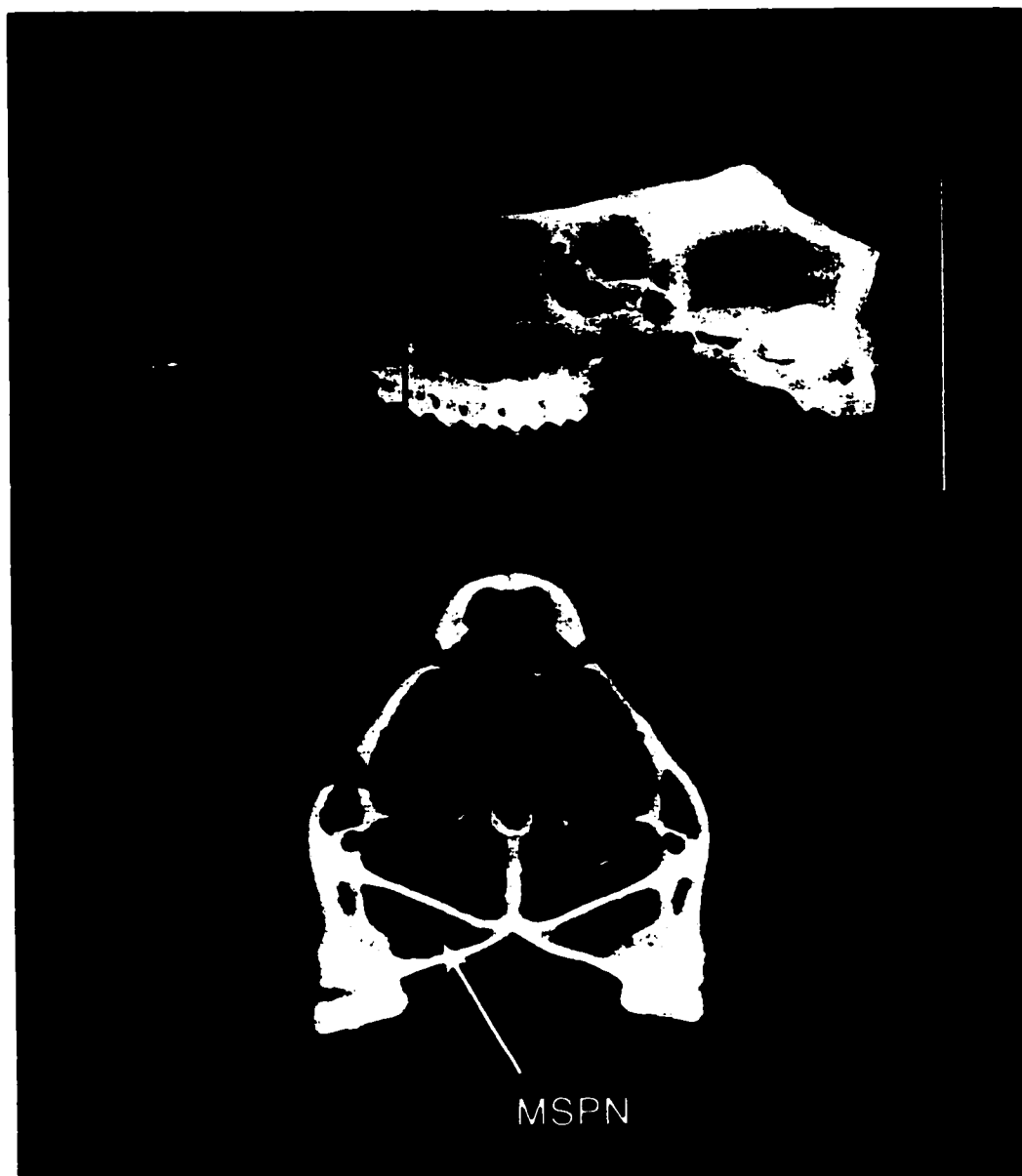


Figure 2-40

Figure 2-41. A frontal and lateral view composite of the deer showing the maxillary sinus both *insitu* and extracted. Note the floor of the sinus covers the dentition and extends into the maxillary tuberosity region in the lateral view.

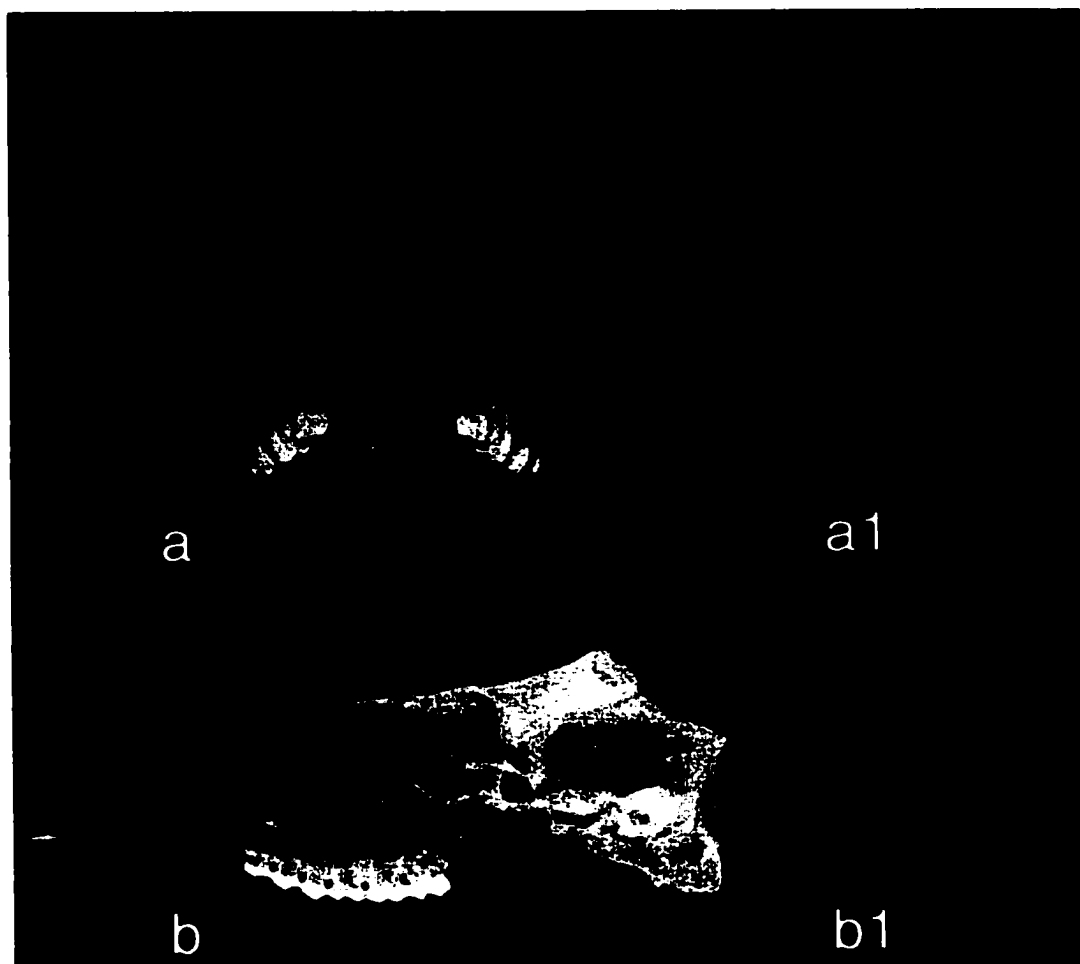


Figure 2-41

Figure 2-42. A composite of coronal views of the deer showing the inferior turbinate. The double scrolled nature of the turbinate with an inroll of one full revolution is shown in (a). The inroll revolutions increases in the next sequential coronal cut seen below (b).

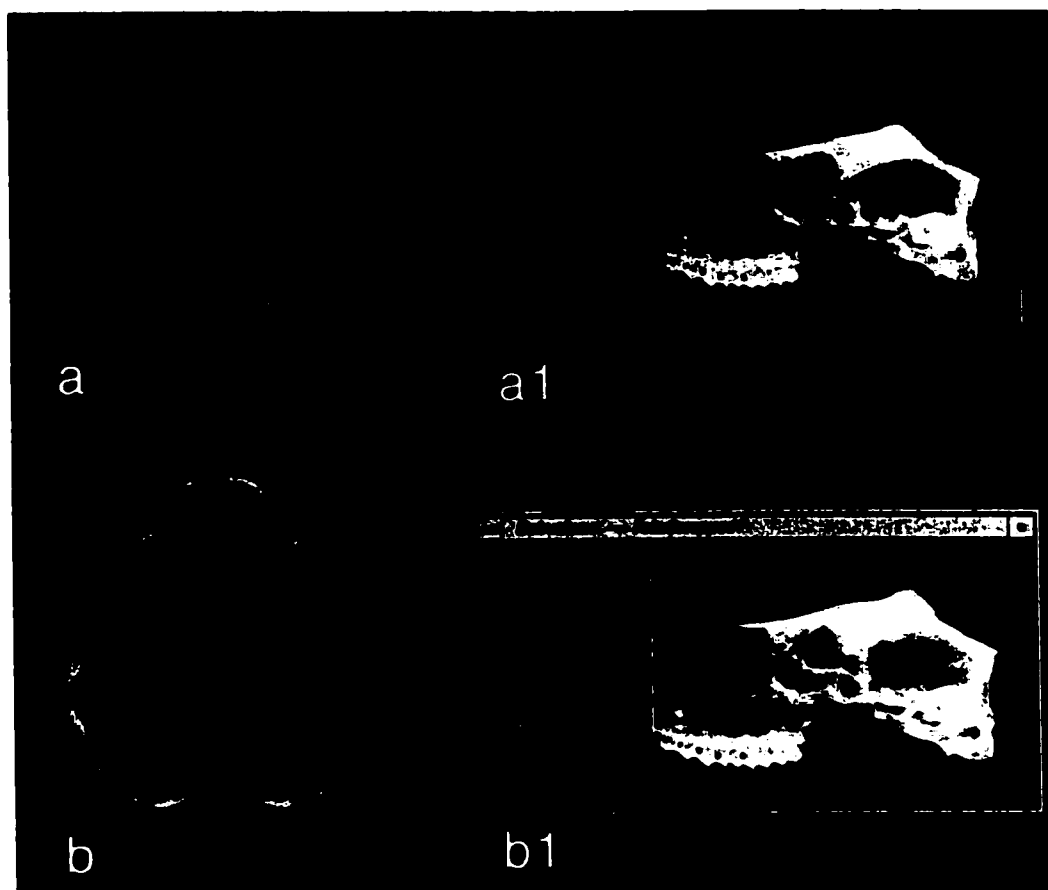


Figure 2-42

Figure 2-43. The upper scroll of the inferior turbinate of the deer begins elaborate inrolling and is larger than its lower scroll partner (a). Note the palatal pneumatization above (a) and the patent communication with the maxillary sinus below (b).

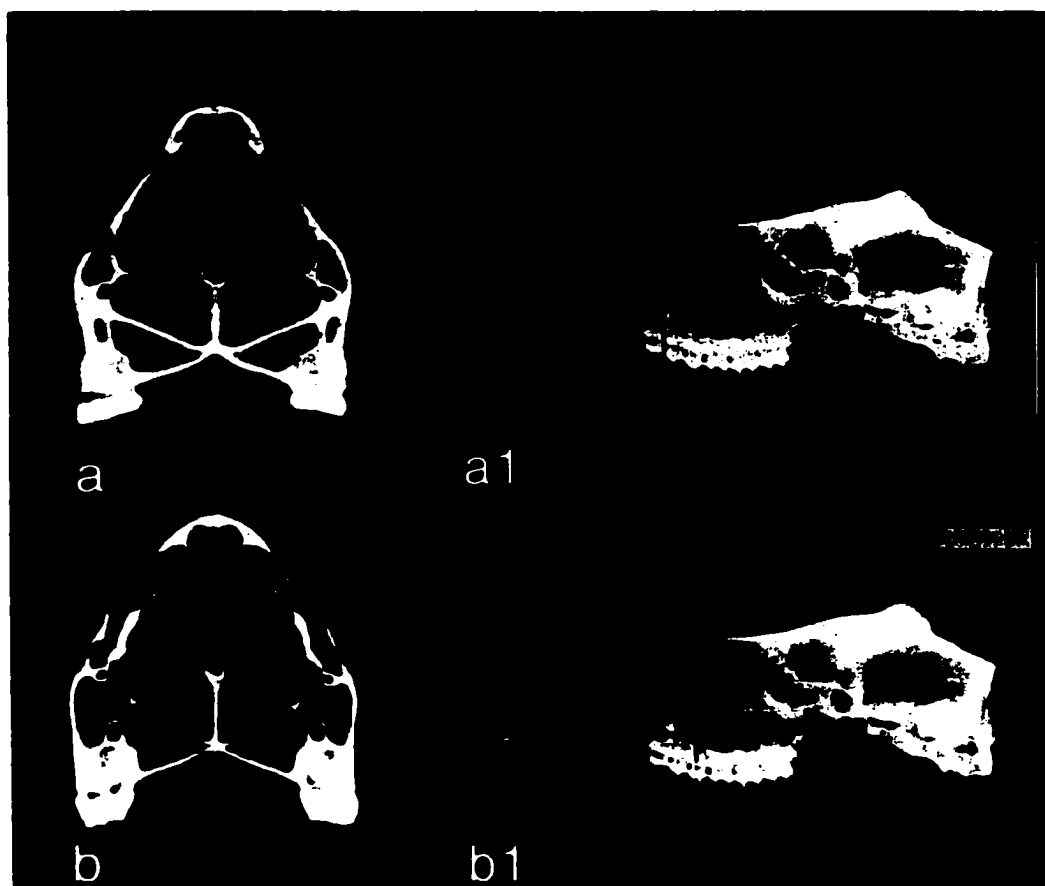


Figure 2-43

Figure 2-44. A coronal cut at the mesial border of the first molar dentition shows the lower scroll with a slight inroll of its extremity while the upper scroll inroll shows a full turn revolution (a). A coronal cut at the midportion of the first molar shows the lower scroll almost absent while the upper scroll has a half turn revolution (b).

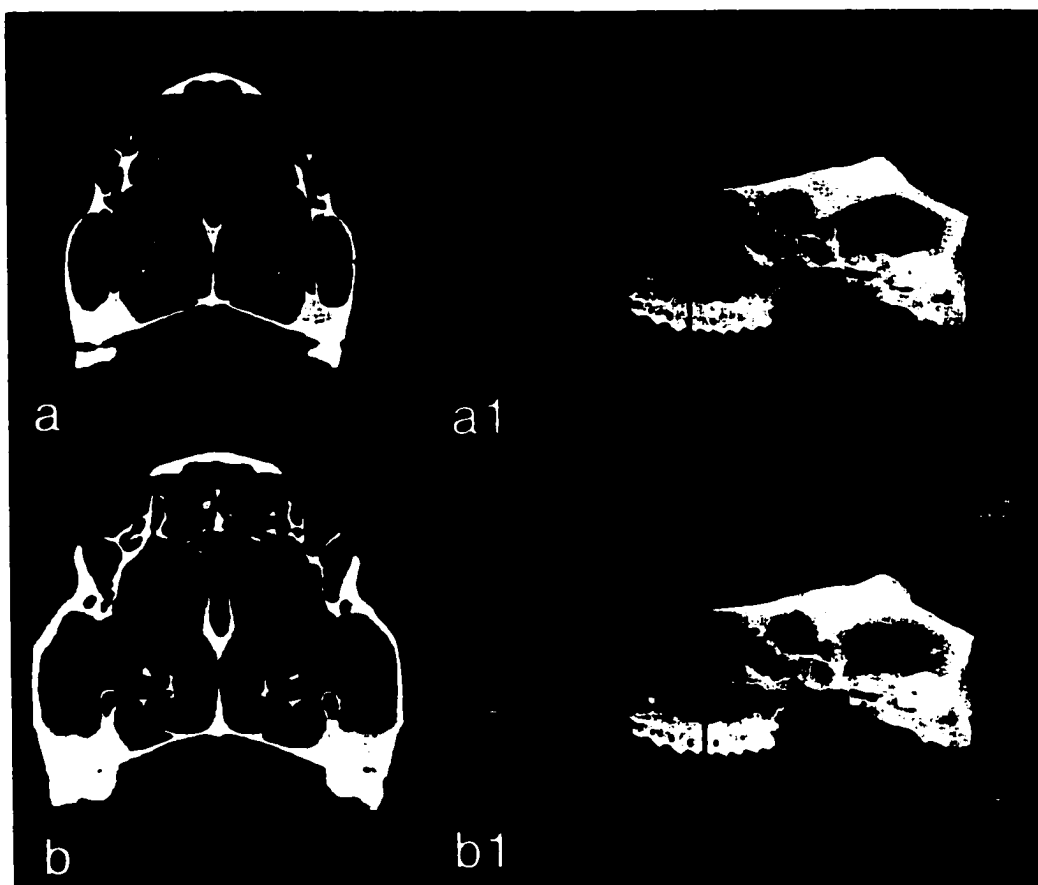


Figure 2-44

Figure 2-45. A coronal cut at the distal border of the first molar dentition of the deer shows only the basal lamella of the inferior turbinate (a). Note that the ethmoturbinates are beginning to appear and proliferate where they are dorsally exposed. Shown in (b) are the ethmoturbinates which coalesce into thick and bony spicules.

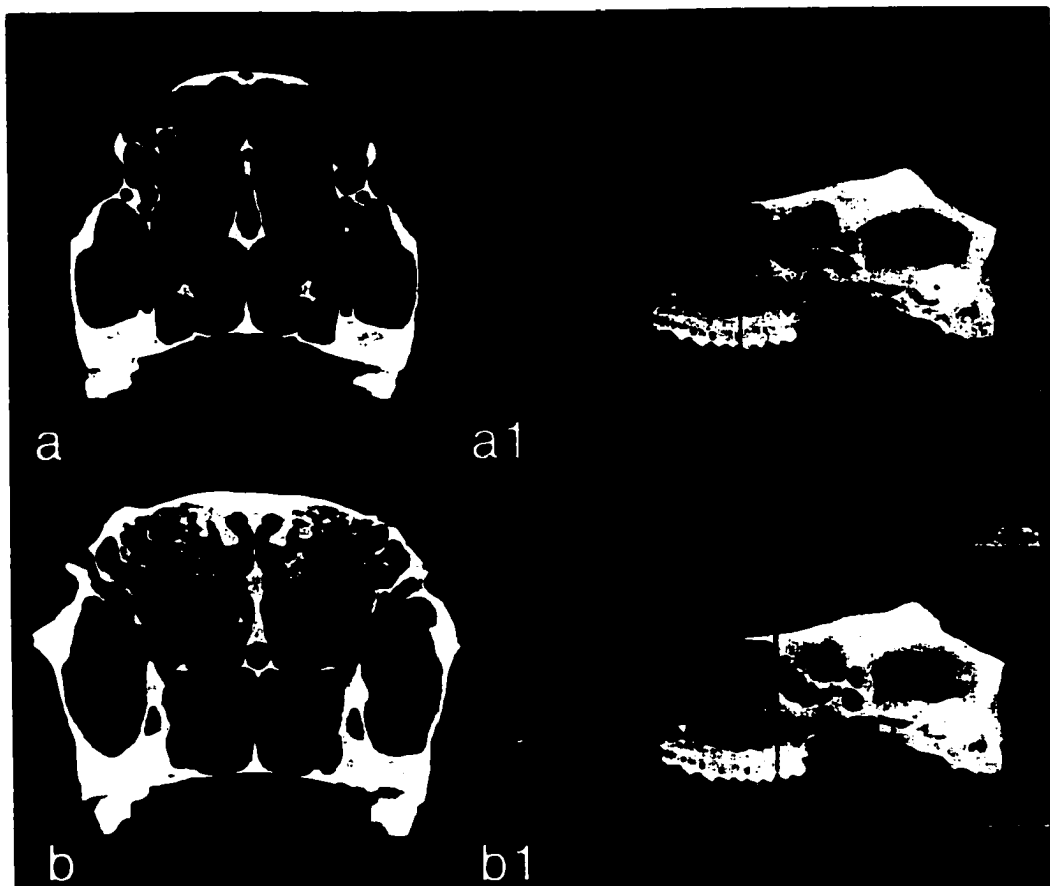


Figure 2-45

Figure 2-46. A coronal cut through the region of the maxillary tuberosity of the deer shows the following structures: Inferior orbital canal (solid white arrows); and choanae (dashed white arrows. Note that the ethmoturbinate mass intrudes into but below the anterior cranial fossa.

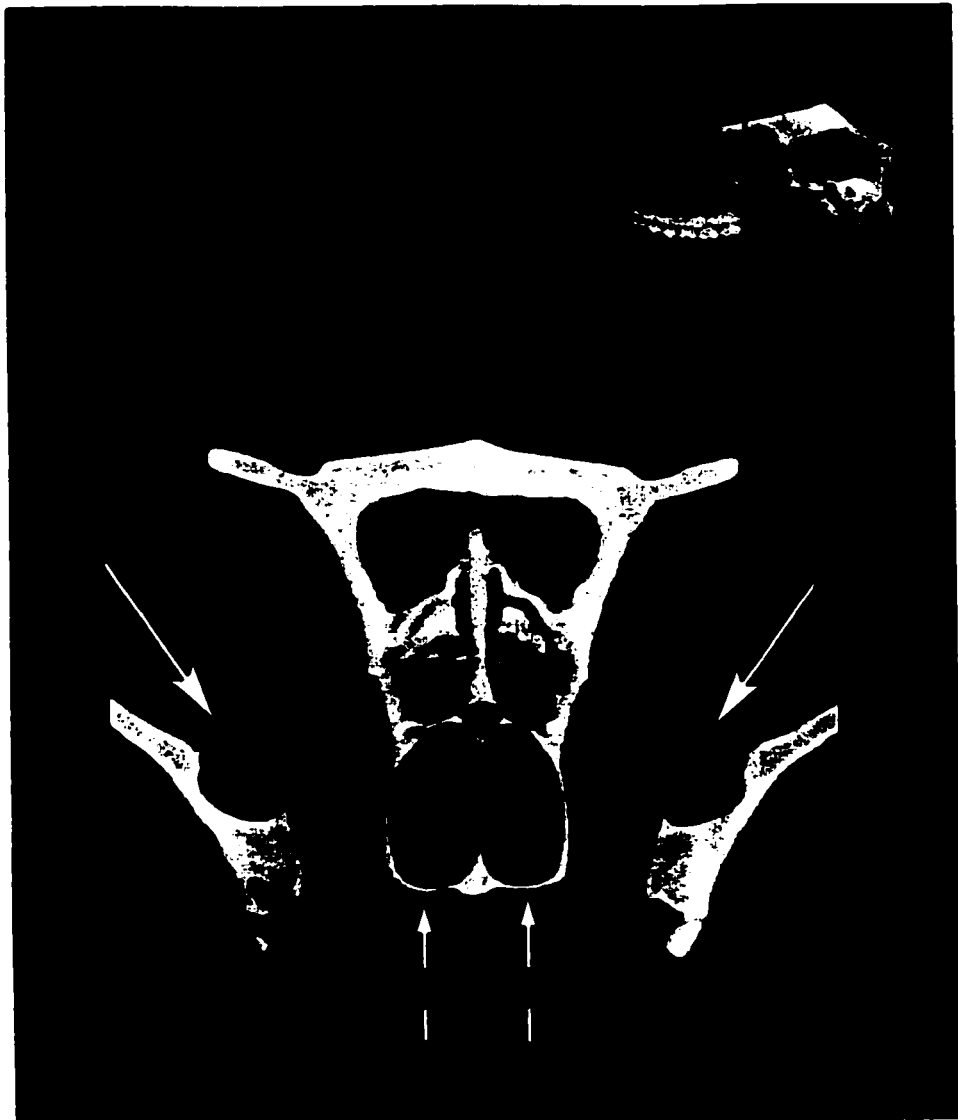


Figure 2-46

2.12. RESULTS FOR THE DOG (*CANIS FAMILIARUS*)

2.12.1 CT scanner specifications and method of analysis

Intensity specifications for CT digital capture scanning were as follows:

DFOV – 21.4 cm, Bone resolution, 130 kV, 120 mA, 1 mm slice thickness/1.0 sp.

Specimen was placed in an axial position and anchored by foam blocks, cotton cloths and cloth tape. The scout, or orientation beams were aligned to ensure that the specimen was in the Frankfort horizontal position. All measurements and observations were obtained through the use of multiplanar CT imaging using VoxelView 2.5 High-Performance 3D Imaging for Biomedicine software. All reference window scout images correspond to specified areas on the multiplanar CT figures.

2.12.2. General remarks

The specimen was an adult based on molar eruption pattern. The specimen exhibited two paranasal sinuses - the maxillary and frontal. The maxillary sinuses appeared markedly symmetrical while the frontal sinuses were well demarcated exhibiting some incomplete septae.

2.12.3. Maxillary sinus – general observations

Maxillary sinus pneumatization was confined within the body of the maxilla with no medial extension into the hard palate. The maxilla forms the dorsal, lateral and ventral walls of the sinus. The medial wall is formed anteriorly and for most of its extent by the lateral lamina of the ethmoid bone. The vertical plate of the palatine

bone forms the posterior area of the medial wall of the sinus. The relative large and oval ostium has its long axis situated vertically and at the anterior end of the sinus. The roof and the floor of the sinus diverge dorsally and ventrally behind the confines of this opening. The most anterior projection of the maxillary sinuses occurred in the coronal plane at the juncture of PM³, with the most posterior excavation observed in the coronal plane of M². The floor of the maxillary sinus extended over the premolar and molar dentition and slightly posteriorly beyond M². The lateral walls of the sinuses at the point of their maximum width were vertically disposed making these cavities appear narrow. Partitions, or septae, were not observed within the sinuses.

2.12.4. Right maxillary sinus

The following observations were made from coronal views with a reference window indicating the corresponding sagittal slice view. The greatest width occurred in the coronal plane at the distal border of M¹. A transverse distance of 6.6 mm was recorded. The greatest height was in coronal plane at the juncture between M² and M³, with a length of 25.1 mm from the most superior to the most inferior point.

From an axial perspective, the greatest anteroposterior length was 27.5 mm. The floor of the sinus nearly approached the level of the nasal cavity floor.

2.12.5. Left maxillary sinus

The lateral and medial bony walls were similar to the right side. The greatest width (6.8 mm) occurred in the coronal plane at the distal border of M^2 (Figure 2-47).

The greatest height (24.0 mm) in the coronal plane was measured at the juncture between M^2 and M^3 (Figure 2-48). From an axial view, the greatest anteroposterior length was 28.7 mm (Figure 2-49 and see Table 5 for summary of maxillary sinus dimensions). The floor of the sinus nearly approached the level of the nasal cavity floor. Figure 2-50 shows the right and left maxillary sinus space digitized and graphically represented both insitu and extracted.

Table 2-5 Linear measures of Dog's maxillary sinus dimensions

	Right Maxillary Sinus	Left Maxillary Sinus
Greatest Width	6.6 mm	6.8 mm
Greatest Height	25.1 mm	24.0 mm
Greatest Length	27.5 mm	28.7 mm

2.12.6. Ethmoid sinus

No ethmoid sinus cells were identified.

2.12.7. Sphenoid sinus

No sphenoid sinuses were detected.

2.12.8. Frontal sinus

Specimen exhibited frontal sinuses encroaching from the lateral portion to the midline of the frontal bone but with no communication with its contra lateral sinus. Sinus pneumatization is moderately extensive encroaching posteriorly to the midportion of the skull (Figure 2-51).

2.12.9. Turbinate morphology

The turbinate system of the dog exhibited a doubled scrolled inferior turbinate and complex ethmoturbinates. Proceeding from anterior to posterior the inferior turbinate begins almost from the piriform aperture entrance and terminates in the coronal plane at the juncture of the third premolar and first molar dentition. As the inferior turbinate terminates the ethmoturbinates first appear with a transverse lamina situated slightly posteriorly to their introduction. Proceeding posteriorly the ethmoturbinates become complex with extensive branching and are housed in the superoposterior portion of the nasal cavity where the olfactory region is demarcated by the transverse lamina (Figure 2-52).

-

Figure 2-47 Frontal view of dog maxillary sinus demonstrating maximum width.
Highlighted area in upper window shows position of slice.



Figure 2-47

Figure 2-48 Frontal view of dog maxillary sinus demonstrating maximum height.
Highlighted area in upper left shows position of slice.

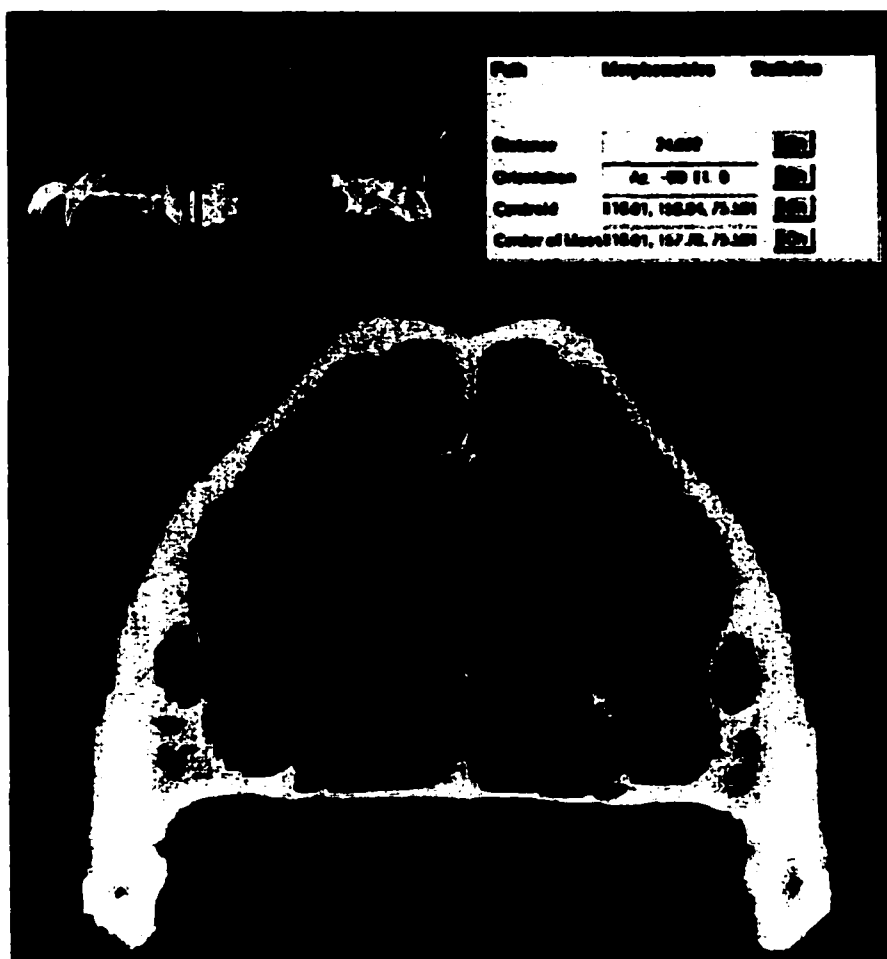


Figure 2-48

Figure 2-49 Lateral view of dog maxillary sinus demonstrating maximum length.

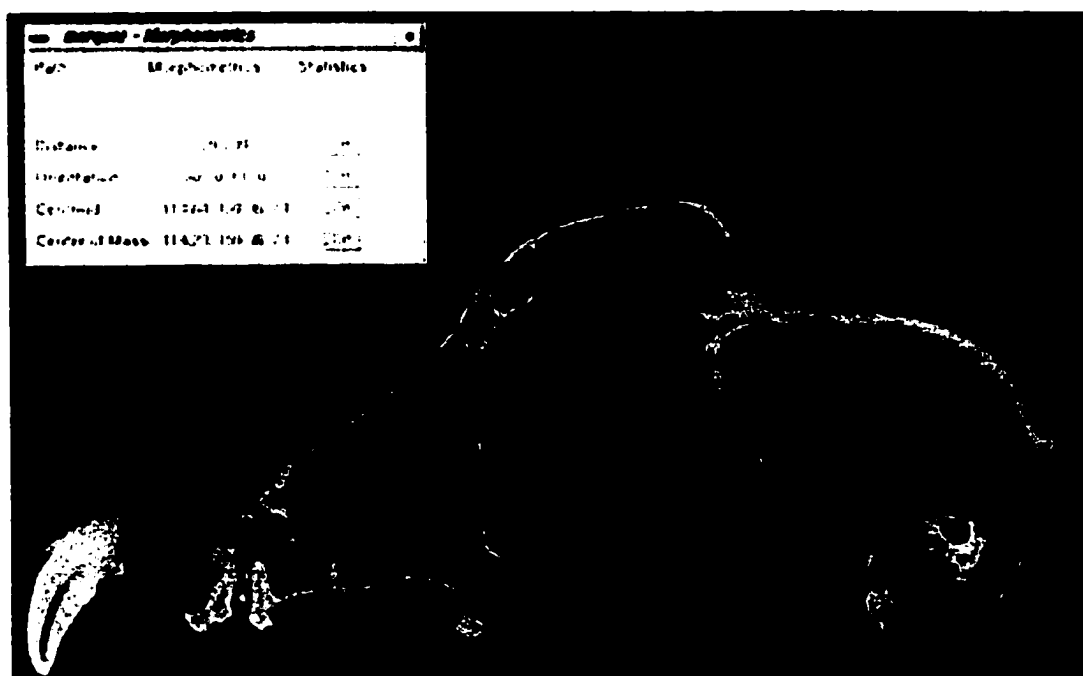


Figure 2-49

Figure 2-50 Highlighted maxillary sinus of the dog *insitu* and extracted. a) Anterior view of maxillary sinus *insitu*. a1) Anterior view of the maxillary sinus extracted. b) Lateral view of the maxillary sinus. b1) Lateral view of the maxillary sinus extracted.

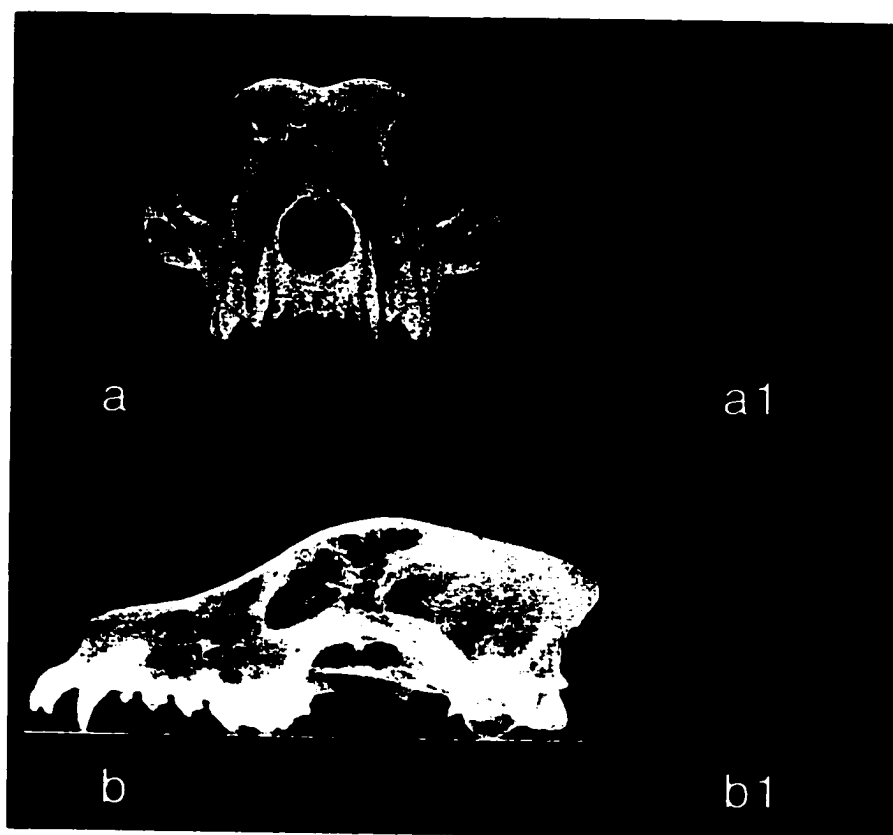


Figure 2-50

Figure 2-51 Lateral view showing frontal sinus (yellow asterisk) with complete (yellow arrow) and incomplete (solid arrowhead) septae.



Figure 2-51

Figure 2-52. The posterior region of the nasal cavity is shown in this frontal view. The nasal cavity floor is demarcated by the hard palate (HP). Note, the transverse lamina (TL) separates the respiratory region (RR) below while above the olfactory region houses the extensive branching of the ethmoturbinates (white asterisk).

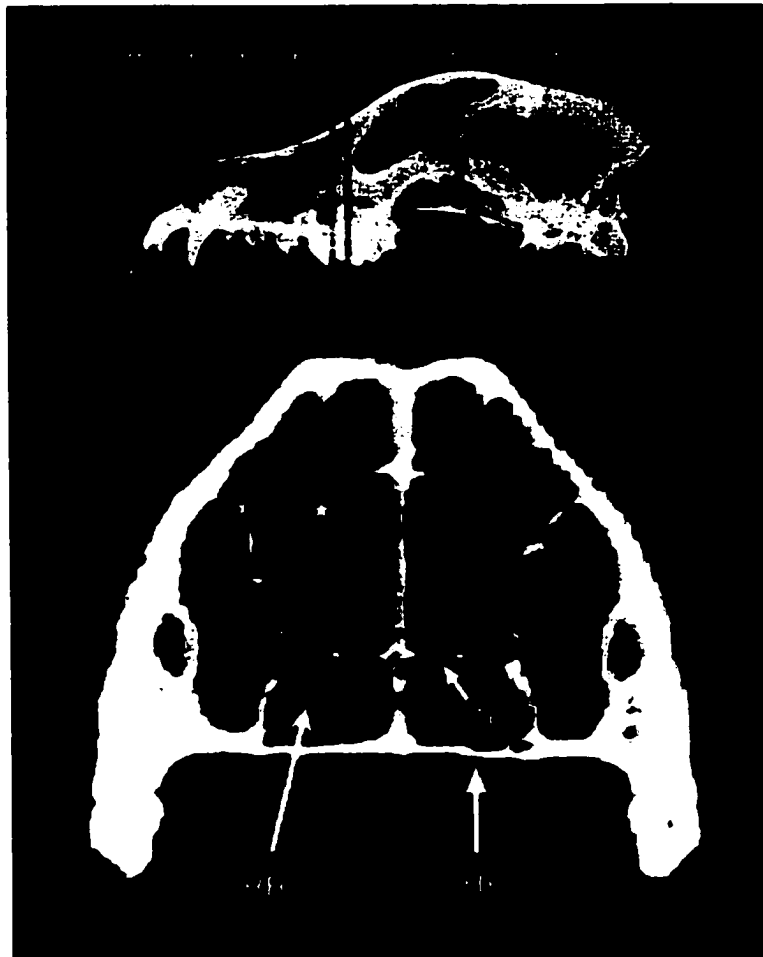


Figure 2-52

2.13. RESULTS FOR THE FOX (*VULPES VULPES*)

2.13.1 CT scanner specifications and method of analysis

Intensity specifications for CT digital capture scanning were as follows:

DFOV – 18.9 cm, Bone resolution, 140 kV, 70 mA, 1 mm slice thickness/1.0 sp.

Specimen was placed in an axial position and anchored by foam blocks, cotton cloths and cloth tape. The scout, or orientation beams were aligned to ensure that the specimen was in the Frankfort horizontal position. All measurements and observations were obtained by the use of multiplanar CT imaging in conjunction with the Microsoft Morphometric tool software program of the NT computer workstation at the Mount Sinai CT scanning facility. All reference window scout images correspond with specified areas designated on the multiplanar CT figures.

2.13.2. General remarks

The specimen was an adult based on molar eruption pattern. The specimen exhibited two paranasal sinuses - the maxillary and frontal. The maxillary sinuses appeared markedly symmetrical and somewhat diminutive while the frontal sinuses were well demarcated exhibiting complete and incomplete septae.

2.13.3. Maxillary sinus – general observations

Maxillary sinus pneumatization was confined within the body of the maxilla with no medial extension into the hard palate and located somewhat posteriorly in the nasal cavity proper. The maxilla forms the dorsal, lateral and ventral walls of the

sinus. The maximum height and width occurs at the coronal plane of the third molar region. The most anterior projection of the maxillary sinuses occurred in the coronal plane at the juncture of M^2 , with the most posterior excavation observed in the coronal plane of M^3 . The floor of the maxillary sinus extended over the molar dentition. The lateral walls of the sinuses at the point of their maximum width were vertically disposed making these cavities appear narrow. Partitions, or septae, were not observed within the sinuses.

2.13.4. Right maxillary sinus

The following observations were made from coronal views with a reference window indicating the corresponding sagittal slice view. The greatest width occurred in the coronal plane at the mesial border of M^3 . A transverse distance of 3.9 mm was recorded. The greatest height was in coronal plane at the distal border of M^3 , with a length of 17.4 mm from the most superior to the most inferior point. From an axial perspective, the greatest anteroposterior length was 22.0 mm. The floor of the sinus nearly approached the level of the nasal cavity floor.

2.13.5. Left maxillary sinus

The lateral and medial bony walls were similar to the right side. The greatest width (4.3 mm) occurred in the coronal plane at the distal border of M^2 (Figure 2-53). The greatest height (18.6 mm) in the coronal plane was measured at the juncture

between M² and M³). From an axial view, the greatest anteroposterior length was 23.4 mm and see Table 6 for summary of maxillary sinus dimensions). The floor of the sinus nearly approached the level of the nasal cavity floor.

Table 2-6 Linear measures of fox's maxillary sinus dimensions

	Right Maxillary Sinus	Left Maxillary Sinus
Greatest Width	3.9 mm	4.3 mm
Greatest Height	17.4 mm	18.6 mm
Greatest Length	22.0 mm	79.2 mm

2.13.6. Ethmoid sinus

No ethmoid sinus cells were identified. The ethmoturbinate branching was extensive and the cribriform plate was curvilinear (Figure 2-54).

2.13.7. Sphenoid sinus

No sphenoid sinuses were detected.

2.13.8. Frontal sinus

Specimen exhibited frontal sinuses encroaching the lateral portion of the frontal bone to the midline of the frontal bone but with no communication with its contra lateral sinus (Figure 2-55).

Figure 2-53 Frontal view of the fox showing maximum width (red line) and maximum height (yellow line) of the maxillary sinus. Yellow arrows are pointing to the extensive branching of its ethmoturbinates.

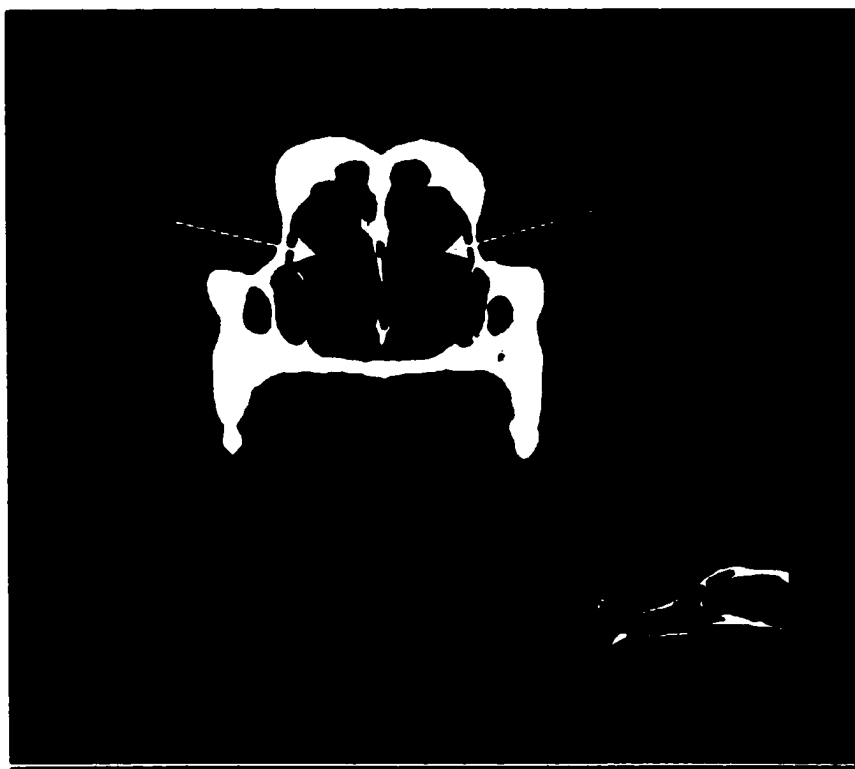


Figure 2-53

Figure 2-54 Frontal view of the fox showing the curvilinear nature of its cribriform plate and how it encircles the anterior portion of the brain (arrows). Note the presence of a transverse lamina (arrowhead).

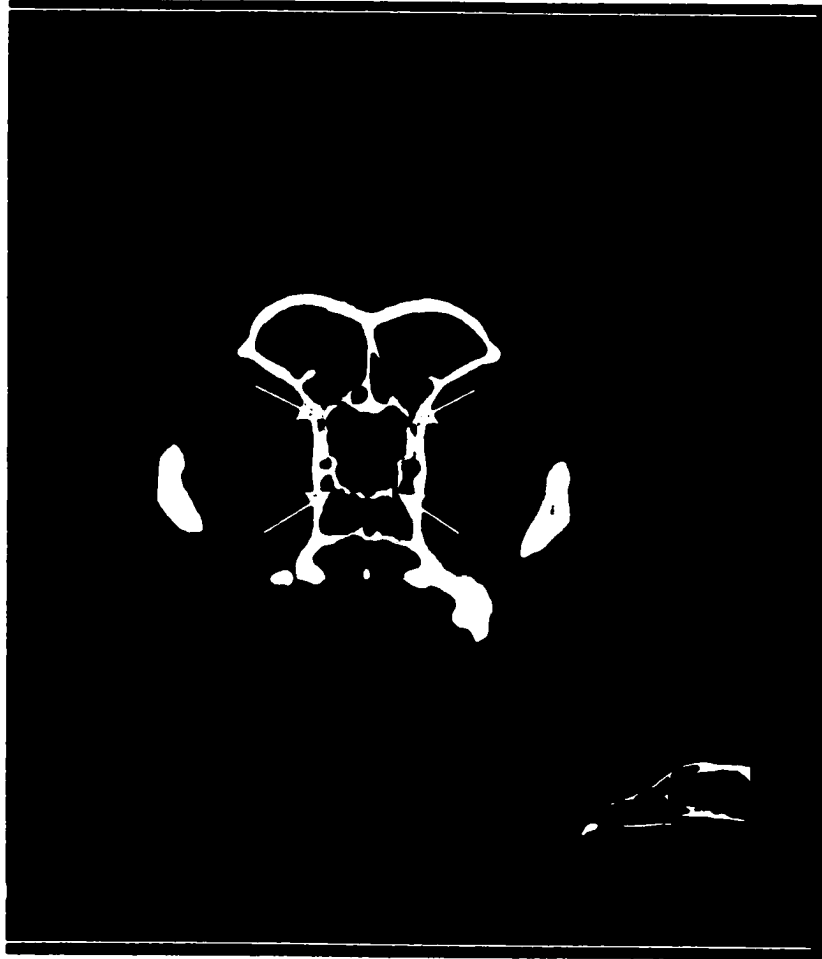


Figure 2-54

Figure 2-55 Lateral (a) and frontal (b) view composite of the fox showing the compartmentalization of the frontal sinus by complete septae.

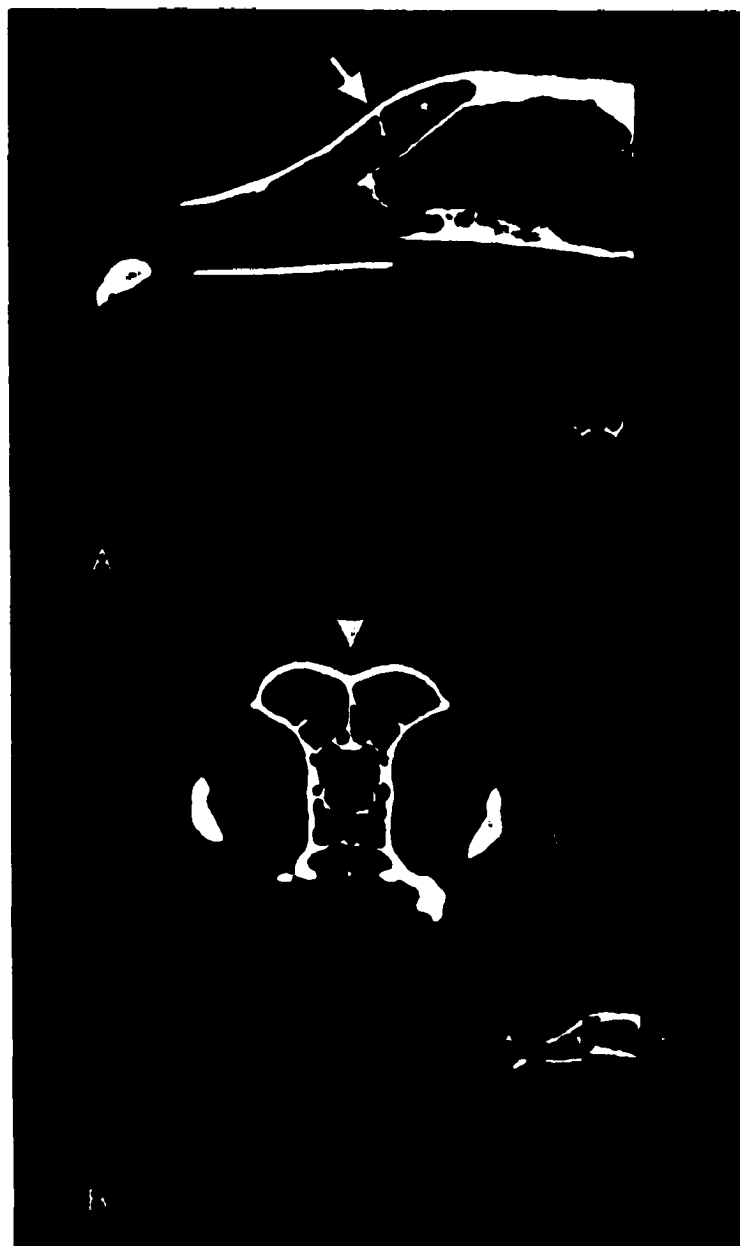


Figure 2-55

2.14. DISCUSSION

This preliminary study using CT analysis of nasal complex and paranasal sinus morphology revealed that there are considerable differences in the morphology of the species studied. The specific reasons for these differences are difficult to ascertain on this limited sample. Although the mammalian specimens used in this study are all considered to be macrosmatic because of their highly developed sense of olfaction, different levels of olfactory acuity may well exist among them.

Since the nasal cavity subserves the function of both olfaction and respiration, mammals classified as macrosmatic would be expected to have their nasal configuration designed in such a way as to reveal this specialization. The basic indicator for the sensitivity of smell lies in the olfactory epithelium which lines a portion of the nasal cavity. Size of the epithelium is the principal indicator of the acuity of the sense of smell. For example, the average surface area of human olfactory epithelium is 10 cm², whereas the surface area of a canine's epithelium is 170 cm². Another factor determining odor discrimination lies in the olfactory receptors, of which, dogs have 100 times more receptor per square centimeter than humans (Bear et al., 1996). However, even without precise knowledge of the histological profile of the olfactory epithelium of the mammalian sample the osteological substrate that serves odor detection could offer insight into the animal's capability of smell.

The olfactory apparatus is principally comprised by the ethmoid bone and its ethmoturbinates which are contained within the upper posterior half of the relatively large snouts of these specimens. Accordingly, variation in the morphological design of this critical skeletal element will determine the level of sensitivity of odor discrimination. While most of these animals demonstrated snout-like prolongation of the nose and mouth, the internal nasal architecture differed widely among them. Consequently, acuity of olfaction could not be predicted by the external craniofacial appearance of the animal. Moreover, no discernable pattern was evident between the presence/absence and size/shape of paranasal sinus morphology and the configuration of the snout within the mammalian sample. Reasons that account for such differences may be that the development of the craniofacial region is olfactory driven in those mammals that places a greater reliance on smell for survival. One advantage of being an omnivore is that it can sacrifice the need for a greater degree of olfactory acuity since their dietary staples vary widely as compared to a carnivore that requires a specific food source. Structural adaptations to increase olfactory proficiency are seen to varying degrees in the species studied by the intricacy of the scrolling of the turbinates, the morphological design of the olfactory plates, and the configuration (planar or curvilinear) and inclination (vertical or horizontal) of the cribriform plate. Moreover, partitioning of the nasal airway into respiratory and olfactory compartments by the formation of transverse bony lamina was noted in certain species in the carnivore sample.

Dietary habits was looked at since upper dentition is intimately related to maxillary sinus morphology given that the floor of sinus covers dental premolar and

molar roots. Again, no clear pattern emerges for the state of paranasal sinuses present and the dental arcade. It was unclear how climate affects the nasal region of the mammals given the limited sample.

CHAPTER 3

ANATOMY OF THE HUMAN NOSE AND PARANASAL SINUSES

This chapter will focus primarily upon the gross structure and development of the human nose and paranasal sinuses. A brief historical treatment for each of the nose and paranasal sinuses will also be presented. The second area of attention is taken to address issues regarding inconsistencies and vagaries in terminology, as these have often been a major source of confusion among those studying the sinuses.

3.1. HISTORICAL PERSPECTIVE

Interest in the human nasal region can be traced back to the Egyptians whose mummification procedures called for a basic knowledge of the anatomy of the passages between the nasal and cranial cavities. References pertinent to the nasal cavities appeared as early as 400 BC, when Hippocrates ascribed the function of the nose to be the reservoir for drainage of mucus from the brain (Stierna and Westrin, 1999). The Greek anatomist Galen made the next major contribution to our knowledge of sinus anatomy 600 years later, although his writings do not mention any of the sinuses by name (see Blanton and Biggs, 1969).

Galen's work was based upon animal models (e.g., monkeys and pigs) rather than human dissections, as the latter methodology was illegal for many centuries (Tange, 1991). The animal research conducted by him perpetuated misconceptions regarding human anatomy for centuries to follow because it was erroneously assumed that the descriptions would be the same. Despite his anatomical errors, Galen remained the unchallenged authority for over a thousand years because of his prestige as an anatomist. His errors were finally revealed when human dissection studies were performed. A leader in this regard was Andreas Vesalius who published, in 1543, the first complete textbook of human anatomy, *De Humanis Corporis Fabrica*. It contains one of the earliest illustrations of the maxillary and frontal sinuses. Among the major anatomical studies that appeared soon afterward were da Vinci's discussion of the maxillary sinus (da Vinci, 1489) and Berengario da Carpi's initial description of the sphenoid sinus (Berengario da Carpi, 1521).

During the 16th century, a major shift occurred away from traditional investigation based on anatomical dissection to philosophical thinking and metaphysical expostulations on the 'existence of being' for the organs of the human body. Most of these works were made by individuals concerned not with detailed, precise anatomy but with theoretical questions addressing functional explanations for the existence of these "hollow" spaces in the cranium (e.g., Bauhin, 1621 and Haller, 1769). The anatomical observations cited by these individuals were not for the systematic assessment of structure, but to buttress their particular functional theories (for discussion see Stammberger, 1989). The middle of the 16th century was populated by medical philosophers who formulated and promoted explanations for the existence of the sinuses. Their ideas were strange, curious, and

bordered on mythological beliefs, with the authors modifying the anatomy to match their philosophies (Stammberger, 1989). Some of these functional theories included: a) a filtering mechanism for air on its way to the brain and ventricles to create the “animus,” or “spiritus vitae;” b) structures containing medullary matter similar to the brain; c) drainage of the brain of its “evil spirits” via the sinuses and the nose; and d) the production of medullary substance to protect the olfactory nerve and provide nutrition to the bone and teeth (Stammberger, 1989). It was precisely this preoccupation with the mechanism of smell that prompted Schneider’s (1655) work on olfaction *Liber de osse cribriformi*. However, his findings were not generally accepted until 200 years later. A statement that best summarizes the prevailing concept during the middle ages about the function of the inner nose and its sinuses is that of Sansovino who in his 1655 work *L’edeficio del Corpore Humano* called the nasal cavity “la cloaca del cerebro” – the drainage pathway of the brain.

It was only in the late 19th century that the first, detailed and systematic anatomic and pathologic description of the paranasal sinuses was published by the great Austrian anatomist Emil Zuckerkandl (1882; 1892a; 1893). His observations and illustrations were so precise and meticulous that they form the foundation for much present day knowledge, and gained Zuckerkandl status as the “father” of modern sinus anatomy (Stammberger, 1989; Lawson, 1991).

During the preantibiotic era in the early 20th century, anatomic studies focused upon descriptions which would improve the operative cannulation and drainage of pathologic sinuses (Schaeffer, 1916a; Myerson, 1932; Simon, 1933; Kasper, 1936; Van Alyea, 1936; Rosenberger, 1938). It soon became apparent that after such treatment,

infection would often recur in the same sinus and spread and infect the other non-treated sinuses. These secondary infections were explained by the intimate anatomic relationships between the paranasal sinuses. This gave impetus to studies on prenatal development to understand sinus interactive anatomy so as to facilitate sinus surgery. This led to the design of a variety of endonasal, transnasal, and external sinus procedures. It was not until the latter part of the twentieth century that technological advances in imaging and instrumentation led to endoscopic sinus surgery, with a primary focus on the role of the ethmoid sinus in recurrent paranasal sinus infection (Schaefer, 1998). Jason Parsons Schaeffer wrote, (1916a) that “the maxillary sinus is often a cesspool for infectious material from the sinus frontalis and certain of an anterior group of cellulae ethmoidales.” This is an example of knowledge lost, only to be rediscovered when interest in the sinuses became renewed by modern sinus surgeons (Wigand et al., 1978; Messerklinger, 1985).

3.2. TECHNOLOGICAL IMAGING ADVANCES

The announcement of the discovery of “X-rays” by Roentgen, in 1895, was received with world-wide enthusiasm and led immediately to its clinical application. A radiograph of the larynx of a cadaver was published the following year by MacIntyre (1896). The advent of plain film radiography provided a considerable improvement in the visualization of the sinuses that had previously been available with transillumination. Subsequently, a stream of technological improvements for the examination of the sinuses followed. In the early 1900’s Dr. Eugene W. Caldwell, an electrical engineer, developed

a motor-driven tilting X-ray table connected with an X-ray tube underneath and a fluoroscopic screen above, a portable X-ray machine, and the first motorized radiograph viewer (Weber, 2000). His contribution to head and neck radiology is recognized by a view of the paranasal sinuses that bears his name, “the Caldwell view”¹ (Berk, 1995). Plain film radiography fueled the development of new surgical procedures. In 1909, with the radiologic advice of Dr. Schüller, Dr. Oskar Hirsch introduced the transsphenoidal approach to pituitary tumors (Weber, 2000). Other notable contributors include the British radiologists, Drs. C. A. Waters and C. W. Waldron, who, in 1914, introduced a projection that defined to greater advantage the paranasal sinuses and facial bones. The “Waters view” is still being used to survey sinus diseases and facial fractures (see Waters and Waldron, 1915).

Further refinements in plain film radiography included the use of contrast medium agents. The first contrast sialogram was performed, in 1912, by Arcelin with a bismuth solution. The use of bismuth salts were later abandoned because of reports of bismuth poisoning (Weber, 2000). Although this technique was used primarily for salivary gland and duct examination, it was employed for investigation of the sinuses. The first nontoxic contrast agent, lipiodol, an iodized oil, was discovered in 1921 by Sicard and Forestier, (Kelves, 1997) and utilized to study the paranasal sinuses by direct instillation (i.e., displacement technique) (Chavda and Pahor, 1996). Technical refinements seen in the last three decades include fluoroscopy with spot imaging, subtraction radiography, and tomography (Weber, 2000).

¹ Dr. Caldwell died of metastatic cancer induced by radiation at the age of 48 as did the many of the early clinical radiologic pioneers (Weber, 2000).

A major shortcoming of plain film radiography is the lack of a detailed depiction of the nasal complex structures because of overlapping in creating a 2-dimensional image (e.g., Márquez et al., 1996a,b). An attempt to improve this initially came in the form of linear tomography² invented by Dr. Ziedses des Plantes of Holland. With this technique, selective tissue planes of variable thickness were captured in detail, with the exclusion of anatomic structures above and below the plane selected. This was achieved by imparting a curvilinear motion to the X-ray tube during exposure, synchronous with motion of the film containing cassette plate in the opposite direction. The shadow of the selected plane remains stationary on the moving film while the shadows of all other planes have a relative displacement on the film and are therefore obliterated, or blurred. The definition achieved of rectilinear tomography was limited by its failure to obscure shadows of linear structures that were oriented in the same direction as the tube-film excursion. This failure in the detailed visualization of anatomic structures caused by reciprocal tube-film movements resulted in the development of circular, elliptic, and hypocycloidal tube motion modifications. The enhanced clarity of these captured images laid the foundation for the next major technological advance in radiographic imaging.

The theoretical framework for computer tomographic imaging (CT) was based on the mathematical principles formulated by the physicist A. M. Cormack, in 1963 and 1964 (Kelves, 1997). Another physicist, Godfrey Hounsfield of Great Britain, provided the link between theory and practical application when he introduced CT scanning technology, in 1972. In the last twenty years, this imaging modality revised the way anatomists and clinicians viewed and defined the fine structure and pathology of the

² Tomography comes from the Greek word *tomos* meaning cutting (section) and *gramma* meaning to write.

sinuses and led to new approaches for the management of sinus disease. CT permits in depth fine visualization and demarcation of both normal and abnormal soft tissue and bone in a defined region. The development of spiral CT in the past few years has allowed a shorter examination time and thinner sections, with the capability of three-dimensional reconstruction. Innovative computer software has permitted the analysis of CT digital data which can be graphically represented three dimensionally. This has promoted a greater understanding of the relationship of the sinus spaces to their contiguous structures and permits precise determination of their morphology and volume. CT has aided the development of functional endoscopic sinus surgery (FESS) by providing detailed analysis of the nasal cavity, especially the lateral nasal wall and ostiomeatal complex.

The next major radiologic milestone was the introduction of magnetic resonance (MR) imaging. This modality provides even greater soft-tissue differentiation and definition of tissue and bone interfaces.

The clinical application of nasal and sinus anatomy has progressed from speculum rhinoscopy to CT with three dimensional reconstruction. The transition from plain film radiography to CT scanning and MR imaging has produced an even greater collaborative interdisciplinary relationship between radiology and otolaryngology over the past century (Noyak, 1997).

Interestingly, Zuckerkandl's precision and accuracy in his description of sinus anatomy a century ago is remarkably comparable to the graphical visualization generated by CT imaging (Stammberger, 1989). Stammberger (1989) and Davis et al., (1996) commented how insightful Zuckerkandl was in illustrating these seemingly new anatomical structures. The congruence of the findings of cadaver dissection with digital

radiologic image capture data on living subjects is testimony to the insight and talent of the traditional anatomists.

3.3. PROPOSED FUNCTIONS OF THE SINUSES

While the last two thousand years has seen vast improvement in the diagnosis and treatment of sinus disease, little investigative interest had been given to sinus physiology until recently. This may have resulted from studies failing to demonstrate a significant physiologic function for the sinuses. While clinical studies by Ingersoll (1906), Skillern (1916), Proetz, (1922) and Negus (1954) proposed hypotheses as to their function, it was only the recent discovery of nitric oxide gas production in the accessory sinuses that indicated an important physiologic role for them (e.g., Lundberg et. al, 1994). Table 3-1 summarizes the plethora of theories ascribing particular functions to these sinuses proposed in the last two thousand years. The various theoretical postulates can be grouped into three categories: architectural; physiological; and a non-functional role. What follows is a brief summary of each hypothesis accompanied by a critical assessment where applicable.

It should be noted that the concept of function is considered controversial in biology. Basically the function of a feature is its action or how it works (Bock and von Wahlert, 1965). It must be emphasized that any aspect of purpose, or design must be removed from any definition of function. Function is used in the sense of physical and chemical properties of the feature and in the sense of the role the feature has in the life of the organism. Many workers in functional anatomy have utilized both meanings as absolute equals when in fact they are not. Accordingly, the distinction between

biological role and functional role will affect the wording of many classical works. With this caveat in mind, the following proposed “functions” were evaluated.

Table 3-1. Historical overview of hypothesized functions ascribed to the paranasal sinuses

Theoretical Function	Authors
1) To Lighten the skull	Galen (circ 130 AD); Cleland, 1862; Paulli, 1900; Schoennemann, 1904; Onodi, 1905; Nemours, 1931; Shea, 1932; Moller, 1969; Buhler, 1972, 1986; Crelin, 1976; Schummer et al., 1979; Davis, et al., 1996
2) To aid in storing a medullary substance	Bartholin (1669) (cited in Libersa et al., 1981)
3) To increase surface area of olfactory mucosa	Braune and Clasen, 1877
4) To effectuate even distribution of inspired air to which aids in olfaction	Strickland, 1932
5) To serve as an adjunct in air conditioning of inspired air	O'Malley, 1924; Eckert-Mobius, 1933; Sato, 1938; Proetz, 1932,1941
6) To humidify inspired air via its mucus secretions	Gannon et al., 1997
7) To impart resonance to the voice	Cleland, 1862; Bignon, 1889; Zuckerkandl, 1892; Dieulafé, 1906; Hartz, 1909; Underwood, 1910; Mosher, 1922; O'Malley, 1924; Eckert-Mobius, 1933; Wegner, 1958; Dyce et al., 1987; Leakey and Walker, 1997.
8) To aid in facial growth and architecture	Eckley, 1904; Dieulafé, 1906; Moss and Young, 1960; Enlow, 1968, Blaney, 1986; 1990; Moore and Persaud, 1993; Davis et al., 1996
9) Part of normal skull pneumatization	Witmar, 1995,1996, 1997a, 1997b
10) Function as pillars for dispersal of masticatory forces	O'Malley, 1924; Badoux, 1966; Enlow, 1968; Preuschoft et al., 1997

- 11) Occupies space between the mechanical bony pillars**
- 12) To provide protection for the brain**
- 13) To assist in regulating intranasal pressure**
- 14) To serve as respiratory reservoirs for mucus secretions**
- 15) To assist in flotation or at some point in time
in its phylogenetic heritage**
- 16) To produces nitric oxide**
- 17) Allow functional decoupling of inner and outer tables
by occupying intervening space**
- 18) To provide thermal insulation for CNS and sense organs**
- 19) To widen the skull base for the support of the large palate to
accomodate the permanent dentition**
- 20) Exists as evolutionary remains of useless air spaces**

DuBrul, 1988; Sicher, 1952
 Riu et al., 1960; Geist, 1971; Schaffer and Reed, 1972;
 Davis et al., 1996
 Coffin, 1905; Neumayer, 1901; Frers, 1909; Suarez,
 1952; Del Cañizo, 1959; Rice and Gluckman, 1995
 Alger, 1938
 Bignon, 1889; Proetz, 1953; Wegner, 1958;
 Rhys Evan, 1992, 1997
 Lunberg et al., 1994
 Paulli, 1900; Weidenreich, 1924, 1941; Moller, 1969;
 Buhler, 1970, 1972
 Bignon, 1889; Bremer, 1940; Proetz, 1953; Verheyen, 1953
 Keith, 1902a, 1902b; Underwood, 1910.

 Ingersoll, 1906, 1922; Negus, 1957a, 1958; Takahashi, 1983;
 Lund, 1988

3.3.1. To Lighten the skull

This is the predominant theory among the majority of the investigators surveyed. That sinuses do actually lighten the skull is indisputable (Proetz, 1922). However, Braune and Clasen (1877) calculated that if the sinuses were replaced with solid bone, the weight of the head would be increased by only one percent. Support for this comes from the experimental electromyographic study of Biggs and Blanton (1970) which demonstrated that the head showed no statistically significant compensatory muscle activity when added weights were placed on the facial region, mimicking the supposedly “filled in” sinuses. One cautionary note is that these studies do not consider the fine adjustment of the head with its muscular and neurovascular configuration to its osteological substrate. These investigations were conducted on stationary subjects, thus the conclusions drawn ignored such critical factors as inertia, angular momentum and equilibrium, which are intimately associated with flight and locomotion. Through natural selection, the finely tuned morphology of the organism adapts to changes in its weight distribution, energy consumption and natural gait, to increase its survivability (e.g., hunting for prey, eluding hunters, and securing water resources). This consideration did not escape Schwalbe (1887) who commented that the head is so evenly balanced that any slight increase would tend to interfere with proper equipoise. The implication that a “one per cent” gain in weight of the head of an animal is inconsequential completely ignores evolutionary biology and the laws of physics.

3.3.2. To aid in storing a medullary substance

This proposal was cited in Libersa et al. (1981) who reported the claim of Bartholin (1669) that the sinuses were used as a storage for medullary matter. Medullary matter was thought of to be of a nutrient nature feeding the delicate nerves that subserve the nasal region (Stammberger, 1989).

3.3.3. To increase surface area of olfactory mucosa

This theory originated with Cloquet (1830) who incorrectly stated that the human maxillary sinus was lined with olfactory epithelium. This hypothesis was furthered by Ingersoll (1906) who carefully established the comparative anatomy of the olfactory organs of many micro- and macrosmatic mammals. Negus (1957, 1958) concurred with Ingersoll and suggested that the ancestral function of the sinus spaces was to house the olfactory conchae. The transverse lamina present in keen-scented mammals serves to separate the olfactory region from the nasal cavity proper. The creation of a system of ethmoturbinals (i.e., olfactory plates) increases the surface area present for contact with inspiratory air thus serving as an adjunct for olfactory analysis.

3.3.4. To effectuate even distribution of inspired air which aids in olfaction

This theory is an extension of theory (3.3.3.) which is based on the erroneous assumption that the sinuses are lined with olfactory mucosa. As such, the multiple

sinuses in humans were thought to be strategically placed for the purposes of reception of inspiratory airflow which would distribute odorous particles for olfactory analysis. The theory that the sinuses house certain elaborate organs of smell is not supported and there is no evidence of any vestiges of these special sense organs in humans.

3.3.5. To serve as an adjunct in air conditioning of inspired air

Although Davis et al. (1996) proposed that the ethmoidal labyrinth appears to have been designed to maximize the mucosal surface area, there exists no experimental evidence that has shown the sinuses to be efficient in this regard. With regard to modification of air temperature, there is minimal air circulation and air exchange even with large and unobstructed ostia between the nasal cavity and the sinuses. Braun and Clasen (1877) have demonstrated that the air pressure varies not more than 8 mm to 12 mm between inspiration and expiration lending support to a non-functional aspect of the sinuses in this regard.

3.3.6. To humidify inspired air via its mucous secretions

Gannon (et al., 1997) contended that the sinuses, principally the maxillary sinus mucosa, can serve a humidification role for processing of the inspiratory airflow. They based this assertion on the strategic position of the maxillary sinus in hiatus semilunaris where it drains into the path of the inspiratory airflow. Although the main role of humidification falls on the nasal cavity mucosa, the production of mucus by the sinuses

may serve as an adjunct for humidifying air in environmentally challenging conditions (i.e., cold and dry climates).

3.3.7. To impart resonance to the voice

The origins of this theory date back to Spiegelhel (1645) and Voltolini (1889) who stated that the sinuses act as resonators – modifying and amplifying the sounds produced at the glottis. At first the theory was not widely accepted but recent investigations have reaffirmed a possible resonating function of the sinuses. Recently, Leakey and Walker (1997) have stated that whatever other functions the sinuses may serve there is no doubt that they act as sound resonators. The study by Dang and Hong (1994) experimentally demonstrated with magnetic resonance imaging that the sinuses serve to effect the timbre of the voice. Howell (1917) reported that the Maori of New Zealand possessed “peculiarly dead voices” and also exhibited an under-development of the accessory sinuses. Wegner (1955/56) also noted that the howler monkeys (i.e., *Alouatta sp*) famous for their “howling” prowess exhibit particularly large paranasal sinuses. However, Proetz (1953) offered a counter-argument with the observation that animals with loud voices such as the lion have small sinuses. Similarly, Negus (1958) noted that giraffes, which possess very large frontal sinuses, are usually silent. Flottes (et al., 1960) also reported that following sinus surgery alteration of the voice of patients has not been observed.

3.3.8. To aid in facial growth and architecture

An active role in the growth and development of the splanchnocranium has been proposed and mentioned in human anatomy textbooks. These sources cite that facial growth lags behind cranial growth, with compensatory development occurred later, with the expansion of the paranasal sinuses and eruption of the teeth. Moss and Young (1960) regarded the role of the sinuses to serve as functional matrices that can actually displace bone. Whether they are morphogenetically “inert” structures that are passively “sucked” into retreating bones during ontogeny is still controversial (Proetz, 1953).

3.3.9. Part of normal skull pneumatization

Witmar (1997a) is the principal proponent of the theory that the sinuses may serve no known function but are merely the result of the interplay of two dynamic developmental forces – the intrinsic expanding nature of the sinuses, and the phylogenetic constraints of the organism. He characterized the paranasal sinuses as “opportunistic pneumatizing machines” (Witmar, 1997b). The constraints impose local biomechanical loading regimes that stimulate bone deposition to maintain structural strength. The result is a compromise between these two competing intrinsic forces. An implied consequence is optimal strength with minimal materials eliminating the need for natural selection. Selection could act secondarily to hone some positive function in particular cases, but basically Witmar believes that the sinuses may have no biological role at all (Witmar, 1997b).

3.3.10. Function as pillars for dispersal of masticatory forces

Ascribing the architectural function of providing maximum strength with minimum materials originates from a central axiom in vertebrate biomechanics. Preuschoft, Witzel, and Witte (1997) were the most recent investigators to suggest that the sinuses are best understood in a mechanical context as “shells” with expanded surfaces, thin-walls, and stress bearing in only two dimensions. Sinuses that take the form of a honeycomb construction such as the ethmoid sinus system are capable of resisting multi-directional forces by dissipating energy over large areas. An explanation as to why a particular species develops solid struts while another closely related species forms a shell, or an assemblage of honeycombs, remains forthcoming.

3.3.11. Occupies space between the mechanical bony pillars

A related hypothesis suggests that the sinuses represent functionless “spaces between the braces,” occupying the area between biomechanically important bony pillars (DuBrul, 1988, pg. 49). It contends that biomechanically unstressed bone has been replaced not by marrow but by an air-filled diverticulum which reduces the weight of the structures.

3.3.12. To provide protection for the brain

The function of shock absorption from facial trauma has been assigned principally to the expanded frontal sinuses of ungulates and bovids, although Riu et al. (1960) also suggested it for humans. Davis et al. (1996) stated that the ethmoidal labyrinth was designed to collapse, thus absorbing the energy of trauma and protecting the eyes and brain. This hypothesis conceives the sinuses having been strategically placed between the site of impact loading and the brain and/or sense organs. Schaffer and Reed (1972) also proposed a spring-like function of the bony septa within the sinuses to assist in dissipating the stresses of impact. Recently, Jaslow and Biewener (1995) experimentally investigated impact loading in goats and found that the sutures were more effective in absorbing shock. Witmar (1997a) is critical of their study since it does not address the potential role of pneumatic spaces in stress absorption. Even if shock absorption is a function of the frontal sinuses in bovids, which is far from established, it does not appear to apply to pneumatic amniotes. As Negus (1957) noted, it does not apply even to the “horned” ungulates as cervids have very small frontal sinuses which are not situated between the antlers and the braincase.

3.3.13. To assist in regulating intranasal pressure

Coffin (1905) was the first to propose this theory, stating that the development and expansion of the sinuses was caused by variations in air pressure which induced resorption of the cancellous tissue. As evidence, it was cited that sinus development

begins at the age when children begin blowing the nose. In 1909, Frers concluded following study of the postembryonic development of the paranasal sinuses, that intranasal pressure changes affected sinus development (Frers, 1909). In support of this he noted that the principle growth of the sinuses occurred after the onset of respiration, the direction of the inspiratory and expiratory streams in relation to the anatomical formation of the nose, and concluded that sinuses were similar to the pulmonary alveoli in being influenced by air pressure (i.e., alveoli of lungs). Frers (1909) also mentioned the study of Neumayer (1901), which demonstrated changing pressure in the sinuses in response to the negative pressure of inspiration and the positive pressure of expiration. The German otolaryngologist, Gustave Killian, disagreed with all of Frers' points and attributed the secondary enlargement of the sinuses to underlying phylogenetic influences (Killian, 1909). Del Cañizo (1959) contended that the sinuses served as regulators of intranasal pressure by dissipating the pressure forces brought on by violent sneezing, or nose blowing.

3.3.14. To serve as respiratory reservoirs for mucous secretions

Alger (1938) was the only sinus investigator to propose that the function of the sinuses was as a respiratory reservoir for mucus secretions. He stated that in patients with acute rhinitis, mucous secretions accumulated in the sinuses because of the negative pressure that resulted from blowing of the nose violently. Alger (1938) claimed that without the sinuses these secretions would pour out of the nose during the night "saturating the pillows," and produce a dermatitis from the copious drainage. He also cited the danger of

aspiration pneumonia during sleep, however, Alger provided only anecdotal rather than experimental evidence.

3.3.15. To assist presently in flotation or at some point in time in its phylogenetic history

The otolaryngologist Rhys-Evans (1992) is the principle proponent of this theory, stating that an understanding of the biological role of the sinuses must be appreciated from a phylogenetic perspective. He contended that if the existence of the sinuses can be explained and shown to be related to some adaptive function, then their susceptibility for sinusitis would be better understood. Employing a comparative sinus investigation would be most appropriate but limiting the sample to only great apes would not because the time period for the last common ancestor would still be relatively recent to properly explain the existence of the sinuses. Rather, the investigation should take place much earlier at the time when apes receded from the savanna and some took to arboreal environments while others sought refuge in water environments. The so-called Aquatic Ape hypothesis proposed by Morgan is based on this principle (Morgan, 1982). Rhys-Evans (1992) extended Morgan's theory viewing the sinuses as a remnant, or carry over from an aquatic adaptation which provided buoyancy for protection of the airway for these apes.

3.3.16. To produce nitric oxide

The discovery within the paranasal sinuses of the production of nitric oxide (NO), a potent neurotransmitter with profound effects on the pulmonary vasculature and tissue oxygenation, as well as carbon monoxide, another aerocrine messenger with a strong local influence on the inflammatory process, has altered the traditional explanations of sinus physiology. It has been shown that NO is continuously released into the upper airway during normal breathing and follows the airstream into the lungs with each inhalation. The autoinhalation of NO contributes to the regulation of pulmonary blood flow (Gerlach et al., 1994), and plays a role in host defense (Lundberg et al., 1996). Lundberg (et al., 1995) demonstrated that large amounts of NO are produced in the human paranasal sinuses. The fact that mammals without paranasal sinuses have a low NO concentration in the exhaled gas of the nasal airway further lends credibility to the concept that the sinuses have a significant role in respiratory physiology (see Márquez et al., 2002).

3.3.17 Allow functional decoupling of inner and outer tables by occupying intervening space

One of the early proponents of the theory that the sinuses allow a functional decoupling of inner and outer tables by occupying the intervening space was by Paulli (1900b) who applied it to mammals. Weidenreich (1924 and 1941) subsequently applied this hypothesis to humans. The theory proposed that the external and internal bony

surfaces served different functions. The outer table was for muscle attachments and the inner table for housing an organ. It is unclear whether an epithelial diverticulum actively separates the bony tables, or that it simply enters the space between the diverging lamellae.

3.3.18. To provide thermal insulation for CNS and sense organs

This theory was originally proposed by Proetz (1953) who likened the paranasal sinuses to “an air-jacket about the nasal fossae closely resembling the water jacket of a combustion engine” (Proetz, 1941, p. 14). Flottes et al. (1960) were critical of this concept stating that polar bears should then possess sinuses whereas brown bears should not, since the latter live in warmer climates. Further contradiction to this theory comes from the works of Koertvelyessy (1972) and Tillier (1975) who noted that Eskimos often possess no frontal sinus while sub-Saharan populations exhibit large frontal sinuses. An extension of this theory was proposed by Dean (1988) who postulated that a thermoregulatory mechanism involving the mucous membrane of the nasal region existed which serves as a cooling agent for brain temperature. Scott (1954) and Hillenius (1992, 1994) hypothesized that the nasal mucous membrane had a role in heat loss from the body. Air flowing over the moist nasal mucous membrane was conceived as cooling the venous blood within the nasal mucosa through the latent heat of vaporization. Venous blood from the scalp, midface and nose communicates with the cavernous sinus intracranially through the ophthalmic veins and the pterygoid venous plexus. The warmer arterial blood in the carotid artery supplying the brain passes through the

cavernous sinus for part of its course in the middle cranial fossa. By this mechanism heat is exchanged with the cooler venous blood from the nose and face, and brain temperature is regulated through the venous return to the cavernous sinus (Dean, 1988). Koppe (et al., 1999) also asserted that the widely assumed purely structural role for the paranasal sinuses is incorrect, with the real function of these spaces directly related to the upper respiratory tract, possibly to aid brain thermoregulation.

3.3.19. To widen the skull base for the support of the large palate necessary to accommodate the permanent dentition

Inspired by the work of Kyle (1899), Keith (1902a) tracked the growth of the maxillary sinus and the surrounding bones and noted the intimate relationship between these morphological structures. The growth trajectory of the sinus continues downward in adult life to a point where the apices of the teeth are separated from its floor by bone of varying thickness, or just by the sinus lining mucosa (Dayal et. al., 1976). This relationship explains the ability of dental disease processes to involve the maxillary sinus and how the retroverted position of the crowns of unerupted third molars are implanted in the posterior segment of the maxilla. Keith (1902a) noted that the expansion of the maxillary sinus resulted from the interplay of the osteoblastic deposition and osteoclastic resorption of bone and was not related to the physical pressure exerted by air within the nasal cavity. He added, its growth “is peculiarly adapted for the purpose of making room for, and bringing into position, the upper molar dentition” (Keith, 1902a, pg. 533). Underwood (1910) was in agreement and stated that the normal anatomy of the maxillary

sinus was largely governed and modified by the development, eruption and arrangement of the molar deciduous and permanent dentition. In this view, the maxillary sinus should be regarded as an adjunct of the dental system.

3.3.20. Exists as evolutionary remains of useless air spaces

Negus (1958) proposed that the sinuses are functionless evolutionary remnants of once functional structures. He considered them as “unwanted” spaces left over after the reduction of the once extensive olfactory nasal conchae. Witmar (1997a) cautioned against the use of the term “spaces” when referring to sinus function as something empty and functionless. He stated that ascribing a hypothetical function to a space, perhaps as a resonating chamber, a shock absorber, a flotation device, a mucus reservoir, an insulator, a useless void between important pillars or as skull tables was thinking in terms of postcranial pneumaticity and was placing a major emphasis on the spaces rather than what lined their walls. Witmar (1997a) concluded that viewing the sinuses as empty bony spaces has misled investigators. He further stated that investigators who suggest a non-functional role to these “spaces” are probably advocating the safest and most conservative position, leaving the burden of proof to other workers that they perform a function.

3.4. MATERIALS & METHODS

Gross anatomic descriptions were undertaken on 90 cadaveric adult human heads at Mount Sinai School of Medicine. Sixty of these consisted of heads midsagittally sectioned for observation and endoscopic visualization by surgeons at the Annual Comprehensive Sinus Surgery Course held at Mount Sinai School of Medicine under the direction of Dr. William Lawson. Twenty one of the heads were used solely for endoscopic visualization, partial and complete turbinectomies as well as other surgical procedures. Nine heads were untouched and provided to me whole.

Progressive dissection from midsagittal plane to lateral aspects of the skull were done for all midsagittal sectioned heads. Nasal complex area was visualized endoscopically in all the whole heads. Nine whole head specimens were sectioned in the coronal plane at intervals of 1.5 cm from the mid-orbit through the sphenoid sinus region. CT scans are included in this chapter for comparative purposes from a preliminary and ongoing study of the common chimpanzee (*Pan troglodytes*, Cat. No. 51382 and *Gorilla gorilla gorilla* Ca. No. 72895 both from American Museum of Natural History) as well as some of our human specimens.

3.5. ETHMOID SINUS

3.5.1. Anatomy and Historical Background

A study of the nasal complex dates back to the time of Hippocrates, in the 5th century BC. The Hippocratic treatise of *Prognostics* remained the most influential

medical works for centuries (Bowman, 1986). Hippocrates considered the function of the nose to be drainage of the excesses of the brain. The next significant contributor was Galen who considered the nose as the primary “respiratory instrument” (*De usu partium*, Book XI, Chapt. 11).

Inheriting the concept of brain breathing that was well rooted in the medical literature, Galen searched for the presence of channels connecting the brain to the nostrils. Three functions were ascribed to these channels. The primary function was to aid in the respiration of the brain; a second was olfactory in odor recognition by the brain; and the third involved “the evacuation of the residues” from the brain. The ancient physicians believed that the brain discharged under stress large quantities of residues, referred to as “rheum, or “coryza”. Galen’s contemporaries called this discharge from the brain “mucus” (*De usu partium*, Book VII, Chap. 6).

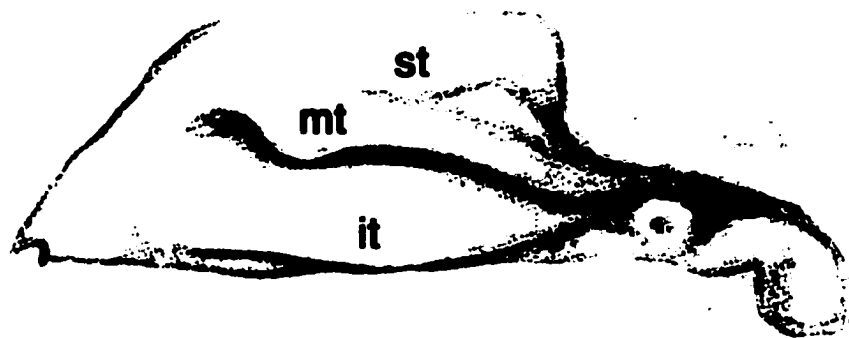
He likened the bone to a sponge and named it *spongoid* because of its porous nature which permitted the passage of air and odorous vapors from the nose to the brain and drained residues downward from the brain. The concern with “brain breathing” led Galen to assign another function to the ethmoid – moderation of the temperature of air entering the brain. He claimed that cold air if allowed to enter the brain directly would “chill it excessively and endanger life itself” (*De usu partium*, Book VIII, Chapt. 6).

Later anatomists, such as Vesalius, adopted the terms *ethmoid*, or *cribriiform*, because of its sieve-like structure (Weir, 1990). The honeycomb appearance of its air cells, combined with its intricate passageways and blind alleys, have led investigators to refer to this bone as an ethmoid labyrinth (Blanton and Biggs, 1969). Van Alyea (1939) stated that the very name “ethmoid labyrinth” implied structural intricacy.

The ethmoid bone has been considered the “keystone in the sinus system” (Terrier, 1991) because each paranasal sinus drainage pathway is through, or adjacent to, its lateral segment. The ethmoid along with the maxilla, inferior concha, lacrimal and the vertical process of the palatine bone contribute to the intricate and irregular surface of the lateral nasal cavity wall (Skillern, 1923

The extensive fetal developmental studies by Schaeffer (1910c, see also 1912a, 1912b, 1920) showed no morphologic changes on the lateral nasal wall to occur until the thirty-eighth to fortieth day of prenatal growth when two shallow grooves appear above and below the region where the inferior nasal conchae, or maxilloturbinal, eventually develops (Figure 3-1). Mesenchymal differentiation about the inferior nasal conchae produces a more prominent fold of the concha and accentuates these grooves, or furrows. The developing folds are considered the primal event in conchal formation, representing the future inferior and middle meatus. Between sixty-three to seventy days of prenatal development, six major furrows develop along with their corresponding ridges, or folds, called the ethmoturbinals (i.e., turbinates arising from the ethmoid). However, not all of these folds and furrows persist during the development of the fetus. From the seventh month to term, only three to five ethmoidal

Figure 3-1. Parasagittal view showing mucosal swellings and evaginations of the future concha of the right lateral nasal cavity wall in a 190-day week old fetus. Note the rudimentary nature of the superior nasal turbinate (*st*), middle nasal turbinate (*mt*) and inferior turbinate (*it*). (Courtesy of Bridget Thomas McKnight, American Museum of Natural History).

**3-1**

Conchae, each with a corresponding intervening meatus are observed. After birth, because of fusion (Negus, 1958), or obliteration (Schaeffer, 1910c), only two or three ethmoidal conchae persist (e.g., middle, superior, or supreme ethmoidal conchae - see Schaeffer, 1920). Although Santorini (1724) was the first anatomist to describe all three ethmoidal conchae, the following commentary by Schaeffer (1910c, p. 614) illustrates the confusion found in the literature regarding the “typical” number of conchae found present at birth:

“Books generally describe and picture two ethmoidal conchae as the typical number, and apparently would have us think that three ethmoidal conchae are rather exceptional.”

In two large cadaver studies, both Schaeffer (1910c) and van Alyea (1939) showed that a supreme conchae was present in 62.5% and 67% of the subjects studied, respectively. Zuckerkandl (1892b) detected a supreme conchae in 80% of his 120 subjects. In contradistinction, Lang and Sakals (1981) reported only 17% of their subjects as having a supreme conchae, and Bingham and colleagues (1991) found no supreme conchae in their material. Consequently, the typical number of ethmoidal conchae present remains unclear.

The first primary furrow of the lateral nasal wall is located between the first and second ethmoturbinals, sometimes referred to as the first interturbinal furrow. The first ethmoturbinal (Figure 3-2) is regarded by most authors as the equivalent of the nasoturbinal found in higher mammals, including New World monkeys (e.g., Howler monkey), and the lesser and great apes (e.g., Gibbons and Orangutans) (see Paulli, 1900; Schaeffer, 1920; Cave and Haines, 1940; Moore, 1981; Stammberger, 1991). In humans,

Figure 3-2. Parasagittal schematic drawing of the lateral nasal cavity wall of an Old World monkey showing inferior turbinate (*IT*), the nasoturbinal (*NT*), middle turbinate (*II*), and superior turbinate (*III*). (Courtesy of Bridget Thomas McKnight, American Museum of Natural History).

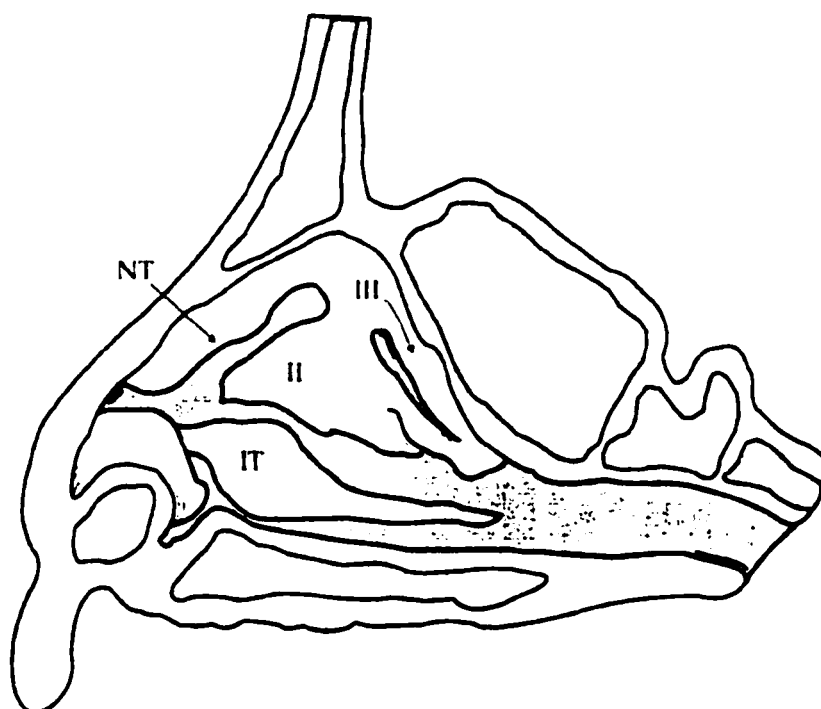


Figure 3-2

the nasoturbinal regresses during later development and never fully evolves into a permanent turbinate. The ramus descendens of this “failed” first ethmoturbinal becomes the uncinate process, and the ramus ascendens becomes the agger nasi, both of which are important landmarks and will be discussed later. The appearance of the first furrow is also an important developmental stage because its descending anterior region becomes the ethmoid infundibulum and the ascending region becomes superiorly the frontal recess. The former is the drainage pathway of a number of the paranasal sinuses. The frontal recess undergoes further development, with additional furrows appearing, or what Kasper (1936) called “pits,” which are outgrowths of epithelium that appear as spherical excavations. Pneumatic invasion of the frontal bone from one of these pits in the frontal recess results in the formation of the frontal sinus (for further discussion see Frontal Sinus section below).

At birth, the ethmoid sinus consists of anterior and posterior divisions. At that time the fluid-filled ethmoids are difficult to recognize on routine radiography (Wasson, 1933). Wolf and coworkers (1993) reported the dimensions of the newborn’s ethmoid sinus system to be 8 mm to 12 mm long (i.e., anteroposterior length), 1 mm to 5 mm high (i.e., superoinferior height), and 1 mm to 3 mm wide (i.e., medial-lateral width). They also found the anterior and posterior ethmoid air cells to be complete in number, although not in size in adult terms. Other studies have confirmed their findings (e.g., Pransky and Low, 1996). By 1 to 4 years of age, the ethmoids have rapidly expanded to 12 mm - 21 mm long, 8 - 16 mm high, and 5 mm - 11 mm wide. The ethmoid labyrinth may be consistently visualized by plain film radiography after the first year postpartum, but only

if the air-filled divisions of the ethmoid sinus are well developed (Shapiro and Jantzen, 1960). At 4 - 8 years of age, the ethmoid sinus system is 18 - 24 mm long, 10 mm - 15 mm high, and 9 mm - 13 mm wide (Wolf et al., 1993). By the twelfth year, the ethmoids have reached nearly adult size, with expansion during puberty primarily involving the bones outside the ethmoid capsule (Van Alyea, 1951).

Architecturally, the ethmoid sinus has been divided into two segments (see discussion in Shambaugh, 1907). During development, the attachments of the various bony structures arising from the ethmoid (e.g., conchae, uncinate process) to the lateral wall are formed by several ground plates, or *basal lamellae* (Figures 3-3 through 3-9). Although the lateral attachments of these lamellae end abruptly, their medial aspects project beyond the labyrinth to form prominences that extend into the nasal cavity. The most anterior of these lamellae is the lateral extension of the uncinate process. The *second lamella* is referred to as the plate of the bulla because its extension into the nasal cavity forms the bulla ethmoidales. The *third lamella* serves as the attachment of the middle turbinate. This is an important anatomic structure, demarcating the division between the anterior ethmoid cells from the posterior cells and directing the drainage patterns of these air cells into the middle and superior meatus, respectively. It is also clinically significant as it is considered a natural boundary to the spread of infection into the posterior ethmoid, and serves as the posterior landmark in anterior ethmoidectomy (Seydel, 1891)(Figure 3-10). As seen in Figures 3-3 to 3-9 and 3-11, this third lamella can be divided into three segments, with the anterior one third having a horizontal orientation and attaching superiorly, the middle third considered the vertical portion coursing obliquely posterior, and the posterior one third assuming an inferior horizontal

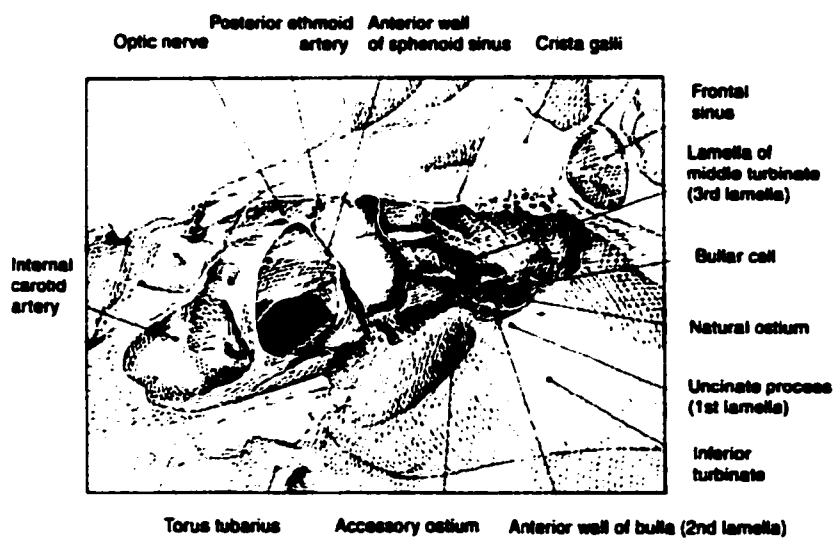
position and attaching laterally. The physical attachment of this basal lamella in three different planes (i.e., superior, vertical, and horizontal) provides much of the structural support of the middle turbinate (Rice, 1995). When this bony plate is removed during posterior ethmoidectomy, the middle turbinate loses its stability (Schaefer, 1998). The ethmoid air cells during development tend to expand to occupy all available space, a phenomenon which Seydel (1891) has called “the struggle for space of the ethmoid.” This results in air cells impinging upon and perhaps distorting the osseous barrier, but the lamella always remains intact and prevents intermingling of cells (Van Alyea, 1939; Stammberger, 1991) (Figure 3-12).

Another important variation in ethmoid anatomy is the *lateral sinus*. This space is bounded laterally by the lamina papyracea, posteriorly by the lamella of the middle turbinate, anteriorly by the posterior aspect of the bulla ethmoidalis, and superiorly by the fovea ethmoidalis (Figures 3-6 and 3-10). When the second lamella does not extend to the fovea ethmoidalis, the sinus lateralis continues anteriorly to the frontal recess. This gives rise superiorly to a space known as the *suprabullar furrow*, or *suprabullar recess*, which communicates with the middle meatus. The *fourth lamella* is at the attachment of the superior turbinate, and when a supreme turbinate is also present, a *fifth lamella* arises lateral to this turbinate.

Figure 3-3. A: Extensively pneumatized sphenoid and ethmoid sinuses. **B:** Several basal lamellae are demonstrated along with both natural and accessory ostia of maxillary sinus. This and the following plates that include a human dissection above and pen drawing below are from Márquez et al., in *Minimally Invasive Surgery of the Head, Neck, and Cranial Base*, (eds. Wackym, Schaefer, and Rice) 2001.



3-3A



3-3B

Figure 3-3. (continued) C: Enlargement of **A** shows sphenoid and ethmoid sinuses. The medial aspect of optic nerve is exposed by ethmoid cells (similar to Onodi cell) and the internal carotid artery is traversing the lateral wall of the sinus. **D.** Extensive pneumatization of the ethmoid bone and extension of posterior ethmoid cells into the sphenoid bone are well demonstrated in this specimen.

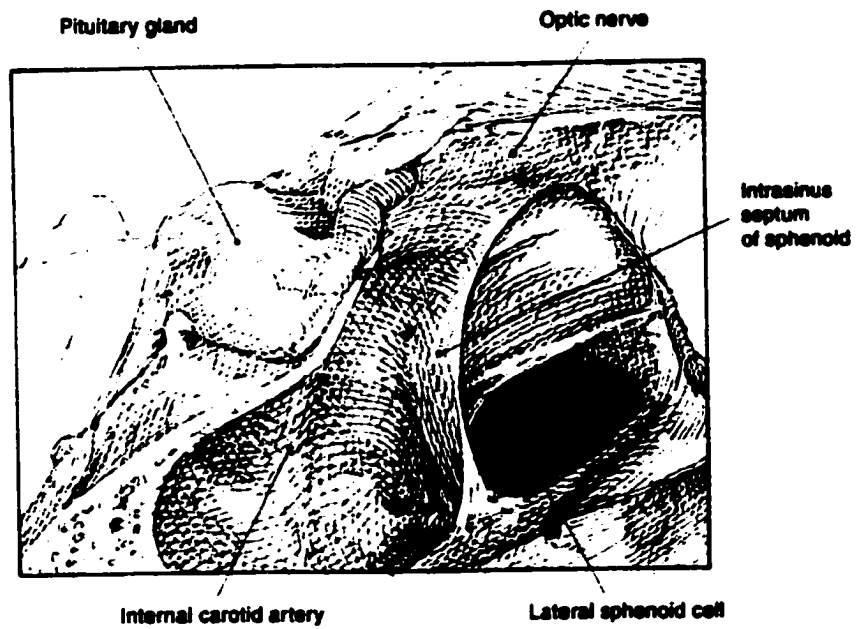
3-3C**3-3D**

Figure 3-4. A: Body of middle turbinate has been removed, leaving an intact rim of middle turbinate. **B:** Diagram of A shows the course of the third lamella or basal lamella, which supports the middle turbinate. This lamella has three segments, a superior horizontal, an anterosuperior to posteroinferior oblique, and an inferior horizontal segment.

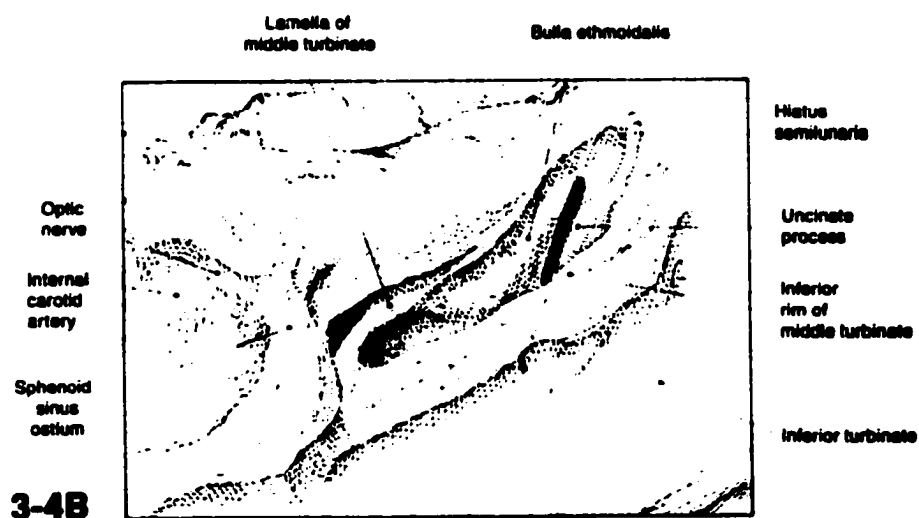
3-4A

Figure 3-5. A: Dissection reveals lateral nasal wall. The ostium of the maxillary sinus is cannulated by a wooden rod. **B:** Diagram of A.

3-5APosterior
ethmoid cellLamella of
middle turbinateWooden rod in
natural ostiumFrontal
recess**3-5B**Agger
nasiEthmoid
infundibulumNatural
ostium of
maxillary sinus

•

Figure 3-6. A: Enlargement of Figure 3-5A. **B:** The diagram illustrates a remnant of the posterior horizontal segment of basal lamella of the middle turbinate. The opening to the lateral sinus is located between the bullar and posterior ethmoid cells.

3-6A

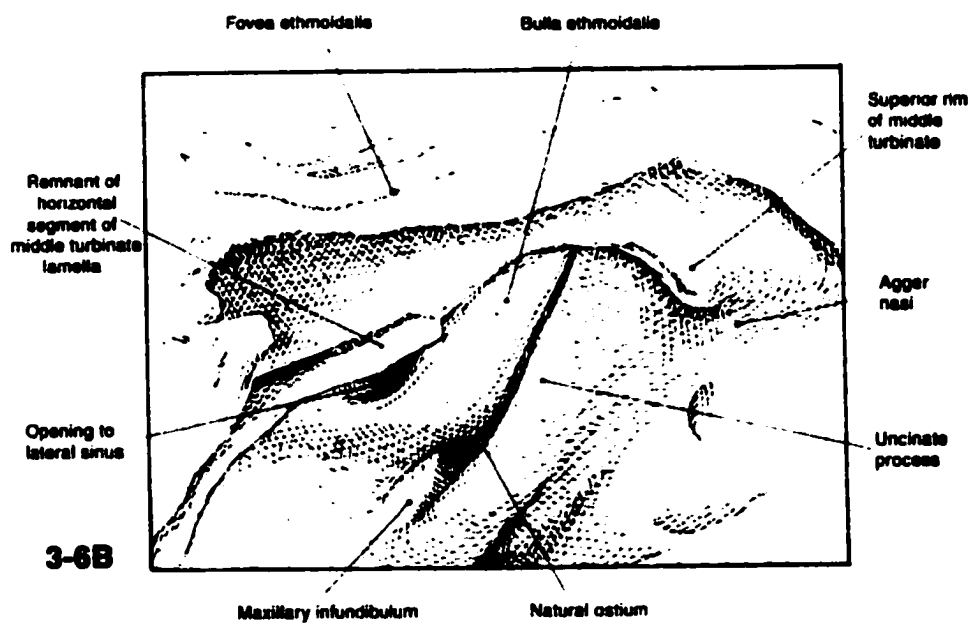


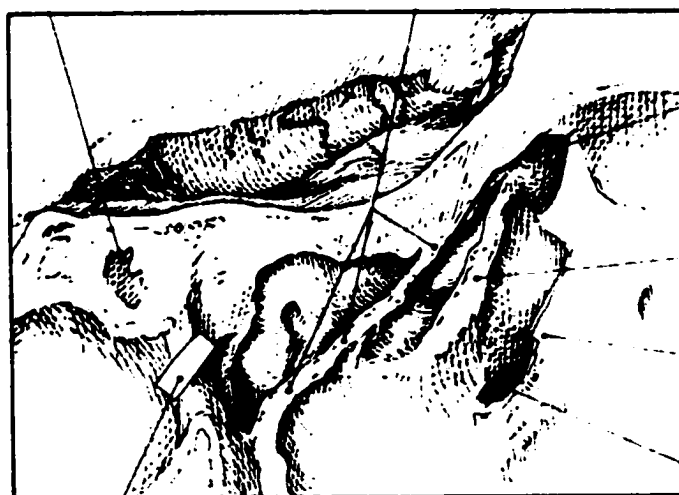
Figure 3-7. A: Medial aspect of bulla ethmoidalis and uncinat process have been removed to reveal lamella of middle turbinate and natural ostium of the maxillary sinus.

B: Three of the lamellae or plates of bone from the lamina papyracea to the lateral nasal wall are illustrated. The most anterior lamella is from the uncinat process. The second lamella is the lateral extension of the anterior wall of the bulla. The third or basal (also known as grand) lamella provides the attachment of the middle turbinate to the lamina papyracea.

3-7A

Posterior
ethmoid cellLamella of
middle turbinate

3-7B



Frontal recess

Anterior wall
of bulla ethmoidalis
(2nd lamella)Lateral remnant
of uncinate
processNatural ostium
of maxillary
sinus

Wooden rod in sphenoid sinus

Figure 3-8. A: Further removal of lateral nasal wall. B: Diagram of A.

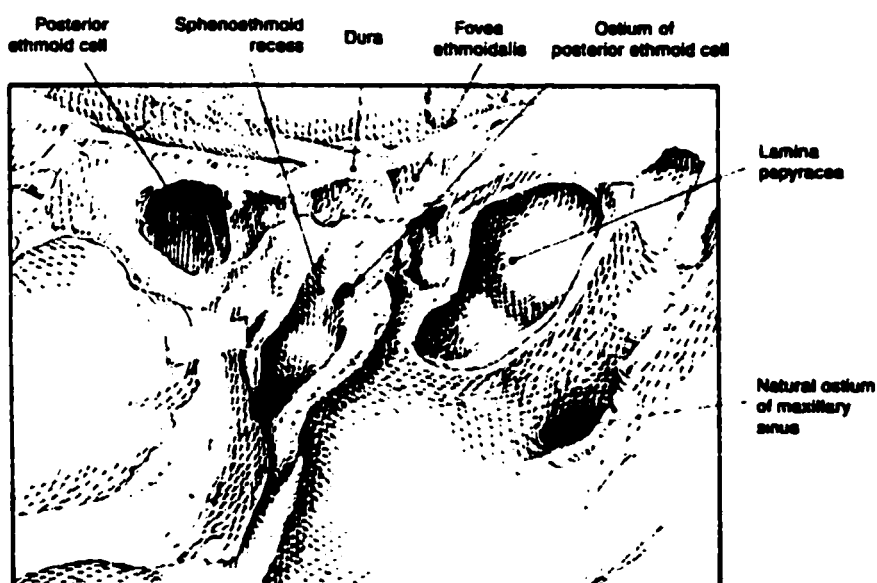
3-8A**3-8B**

Figure 3-9. A: All ethmoid cells have been exposed to reveal their location within the ethmoid and adjacent bones. **B:** Note the relationship of the agger nasi (extramural infundibular cells) to the frontal sinus, and the most posterior ethmoid cell to the sphenoid sinus. The latter is important because extramural ethmoid cells may be confused with the sphenoid sinus.

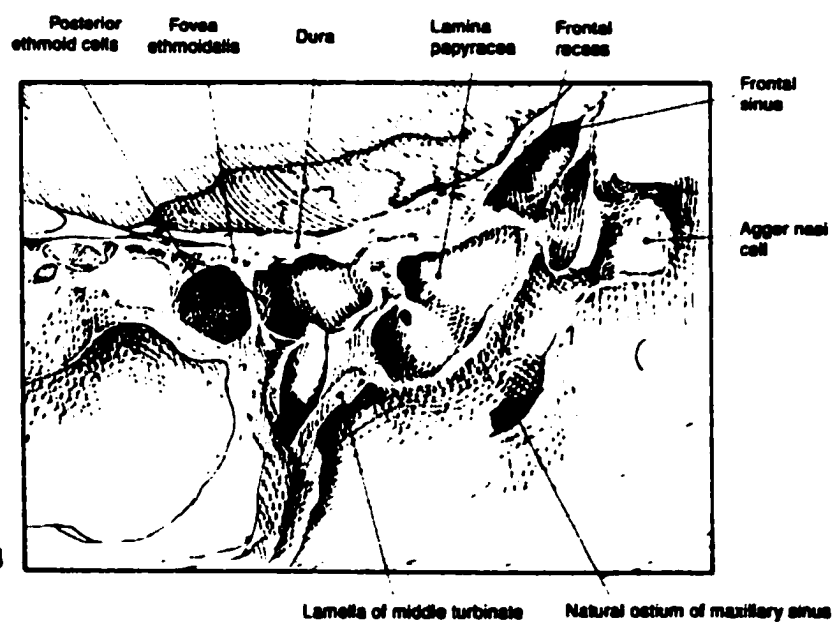


Figure 3-10. Diagram in axial plane of right lateral nasal wall. Note the lateral sinus between posterior aspect of bulla ethmoidalis and third lamella or basal lamella of the middle turbinate.

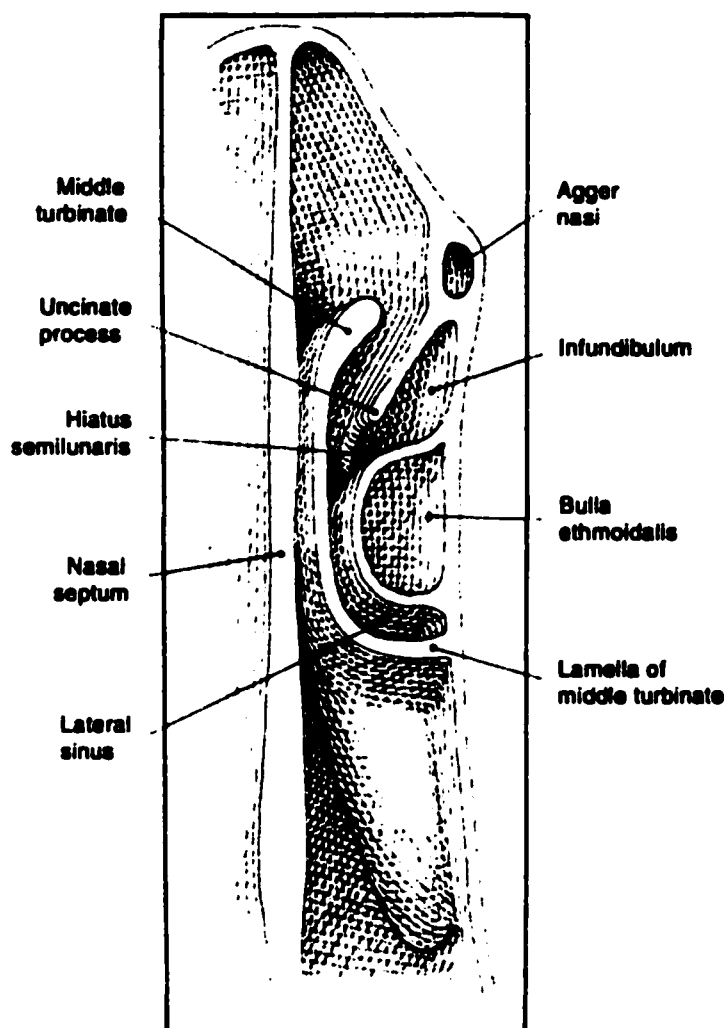
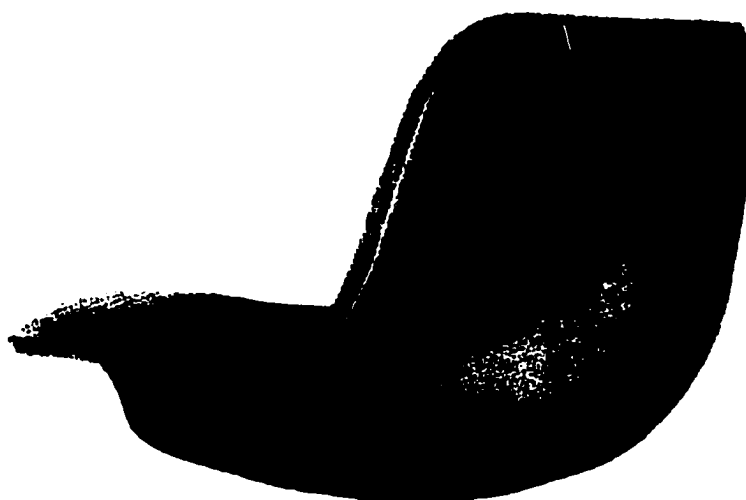
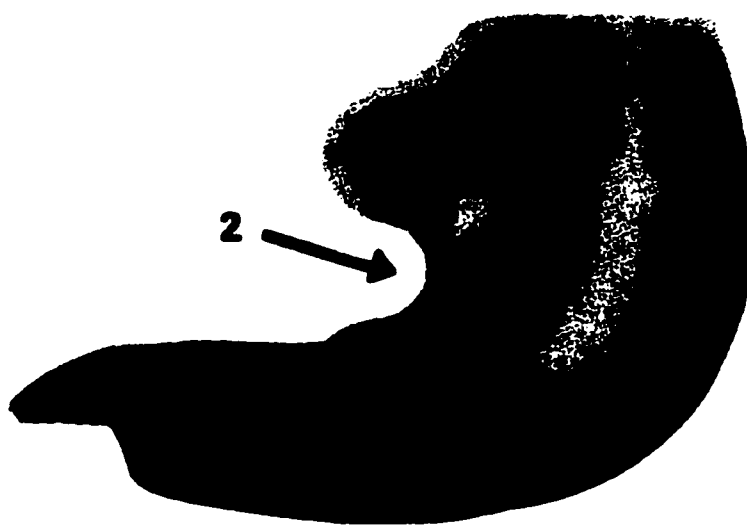
**3-10**

Figure 3-11. On the lateral surface of middle turbinate where the light grey border signifies the areas of attachment of the lamella. Note the anterior one third attaches superiorly, the middle third attaches to the lateral wall of nasal cavity in a somewhat vertical manner, and the posterior one third although, also attaching to the lateral wall, does so in a horizontal manner. (Adapted from Stammberger H *Functional endoscopic sinus surgery*. In Hawke M ed., Philadelphia: B.C. Decker, 1991).



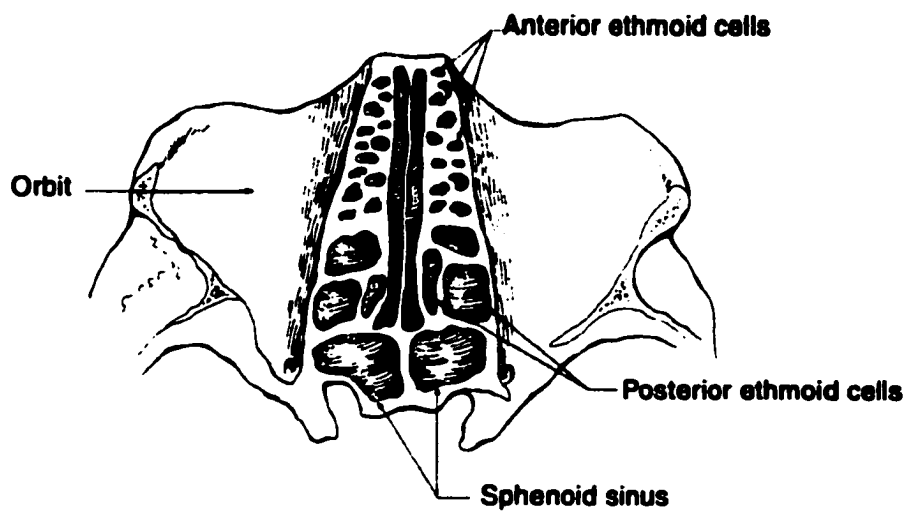
3-11

Figure 3-12. The basal lamella may become somewhat distorted because of the impinging ethmoid air cells, but the integrity of the barrier is nevertheless maintained. 1, indentation by anterior ethmoid cells; 2, indentation by posterior ethmoid cells. (Adapted from Stammberger H *Functional endoscopic sinus surgery*. In Hawke M ed., Philadelphia: B.C. Decker, 1991).



3-12

Figure 3-13. A transverse view of the ethmoid shows the width of the labyrinth increasing from anterior to posterior, whereas the number of cells decrease in the same direction. (Courtesy of Mr. Robert Fenn, Medical Illustrator).

**3-13**

3.5.2. Clinical implications

In the adult, the ethmoid sinus viewed in a transverse section forms a pyramid, with the blunted apex located anteriorly and the wider base located posteriorly (Figure 3-13). The entire sinus measures 4 to 5 cm anteroposteriorly, 2.5 cm inferosuperiorly, and 0.5 cm mediolaterally anteriorly and 1.5 cm posteriorly (Mosher, 1929). Various descriptions of the ethmoid roof, such as fovea, or foveolae ethmoidales, have caused considerable confusion over the years. Lateral to the cribriform plate and the insertion of the middle turbinate, numerous ethmoid air cells open superiorly and are closed by the frontal bone. Mosher (1904, p. 832) described this anatomy as follows:

“[U]pon the whole length of the ethmoidal notch of the frontal bone there is a row of little half cells which is matched and completed by a similar row of cells upon the upper surface of the lateral mass of the ethmoid bone.”

Because the indentations or foveolae³ of the frontal bone cover the corresponding clefts and cells of the ethmoid, the frontal bone is anatomically considered the roof of the ethmoid complex (Stammberger et al., 1995) (Figure 3-14). Use of the term fovea to describe the entire ethmoid roof does not distinguish between the endonasal view and the endocranial perspective as viewed from the olfactory groove. These air cells are at and usually above, the level of the cribriform plate. The fovea, or *foveola ethmoidalis* (fovea meaning “pit,” rather than roof, or tegmen), extends on an average 2 to 3 mm above the more medial cribriform plate (Figure 3-15).

³ Foveolae from the Latin, foveolae ethmoidales ossis frontalis, meaning ethmoid pits of the frontal bone.

The plane of the fovea slopes inferomedially, with this bony plate sometimes at an acute angle to the cribriform plate. In such cases, the fovea is particularly vulnerable to penetration along the medial aspect. The lateral wall of the ethmoid bone is termed the *lamina papyracea* (i.e., *orbital plate*) and forms its most constant component (Figures 3-15 and 3-16).

The actual size of the sinus and the number of cells present vary in each reported series. Van Alyea (1939) examined 100 specimens, finding a range of 4 to 17 cells, averaging 9 cells per specimen. Schaeffer (1930) found the most simple ethmoidal labyrinth to consist of only 3 cells and the most complex of 16 cells. When few cells occupy the ethmoid labyrinth the cells are large, but when 12 to 16 cells are “massed” together in the ethmoid region, each cell “struggles for space,” resulting in the highly variable and irregularly formed ethmoidal air cells observed. The fact that the sinus is known as the “ethmoid labyrinth” attests to the intricacy of the structure and challenges our understanding of the anatomy.

3.5.3. Classification of Ethmoid Sinus Cells

For this discussion, cells are divided into those that are within the ethmoid region, or *intramural*, and those that are outside the ethmoid, or *extramural*. The intramural cells are further divided into the smaller but more numerous anterior cells and the larger posterior cells, with some authorities calling the ethmoid bulla the “middle cells” (Figure 3-17). However, descriptions of a “middle ethmoid,” or of “middle ethmoid cells,” are considered incorrect because they are not based on developmental, anatomical,

Figure 3-14 Schematic drawing shows the relationship between the ethmoid and frontal bones. Also illustrated are the crista galli (1), lamina cribrosa (2), septum (3), lamina lateralis of lamina (4), fossa olfactoria (5), lamina papyracea (6), middle concha (7), superior concha (8), ethmoidal clefts and cells open superiorly (9), and os frontale with foveolae ethmoidalis. (Courtesy of Mr. Robert Fenn, Medical Illustrator).

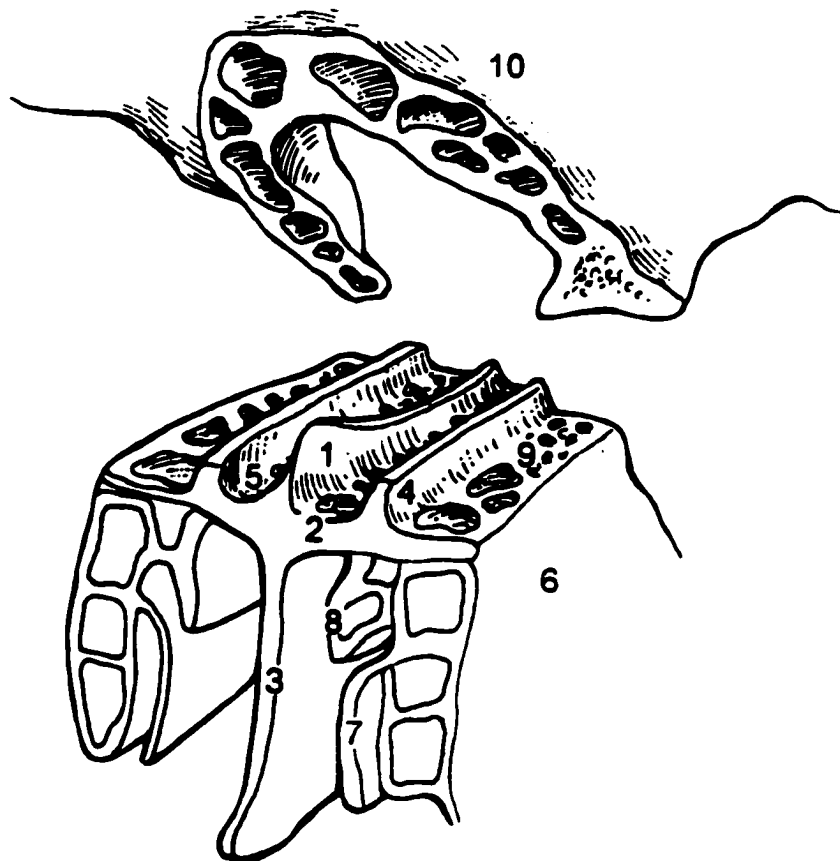
**3-14**

Figure 3-15. A: The anterior surface of the coronal section contiguous with Figure 3-20C is shown. It is at the level of the ventral aspect of the maxillary sinus. **B:** Note the continuation of the infundibular cells. The most constant of these cells is the agger nasi, or pneumatization of the lacrimal bone. **C:** Posterior surface of specimen in Figure 3-6A is shown. It includes the ventral portion of the maxillary sinus.

3-15A



3-15B

Infundibulum of maxillary sinus

Uncinate process

3-15C



Figure 3-15. (continued) D. Residual infundibular and supraorbital cells are shown in this section. **E.** Plain film radiograph of the specimen shown in **A** through **C**.

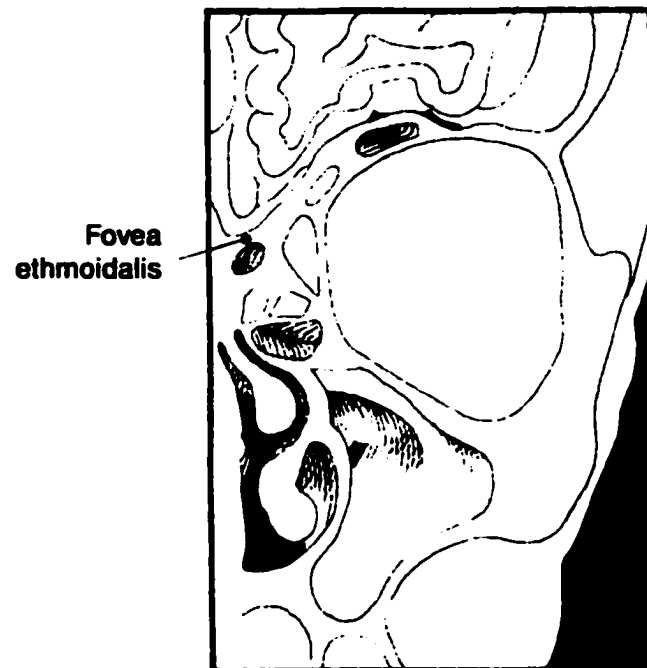
**3-15D****3-15E**

Figure 3-16. A: The anterior surface of the coronal section contiguous with specimen in Figure 16-15C is shown, which includes the midportion of the maxillary sinus. **B:** On the right of the specimen are several middle ethmoid cells, including bullar cells. On the left is a large bullar cell. **C:** The posterior surface of the specimen in **A** is shown, which exposes the middle ethmoid or bullar cells.

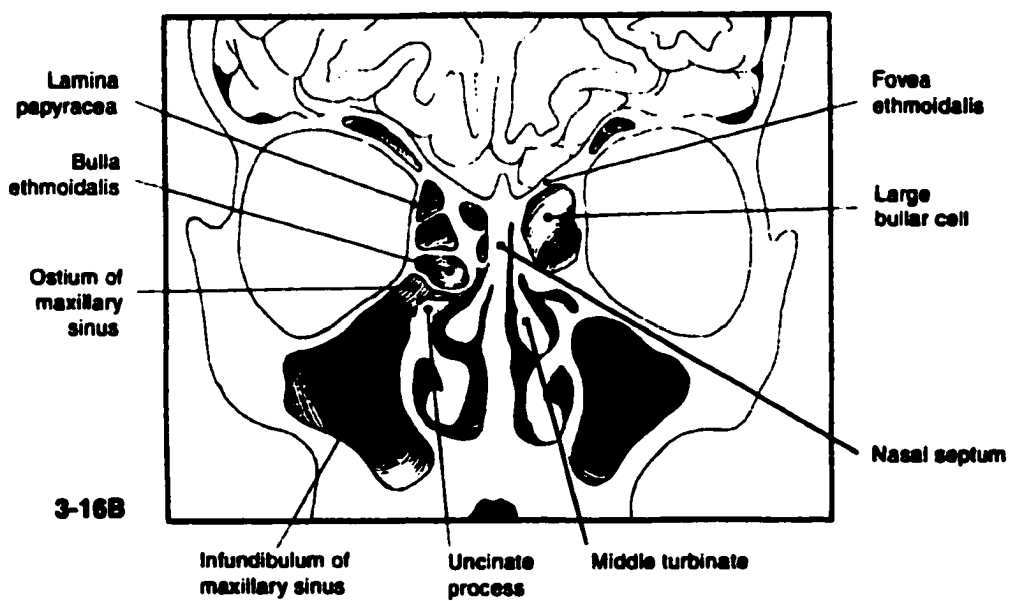
**3-16A****3-16B****3-16C**

Figure 3-16. (continued) D: The illustration shows the middle ethmoid cells seen in C.

E: Plain film radiograph of the specimen in A through C. Note the uncinate process projecting several millimeters superiorly (*curved arrow*). The *large arrow* points to membranous meatus.

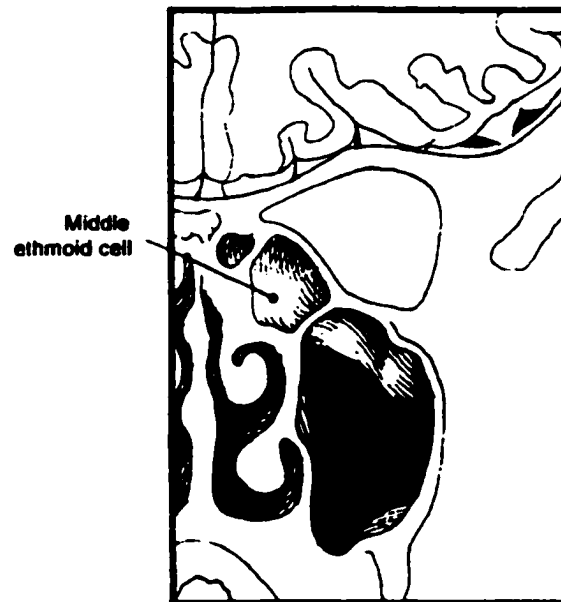


Figure 3-17. A: Parasagittal section through the middle turbinate is shown. **B:** Extensive pneumatization of the ethmoid bone is represented by the anterior and posterior ethmoid sinuses.

3-17A



Sphenoethmoid recess

Sphenoid
sinus

3-17B

Frontal
recessFree edge
of middle
turbinateInferior
turbinate

or functional grounds (Stammberger et al., 1995). The anterior ethmoid cells can be further subdivided based on their location, or that of their ostia (Van Alyea, 1939). However, cells of a given origin frequently invade the territory usually occupied by cells of another origin and one investigator favors classification by the location of their ostia (Hollingshead, 1968). Examples of several classifications are given in Table 3-2.

Among the various classifications proposed, the Ritter nomenclature system conveys most clearly the origin and drainage of the ethmoid cells. Using Ritter's classification, the most anterior cells are the frontal recess cells (range, 0 to 4 cells), which arise from the anterosuperior growth of the ethmoid cells into the frontal bone (Figures 3-4 and 3-11). These cells may come to rest within the frontal bone by either forming the frontal sinus, giving rise to the *frontal bullae*, bulging into the frontal sinus floor, or forming the *supraorbital ethmoid cells* as they pneumatize the orbit (Zuckerkandl, 1893; Ritter, 1978). The inferior expansion of these cells can displace the nasofrontal duct, resulting in a torturous or serpentine course of the duct (see Frontal sinus discussion).

The infundibular cells (range, 1 to 7 cells) are the second most anterior cells (Figures 3-18 to 3-20). The most constant of these cells form the extramural cells, the *agger nasi*, through the pneumatization of the lacrimal bone (Van Alyea, 1939). These cells are located on the lateral nasal wall immediately anterior to the middle turbinate and constitute an important landmark in both intranasal procedures and external ethmoidectomy. They drain into the three dimensional space of the *ethmoid infundibulum*, a pouch or trough that ends superiorly in the frontal recess (Figures 3-3 and 3-5). In some individuals, the infundibular cells may be the origin of the frontal

Table 3-2 **Anatomical Classification of Ethmoid Sinus Cells**

Middle meatus	Anterior ethmoid cells	Anterior ethmoid cells
Infundibular cells	Fontal recess	Fontal recess
Agger nasi	Infundibular	Infundibular
Terminal	Bullar	Bullar
Suprainfundibular	Conchal	Conchal
Inferior	Extramural (i.e., agger nasi)	Extramural
Superior meatus	Posterior ethmoid cells	Posterior ethmoid cells
Posterior cells	Intramural	Intramural
	Extramural (Ritter, 1978)	Extramural (Hollingshead, 1986)
Supreme meatus		
Postreme cells (Van Alyea, 1939)		

sinus (Schaeffer, 1916a)(Figure 3-21). The *ethmoid infundibulum* lies anterior to the bulla ethmoidalis and is bounded medially by the middle turbinate (Figure 3-5). The infundibulum is also the site of drainage for the frontal sinus and other anterior ethmoid cells involving the adjacent frontal, lacrimal, and nasal bones. Since Baron Alexis de Boyer first coined the term *infundibulum*, a Nomina Anatomica [NA] term, cells draining into this trough are also known as *Boyer's cells* (Zuckerkandl, 1893).

The bullar cells (range, 1 to 6 cells) are the most constant of the anterior ethmoid cells and together form a partial sphere lateral or beneath the middle turbinate, the *bulla ethmoidalis* (Van Alyea, 1939) (Figures 3-4 to 3-9, 3-16, 3-17, and 3-21). The term *bulla ethmoidalis* was first used by Zuckerkandl (1893), although Grünwald (1925) used the term *lateral torus*. Lang (1989) gave its dimensions as 18 (9 to 28) mm long and 5.4 (2 to 13) mm high, whereas Zuckerkandl (1893) reported lengths of 20 and 26 mm. By definition, this region of the ethmoid bone would not be called the bulla without pneumatization. A variable number of ethmoid air cells generally develop in the lamella of the bulla, producing the characteristic swelling described as the *bulla ethmoidales* (Mosher, 1904). Even though the extent of pneumatization of the bulla is highly variable, a prominence is always detectable endoscopically and radiographically (Lawson, 1994). The bullar cells drain into the middle meatus through crescentric ostia that lie superiorly, posteriorly, and parallel to the much larger semilunar cleft in the lateral nasal wall, the entrance of which Zuckerkandl described as the *hiatus semilunaris* (Schaeffer, 1916a; Van Alyea, 1939). The hiatus semilunaris forms the curved groove between the bulla ethmoidalis that borders it posteriorly and the uncinate process, a ridge of bone formed

Figure 3-18. A: The posterior surface of the coronal section at the ventral aspect of the frontal sinus is shown. **B:** This section is sufficiently ventral to the body of the frontal sinus to include only a remnant of the frontal recess cells of the anterior ethmoid. **C:** Plain film radiograph of the specimen shown in A.

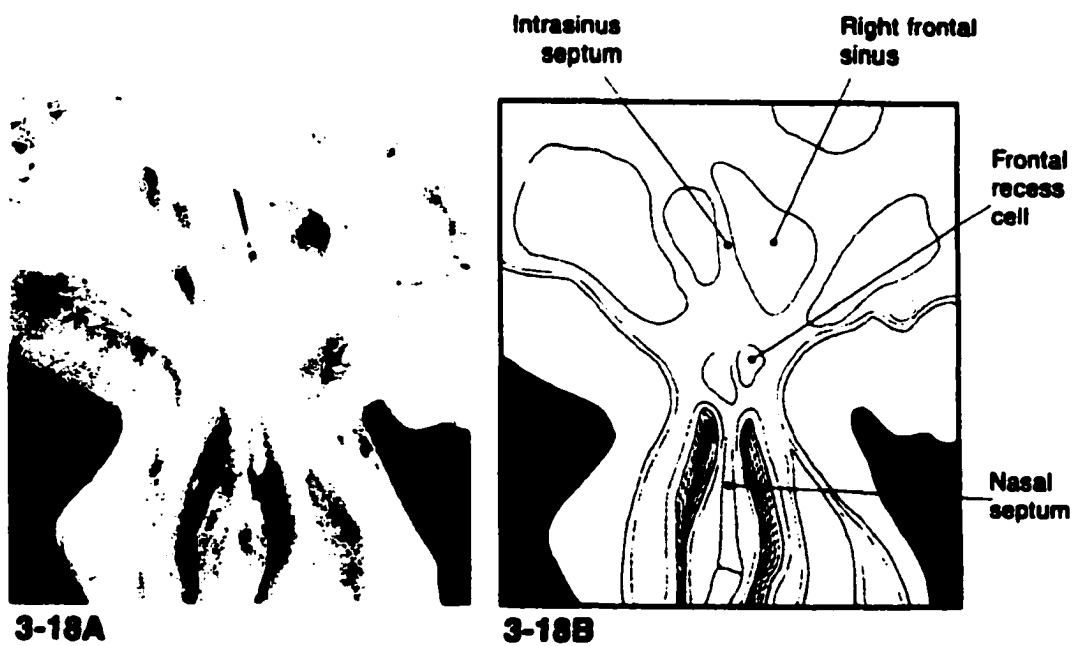
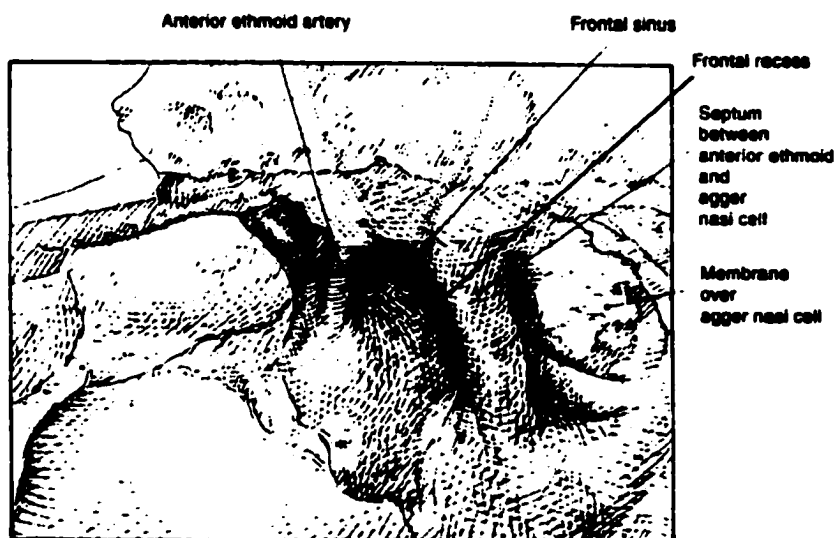


Figure 3-19. A: Frontal recess of left ethmoid bone. B: Diagram of A. The relationship of the frontal sinus to the nose may be compared to an hourglass. The upper body of the glass is the frontal sinus, the neck is the ostium, and the lower body is the frontal recess.



3-19A



3-19B

Figure 3-20. A: Anterior surface of coronal section through frontal sinus contiguous with the section in Figure 3-18A is shown. **B:** Note frontal recess cells seen in coronal section in **A**. These cells are among the several possible origins of the frontal sinus.

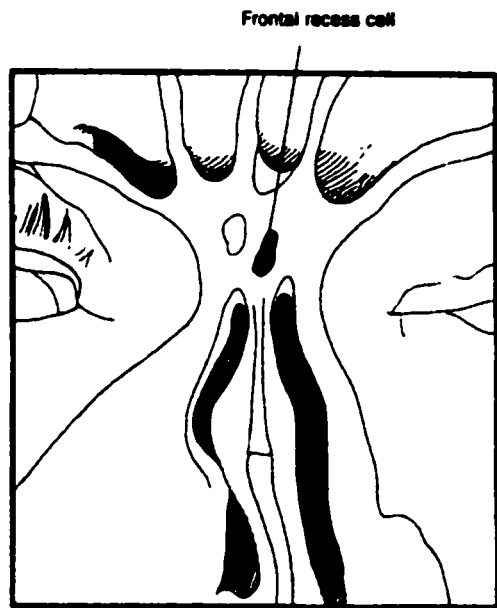
**3-20A****3-20B**

Figure 3-20. (continued) C: Posterior surface of specimen in **A** is sectioned immediately dorsal to the principle cavity of the frontal sinus. **D:** Supraorbital ethmoid cells are shown immediately superior to infundibular cells of the anterior ethmoid. The lateral boundary of these cells is the lamina papyracea, which is the most constant structure in the ethmoid bone. **E:** Plain film radiograph of the specimen shown in **A** through **C**.

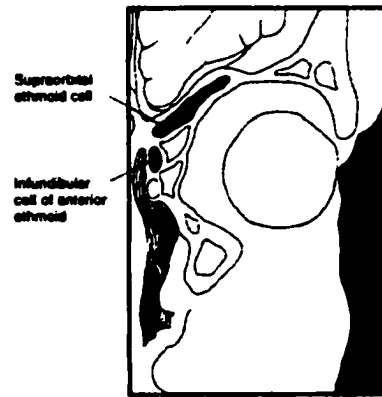
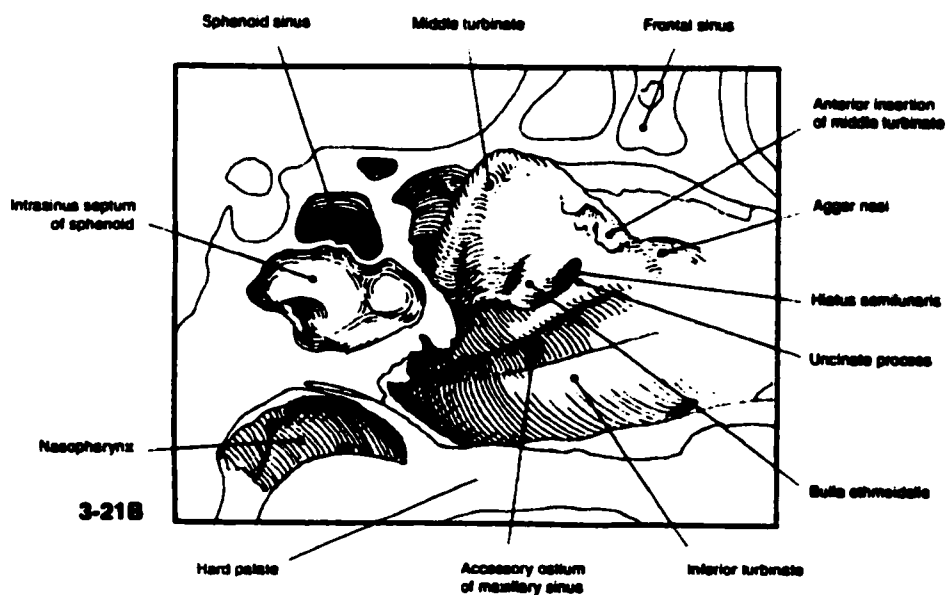
**3-20C****3-20D****3-20E**

Figure 3-21. A: Midsagittal section shows the anatomy of the lateral nasal wall. Middle turbinate has been reflected superiorly to reveal the surface anatomy of the ethmoid sinus.

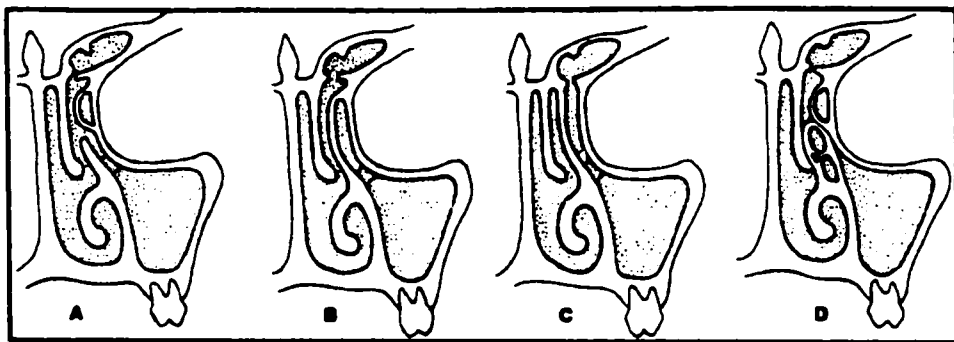
B: The hiatus semilunaris appears as a depression between the bulla ethmoidalis and the uncinate process. Anterior to the uncinate ridge is the agger nasi, which is formed by the pneumatization of the lacrimal bone by the infundibular cells of the ethmoid. The accessory ostium of the maxillary sinus appears above inferior turbinate.

3-21A



by the ramus descendens of the first ethmoturbinal, that borders it anteriorly (Mosher, 1929) (Figures 3-10 and 3-21). The relationship of the hiatus to the middle turbinate is variable and is observed most commonly 11 mm to 20 mm posterior to the anterior aspect of the turbinate (Myerson, 1932). Superiorly, the hiatus communicates with the *ethmoid infundibulum* (Figure 3-5). The anteroinferior boundary of the hiatus semilunaris is the *uncinate process*, also a semilunar structure, which has an anterosuperior to posteroinferior sagittal orientation. It ranges from nearly flat to 4 mm high and 14 to 22 mm long with its free margin occasionally projecting into the nasal cavity (Myerson, 1932)(Figures 3-4 to 3-10, 3-21 and 3-22). The uncinate process, which is immediately posterior to the agger nasi bone, makes its visualization on the lateral nasal wall dependent on the anterior and inferior expansion of the middle turbinate.

Figure 3-22. Variations in the uncinate process include the most common appearance of the uncinate process: (A), the uncinate process inserting on the lamina papyracea to form a sinus terminalis (B), the uncinate process fusing with the fovea ethmoidalis (C), and an extensively pneumatized uncinate process partially obstructing outflow from the ethmoid and maxillary sinuses (D).



3-22

The uncinate process is considered one of the most important surgical landmarks of the lateral nasal wall for endonasal sinus surgery. Its medial appendage is strategically located near the osteomeatal complex (OMC)⁴. The dynamics of this region are such that any abnormal growth or excessive pneumatization of the uncinate process can potentially narrow and ultimately obstruct the outflow tract of multiple sinuses. Moreover, normal variations in the morphology of the uncinate process give rise to several patterns of drainage from the OMC (see discussion in Isobe et al., 1999 and Figure 3-22). The first variation is an uncinate process coursing superolaterally to insert on the lamina papyracea (Figure 3-22B). This variation leads to closure of the superior aspect of the infundibulum to form a blind pouch known as the *recess terminalis* and results in the communication of the frontal recess with the middle meatus medial to the ethmoid infundibulum. The frontal sinus drains into the nose medial to the ethmoid infundibulum and lateral to the middle turbinate. A second variation is an uncinate process extending superiorly to insert on or approximate to the fovea ethmoidalis, causing the frontal sinus to drain directly into the ethmoid infundibulum through the frontal recess (Figure 3-22C). Another variation is extensive pneumatization of the uncinate process, which can potentially obstruct drainage through the infundibulum (Figure 3-22D).

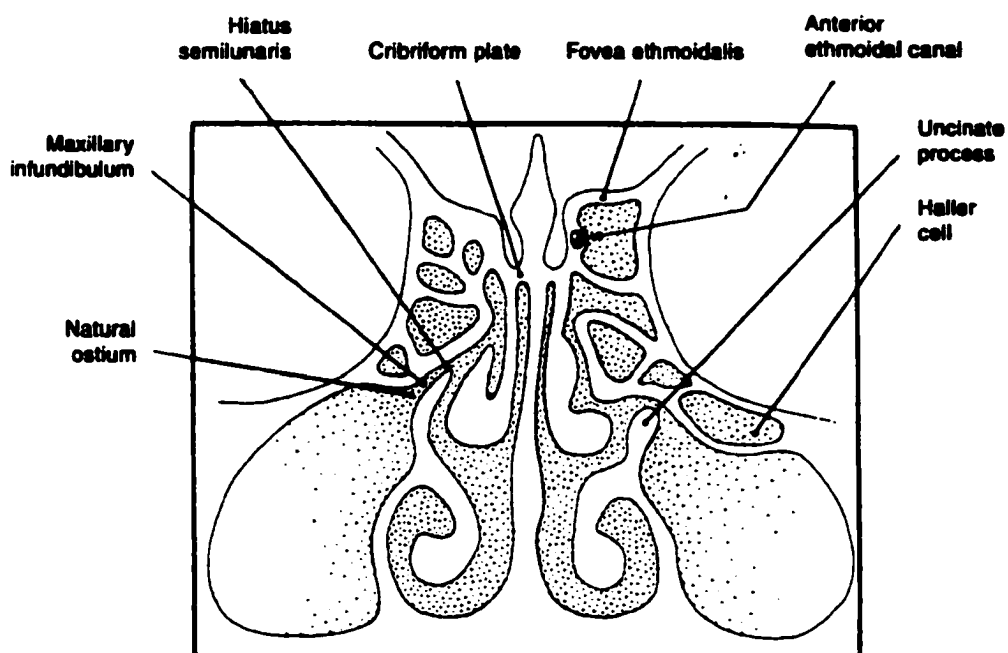
The terminology regarding the anatomic boundaries of the hiatus semilunaris invites confusion. Some investigators prefer to divide the hiatus semilunaris into anterior and posterior portions, but others tend to describe it as extending from the superior terminal of the frontal recess to the posterior aspect of the bulla, thereby substituting the

⁴ Naumann (1965) coined the term OMC to describe the region between the insertions of the inferior and middle conchae where the confluence of the frontal, ethmoid and maxillary sinuses all drain into before entering the nasal cavity.

anterosuperior portion of the hiatus for part of the ethmoid infundibulum. Others consider the infundibulum to be the bottom or most lateral region of the hiatus when describing the anterosuperior aspect as the ethmoid infundibulum (e.g., frontal recess to the bulla ethmoidalis), thereby designating that part of the infundibulum that communicates with the natural ostium of the maxillary sinus as the *maxillary infundibulum* (Mosher, 1929; Myerson, 1932) (Figure 3-5). Various descriptions are given of the hiatus that include part of the infundibulum. The consensus is that the hiatus should be viewed as a two-dimensional structure, as Zuckerkandl (1882) originally described, and should be regarded as the entrance into the infundibulum (Stammberger et al., 1995). Whatever terminology is used, these structures are important landmarks and constitute the route by which secretions can flow from the frontal and anterior ethmoid cells into the ostium of the maxillary sinus (Schaeffer, 1916a). Sometimes, a bony process develops from the attachment of the middle turbinate and projects laterally toward the orbit, but this is a rare event. Pneumatization of this process produces what is called a *Haller cell* (Figure 3-23). Because this cell is at the inferomedial aspect of the orbital rim, extensive pneumatization can impair the outflow from the maxillary sinus, serve as a primary site of ethmoiditis, or increase the vulnerability of the eye to injury during endoscopic ethmoidectomy.

Conchal cells are ethmoid air cells that invade the middle conchae, and when these cells are located in the anterior aspect of the conchae, the condition is referred to as a *concha bullosa* (Zuckerkandl, 1893; Schaeffer, 1910a)(Figure 3-17). The bullosa cells

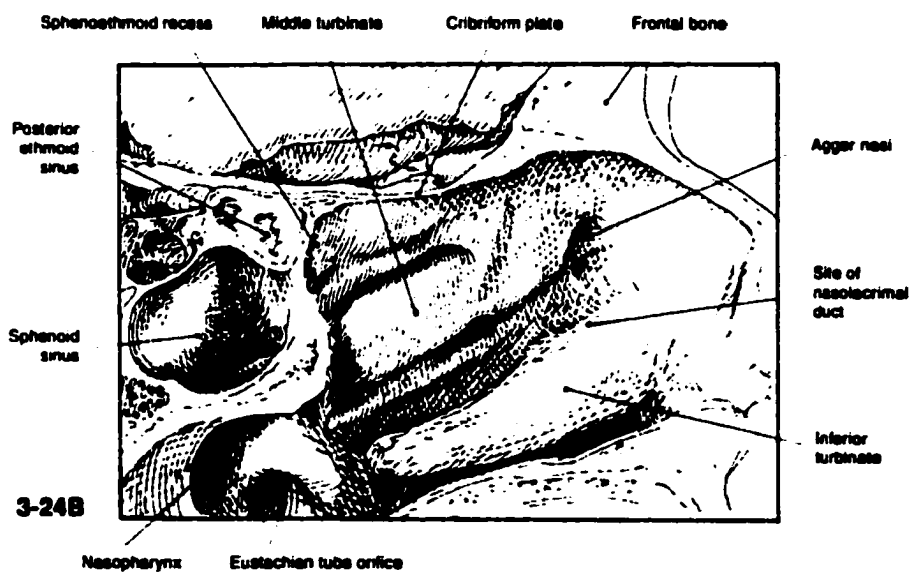
Figure 3-23. Schematic of the relationship of the paranasal sinuses to anterior cranial fossa and orbit. The anterior ethmoidal canal varies from 2 mm inferior to 4 mm superior to cribriform plate and the posterior canal ranges from 0 to 3.1 mm superior to the cribriform. Pneumatization of inferomedial orbit is known as a Haller cell.

**3-23**

are clinically important because they can be an isolated source of recurrent ethmoiditis, or may obstruct the middle meatus. The *middle turbinate* being a medial appendage of the lateral nasal wall overhangs the bulla ethmoidalis, the hiatus semilunaris, and the uncinate process (Figure 3-14). Occasionally, the uncinate process and hiatus semilunaris are not covered by the downward expansion of this 3.5 to 4 cm long important bony structure. Anteriorly, the middle turbinate is attached superiorly to the cribriform plate, with a 15° slope posteroinferiorly so that the posterior tip lies at or immediately inferior to the sphenopalatine foramen (Ritter, 1978) (Figure 3-24).

The *posterior ethmoid cells* (range, 1 to 7 cells), which invade the posterior ethmoid capsule, may also involve the middle turbinate, the sphenoid, the palatine, and the maxillary bones (Figures 3-3, 3-5, 3-6, 3-16, and 3-17). An important form of the extramural extension of the posterior ethmoid cells is the migration of these cells to the medial aspect of the optic nerve within the sphenoid bone. Such cells located superiorly and inferiorly to the optic nerve are called *Onodi cells* (Lang and Haas, 1988). In a clinical study by Basic and coworkers (1999) they found a 10.4% rate of Onodi cells in their sample of 212 patients. These cells are clinically important because the optic nerve may be covered by relatively thin bone and is vulnerable to injury by dissection posterior to the anterior face of the sphenoid bone [anatomic relationships between the optic nerve and paranasal sinuses are reviewed by Loeb, 1909 and in Figure 3-3]. At the junction of the lamina papyracea and the frontal bone, the posterior ethmoidal artery enters the posterior ethmoid cells approximately 2 to 8 mm (average, 5 mm) anterior to the optic nerve. The *anterior ethmoidal canal* (Figures 3-3 and 3-23) containing the artery (AEA) and the nerve of the same name runs between 1 mm inferior and 4 mm superior to the

Figure 3-24. A: Most medial of a series of progressive dissections of the left lateral nasal wall. **B:** Diagram of **A** illustrates the surface anatomy.



cribriform plate. The extraordinary course of the AEA originates from the orbital region and passes through the anterior ethmoid onto the anterior cranial fossa to finally enter the nasal cavity (Kainz and Stammberger, 1989). A significant number of individuals have a natural dehiscence of this canal as it crosses the posterior aspect of the frontal recess at a region called *the dome of the ethmoid* (Kennedy, 1985; Lang and Hass, 1988). Injury to the AEA results in bleeding into the nasal cavity that can potentially cause the retraction of the vessel into the orbit, which leads to intraorbital bleeding and the danger of blindness. The *posterior ethmoidal canal* traverses the ethmoid bone at a plane approximately 1.5 mm above the cribriform plate, and it may also be partially dehiscence of bone.

3.6. MAXILLARY SINUS

3.6.1. Anatomy and Historical Background

The sporadic works appearing in the last two thousand years have cumulatively contributed to our knowledge of the nose and paranasal sinuses. However, a survey of the literature has identified investigators who have made landmark contributions. During this period, great scientific achievements have suffered from theologic preoccupation, indifference, narrow-mindedness, or mythologic preconceptions. The recognition of these significant discoveries often depended on the time of their appearance.

The first important historical event in the study of maxillary sinus anatomy was the treatise *Corporis Humani Disquisitio Anatomica* by Nathaniel Highmore, that described and illustrated the “antrum magnum maxillae superioris” (Highmore, 1651, pg. 226). The maxillary sinus has since been referred to as the Antrum of Highmore in honor of this English physician. Clinical texts and biographical profiles, however, continue to incorrectly credit Highmore as being the first to describe this sinus (see, for example, Anon et al., 1996 and Gillispie, 1970). Although the text by Highmore is principally concerned with the circulatory system of the various regions of the human body, undoubtedly due to his admiration and for close association with Harvey⁵, he is best remembered for the illustrated description of the maxillary sinus (Figure 3-25).

⁵ During 1642, while conducting studies on the embryonic development of the chick, Highmore and William Harvey became close colleagues. Highmore's 1651 treatise was the first anatomical textbook to accept Harvey's theory on the circulation of the blood as reflected in the translation of his full title: “An anatomical investigation of the human body, in which the circulation of the blood in any part of the body in many new ways, and of medical mysteries, is set out and described clearly and concisely” (Translation from Hamilton, 1973).

However, Highmore's brief description of this sinus is deficient by modern anatomical standards. This is reflected in the English version translated from the original Latin:

"This hollow, one on each side under the lower part of the eye where the bone swells out to a certain extent to protect the eye, is situated near the lower side of the nose. It is markedly hollow, spherical but somewhat elliptical in shape, and sufficiently large for the last joint of the big toe to be inserted in it. It is covered by thin bone or bony scale; for the bone which encloses it and which separates it from the sockets of the teeth, barely exceeds the thickness of packing paper. In the base of this, certain swelling projections are seen. In these the finer points of the teeth are enclosed. The sockets of the teeth are cut into the edges of this lower bone in which the teeth are fixed. This hollow is more often empty, but sometimes is found full of mucus, into which fluids from the head through a channel from that space in the bone of the forehead, and from the ethmoid bone can distil" (translation from Hamilton, 1973, pg. 165).

Figure 3-25. The original illustration of Highmore's description of the maxillary sinus as it appears on page 227 in his 1651 publication, *Discussion of the Human Body Anatomy and of the Blood Circulation*. (Courtesy of the New York Academy of Medicine Library, New York, NY).



Highmore is also credited with the first written description of odontogenic sinusitis case as seen in the following English version of Highmore's original description by Cowper in 1707:

An instance of this is mention'd by Dr. Highmore in a Gentlewoman, who had the Dens Caninus drawn upon the account of Pain, proceeding from an Invertebrate Defluxion of sharp Humours that had destroy'd most of her Teeth; who upon thrusting a Silver Bodkin into the Alveolus, was exceedingly frighted to find it pass, as it did, almost to her eyes. And upon farther Trial with a small Feather stript of its Plume, which she thrust up a Hand's breadth or more, was so terrify'd at it as to consult the Doctor and others about it, imagining nothing less than that it had gone to her Brain. But they considering the Circumstances of the matter, found that the Feather had doubled only in this Cavity, and gave the Lady full satisfaction in that point" (Harle, 1992, pg. 79).

Despite the eponymic celebrity of Highmore, careful scrutiny of the literature reveals that it was Leonardo da Vinci who both illustrated and described this sinus, in 1489 (Sperber, 1980; Wendler, 1986; Stoney et al., 1991; see Table 3-3 for an overview of the earliest known investigators of the paranasal sinuses). Da Vinci also offered an imprecise and archaic description as is illustrated in the passage from the Dell' Anatomia, Fogli B:

"I wish to elevate that part of the bone, the support of the cheek – to demonstrate through the exposed opening, the size and depth of the two cavities which are hidden behind it. The eye, the instrument of vision, is hidden in the cavity above and in that below is the humor which nourishes the roots of the teeth. The cavity of the cheek-bone has a resemblance in depth and size to the cavity which receives the eye within it, and in capacity it is very similar to it and receives in its interior some veins through the opening, which descend from the brain, passing through the sieve (cholorio) (Ethmoid) which discharges into the nose the superfluities of the humors of the head." Translation from Sperber (1980, p. 381.)

Table 3-3 **Paranasal Sinus Anatomy History**

Paranasal Sinus	Synonym	First Described	Studies
Maxillary sinus	Antrum of Highmore	Leonardo da Vinci, 1489	da Vinci, 1489
Sphenoid sinus		Giacomo Berengario da Carpi, 1521	da Carpi, 1521, Tillaux (1862)*
Frontal sinus		Volcher Coiter (1534-1576)	cited in Libersa et al., 1981
		Basilius (n.d.)	cited in Douglass, 1906
Ethmoid sinus		Galen, (131-201 A.D.)	Galen

*** Tillaux was the first to suggest that the sphenoidal sinus was part of the facial sinuses although Johann Riolan (the younger) in 1649 was the first to recognize the paranasal sinuses as an entity (Stammberger, 1989).**

~According to Douglass (1906, p. 21), Basilius was the first to describe of the frontal sinus but offers no citation as does Libersa et al., 1981 which cites Coiter as the first to describe this sinus.

Other workers that preceded Highmore in describing the maxillary sinus and who have not been justly credited are Vesalius, in 1543, and Peter Paaw, in his 1615 book *Succenturiatus anatomicus* (Harle, 1992). Thus, the so-called first original description of the maxillary sinus has been undeservedly credited to Highmore by uncritical writers (Stoney et al., 1991). Nevertheless, the sinus description by all of these investigators failed to define the entire paranasal sinus complex. The assumption of subsequent sinus investigators and clinicians was that that this had already been done and reported by several workers in the mid-seventeenth century.

This is highlighted by a report by Chapin A. Harris, the founder of the American Society of Dental Surgeons, delivered on July 20th, 1842 entitled - *Dissertation on the Diseases of the Maxillary Sinus*. In his address, he commented that “it will be unnecessary to give a full description of this cavity, inasmuch as that has been done, by nearly every writer on general anatomy, since the middle of the seventeenth century” (Harris, 1842, pg 21). Chapin then briefly described some aspects of maxillary sinus morphology noting that it drained through an ostium between the inferior and superior meatus. In the same issue of the journal appears a critical commentary by Hayden:

“We should feel greatly obliged to our friend, the doctor, if he had particularized, or named even one or more of the writers on general or particular anatomy, that has given ‘a full description of this cavity,’ ‘since the middle of the seventeenth century,’ or even until *now*, nearly the middle of the nineteenth century, for we are bold to say that no one author, whose works have been published, has *ever given* a full and accurate *physiological* view of those cavities, not even to the day, inclusive, on which the American Society of Dental Surgeons met in the principal lecture room of the Medical College, in Mason street, Boston” (Hayden, 1843, pg.206).

Hayden's observation was correct in that no such anatomical account had been published up to that day in 1843. That landmark anatomical account would come nearly forty years later with the first detailed report of the normal and pathologic anatomy of the sinuses by Zuckerkandl (1882).

3.6.2. Anatomy of the human nasal complex

A proper appreciation of the nasal cavity and the paranasal sinus system requires an understanding of its two components. These are the osteological construction and its mucosal coverings which have separate developmental origins but act together as a functional unit. Not only is the mucosal lining essential conditioning the inspired air but it also contributes to the shape of the underlying framework. The mucosa helps to define the spaces and clefts of the ethmoid region and determines the drainage pathways of the sinuses. Accordingly, structures such as the nasal fontanelles and the accessory ostia of the maxillary sinus cannot be fully appreciated in the dry skull. A brief osteological review is presented before describing the clefts and spaces of the lateral nasal wall,

Bones involved with the adult maxillary sinus are the maxilla, the horizontal plate of the palate, and the zygoma. The osteological framework of the medial wall of the maxillary sinus consists of the thin portion of the corpus maxilla surrounding the hiatus maxillaris, and also the lamina from contiguous bones partially filling in the hiatus. The lamina, which form the incomplete portion of the wall, are the maxillary process, the ethmoid process of the inferior turbinate, perpendicular plate of the palate, the uncinate

process of the ethmoid, and the posteroinferior portion of the lacrimal bone. The extent of pneumatization into the different bony regions requires description.

The maxillary sinus, lying within the body of the maxillary bone, is the largest and most constant of all four paranasal sinuses. Asymmetries in the size of the maxillary sinus have been reported (Hajnis et al., 1967), but without a dominant laterality (Schaeffer, 1910b, Koppe et al., 1997). Different descriptions of its shape exist, probably because of the great variability in its development (Anon et al., 1996). Cullen and Vidic (1972) classified its prenatal morphology as elliptical, triangular, irregular, rectangular, and spherical. Anagnostopoulou and associates (1991) analyzed 119 casts of adult maxillary sinuses from 60 dry skulls and characterized them as semi-ellipsoid, paraboloid, hyperboloid, and conical. It is generally described as being pyramidal (Harris, 1842; Davis, 1918; Skillern, 1923; Turner et al., 1936; Alberti, 1976), although Anon (et al., 1996) preferred the term tetrahedral to represent its morphology in three-dimensional space. An analogy with a pyramid is misleading because the term pyramid implies a quadrilateral base with its apex directed superiorly. The pyramidal body of the maxillary bone with its hollowed out sinus cavity has its base facing the lateral wall of the nose and its apex orientated towards the superior junction of the zygomatic and maxillary bones. The maxillary bone has four processes: the frontal process which extends to the frontal bone and forms the root of the external nose, the zygomatic process which extends laterally to articulate with the zygoma, the palatine process which forms the anterior two-thirds of the hard palate, and the alveolar process which houses the upper dentition. Its anterior wall is the facial surface of the maxilla upon where the facial vein and artery course, and the posterior wall is the infratemporal fossa where the path of the

maxillary artery⁶ and vein are located. The medial wall constitutes the lateral wall of the nasal cavity where a number of vascular structures are situated (i.e., branches of the sphenopalatine, the septal branch of the superior labial, and ethmoidal arteries). The superior wall, or roof of this sinus is the floor of the orbit, and the floor of this sinus is the alveolar process of the maxilla. The topographic relationship of the maxillary sinuses to several contiguous structures permits spread of infectious and neoplastic processes in multiple directions (Almagro et al., 1995; Boocock et al., 1995).

Development of the maxillary sinus has begun by the sixty-fifth day of gestation, making it the first sinus to develop *in utero* (Amedee, 1993). Various researchers have reported different times of onsets of its development. This was reported by Schaeffer (1910b) to be on the seventieth day; Kallius (1905) timed it by an evagination appearing in the middle of the third month; and Brandt and Roper-Hall (1943) and Aubert (1929) cited the fourteenth week as the beginning of maxillary sinus prenatal development. The initial stage of development of this sinus has been described primarily as a mucosal evagination (i.e., bud) into the lateral cartilaginous environment of the nasal capsule. However, Wang (et al., 1994) suggested that the mucosal evagination, or outpouching of the nasal mucous membranes, should be considered a secondary event rather than the primary force. Although Schaeffer (1910b) described this pouch as a minute epithelial sac forming the anlage of the sinus, its presence precedes the appearance of the cartilage that later surrounds it. Wang (et al., 1994) showed that during the nineteenth week *in utero* the mucosa of the maxillary sinus makes direct contact with the maxillary bone

⁶ Based on the Nomina Anatomica [NA] adopted in Paris 1955. The maxillary artery, in the older Basle Nomina Anatomica [BNA], was referred to as the "internal maxillary artery" to distinguish it from the "external maxillary artery" which is the "facial artery" in the NA.

only after the surrounding cartilaginous wall of the maxillary sinus begins to disappear through degeneration and absorption of its cartilaginous cells. The exact location of this maxillary sinus outpouching stems from the primitive ethmoid infundibulum, also known as the uncibullous groove, which become the future uncinate and bulla ethmoidales structures. These structures demarcate the portal between the ethmoid infundibulum and nasal cavity (Schaeffer, 1910b). This developmental stage explains why the drainage from this sinus passes through the ethmoid infundibulum before reaching the middle meatus.

The term infundibulum refers to one specific space in the anterior ethmoid region. To clarify the topographic relationship, the term infundibulum should always be accompanied by the adjective “ethmoidal” (Stammberger and Hawke, 1993). Key to understanding the ethmoidal infundibulum is its perception as a cleft-like three-dimensional space in the lateral wall of the nasal cavity that is a component of the anterior ethmoid. The medial wall of this space is provided by the entire extent of the uncinate process and its mucosal covering. The major portion of the lateral wall of the ethmoidal infundibulum is provided by the lamina papyracea of the orbit, with the frontal process of the maxilla, and in rare cases, the lacrimal bone providing the remainder of its lateral wall anterosuperiorly. The anterior border of the uncinate process fuses with the bones of the lateral nasal wall at an acute angle and connects inferiorly with the inferior turbinate. Bony defects in this area may be covered by either dense connective tissue (i.e. periosteum), mucous membrane, or both, thus sealing off the area of the anterior nasal fontanelle. Along the line of attachment of the anterior margin of the uncinate process to the lateral nasal wall, the ethmoidal infundibulum ends blindly anteriorly in an acute

angle. This is the reason that the lumen of the ethmoidal infundibulum appears to be “V” shaped in a horizontal section (Figure 3-10).

At birth, the sinus has an average volume of 6 to 8 mL and is fluid-filled, making interpretation of plain film radiographs difficult (Schaeffer, 1920; Wasson, 1933).

However, Weiglein and colleagues (1992) reported that this sinus is of appreciable size at birth and can be identified on a Caldwell view. The maxillary sinus then undergoes two periods of rapid growth: one between birth and 3 years; and the other between 7 and 12 years (Schaeffer, 1910b, 1920). Between these two growth periods, at about 4 years of age, the sinus extends laterally beyond the infraorbital canal (Scuderi et al., 1993).

Subsequent expansion after the second period of rapid growth (see Table 3-4) involves pneumatization of the alveolar process of the maxilla. Before growth is completed, there is a descent of the maxillary sinus from 4 mm above the floor of the nasal cavity at birth to the level of the nasal floor at age 8 to 9 years, and then a final drop of 4 - 5 mm below this level by adulthood (Van Alyea, 1951, see Figure 3-26). Because the descent of this sinus coincides with dental molar eruption, it was long believed that a close inter-relationship between these two developmental growth trajectories existed (see Keith, 1902, Underwood, 1910 and Turner et al., 1936). However, Libersa (et al., 1981), Márquez (et al., 1998) and Lewis (et al., 1999), have that the relationships between molar eruption pattern and adult maxillary sinus form, and between molar volume and adult sinus size, respectively, were not statistically significant.

Table 3-4 **Embryologic Pattern of Development**

<u>Paranasal Sinus</u>	<u>Embryologic Appearance</u>	<u>Postnatal Appearance</u>	<u>Growth Spurt Interval</u>
Ethmoid sinus	Development begins in third fetal month	Present at birth	First growth spurt between first and 4 years; second growth spurt between fourth and eighth years
Maxillary sinus	65th day of gestation	Present at birth	First growth spurt between birth and 3 years; second between 7 and 12 years
Frontal sinus	Development begins in fourth fetal month	Detected at 7 - 12 years of age	Adult size is completed by 20 years
Sphenoid sinus	Development begins in third fetal month	Detected at 3 - 4 years of age	By seventh year, sinus begins to extend posteriorly toward the sella turcica

Figure 3-26. A three dimensional CT reconstruction of an adult human crania (the author's) is shown in frontal view to illustrate the descent of the maxillary sinus floor (arrows) below the level of the nasal cavity floor (arrow head).

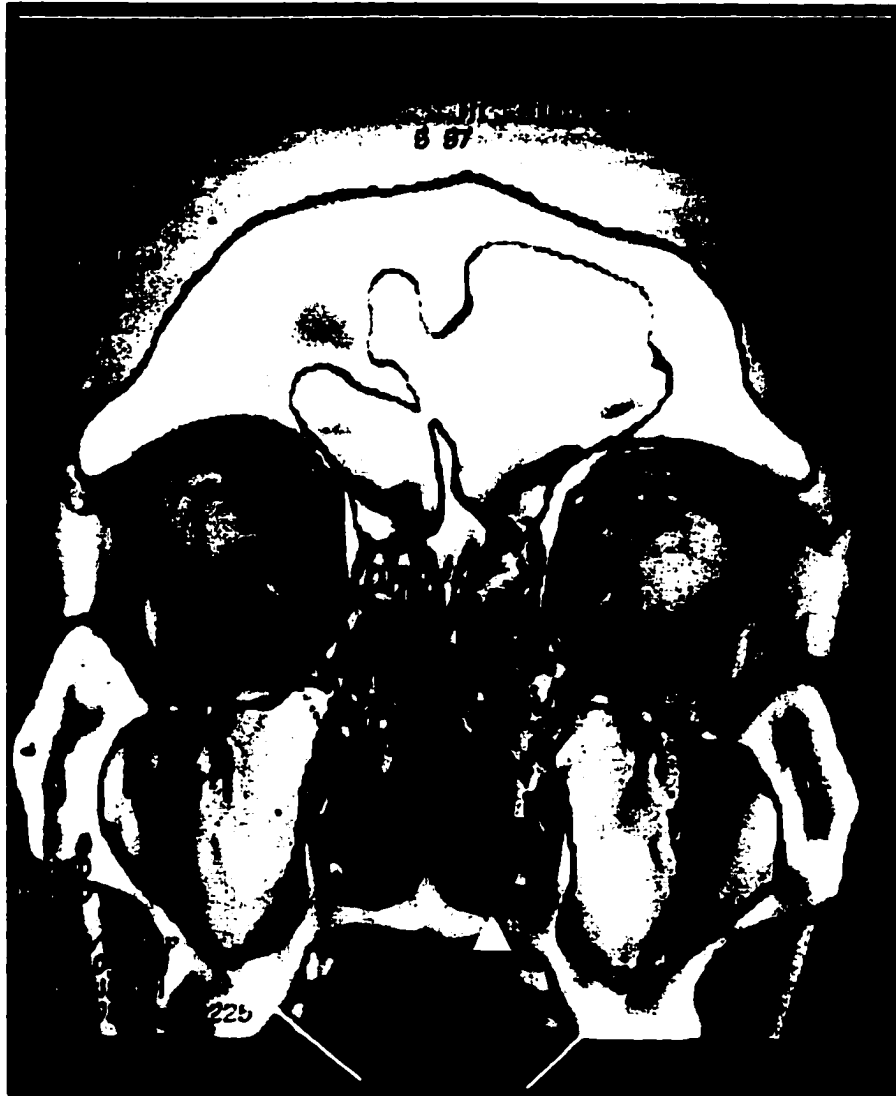


Figure 3-26

The medial wall is considered the most clinically important for the following reasons: it contains the sole opening into the sinus; it is the first to show pathological changes when the sinus is affected; it is the thinnest and presents the easiest point of entry into the sinus cavity for diagnostic or therapeutic purposes. The anterior wall is clinically significant as radical operative procedures are usually made through this structure. Its thickness can range from as thin as paper (4 to 8 microns) to several millimeters thick, depending upon the age and the construction of the facial bones. Resorption can occur with age and portions of the wall may lose entirely its osseous tissue with only the periosteum and sinus mucosa remaining. The thinnest portion of this wall is in the center of the canine fossa, and is the point of election for creating an opening in external radical operations. The infraorbital foramen lies in this wall close to its upper margin directly over the canine fossa. The topographical relationships are important clinically when performing extensive surgical resections. The posterior wall has a uniform thickness and is the point of entry into the pterygomaxillary space for surgery to control epistaxes, for vidian neurorectomy for vasomotor rhinitis, and for the excision of neoplasms. The roof of the sinus is the orbital floor and may contain natural dehiscences in the area of the infraorbital canal which may serve to propagate infections and tumor into the orbit. (Zuckerkandl, 1893).

In the adult, the maxillary sinus can be roughly described as triangular in shape, measuring 25 mm along the anterior limb of its base, 34 mm in depth, and 33 mm in height (Schaeffer, 1920; Van Alyea, 1951). The sinus may be partially compartmentalized by complete, or incomplete septa. Knowledge of the incidence and morphology of maxillary sinus septa has clinical implications, especially in sinus lift

operations performed preparatory to the placement of dental implants (Krennmair et al., 1997). In rare cases, separate cavities can exist in the posterior part of the sinus, which can be a source of persistent infection (Som et al., 1984). The primary or *natural ostium* of this sinus is located in the superior aspect of the medial wall of the sinus and drains through its infundibulum into the hiatus semilunaris (Figures 3-3 and 3-5 to 3-9). Despite a marked variation in position, most investigators see the ostia as being in the region of the posterior half of the ethmoidal infundibulum, or posterior to the midpoint of the bulla ethmoidalis (Schaeffer, 1920; Myerson, 1932; Van Alyea, 1936). Lang and Papke (1984) found the ostium located 1.3 mm to 11.5 mm (average, 4 mm) from the nasolacrimal duct (Figure 3-27); this proximity of the duct to the natural ostium makes it vulnerable to injury during middle meatus antrostomy. The pneumatization of the ethmoidal bulla and the height (e.g., medial and superior projection) of the uncinate process form a canal leading to the maxillary sinus, which was incorrectly called the *maxillary infundibulum*⁷. This structure varies in depth (average, 5 mm) (Schaeffer, 1910b), orientation, and accessibility through the nose (Myerson, 1932).

The natural ostium tends to be elliptical, measuring from 1 to 20 mm in length (Schaeffer, 1910b). Accessory maxillary sinus ostia were found in 15% to 40% of subjects examined by various authors (see Schaeffer, 1910b; Myerson, 1932; Van Alyea, 1936)(Figures 3-3 and 3-21). These ostia may be located in the infundibulum, or the

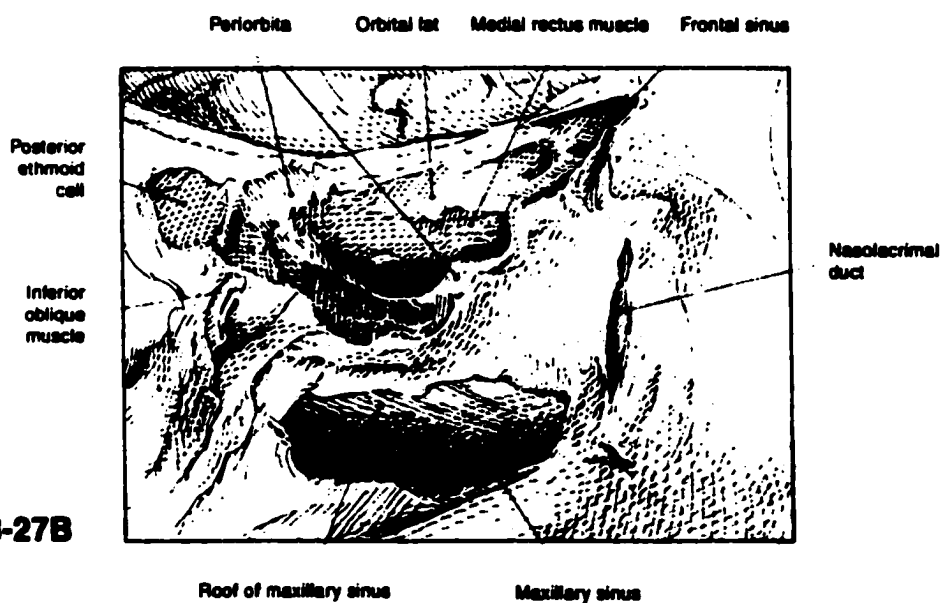
⁷ The maxillary infundibulum and frontal infundibulum are totally within their respected sinuses appearing as funneling tunnels whose orientation is toward their natural ostia (Stammberger et al., 1995).

Figure 3-27. A: The lateral nasal wall has been exenterated to show the medial orbit, maxillary sinus, and nasolacrimal duct. **B:** The illustrated version of **A**.

3-27A



3-27B



membranous region of the medial sinus wall, with the latter being only a reduplication of the mucosa of the sinus and the lateral nasal wall. This membranous wall is known as the *membranous meatus*, or *fontanelle*. This region is located inferior to the uncinate process and superior to the insertion of the inferior turbinate. Clinically, this site is important because it may serve as an alternative opening when the natural ostium cannot be found during the performance of a middle meatus, or supra-inferior turbinate antrostomy.

During the seventeenth century, antral trephination for suppuration was the most common maxillary sinus operation performed, followed by molar tooth extraction to create an oral-antral fistula for dependent drainage of an infected maxillary sinus (Tange, 1991). Historically, the next procedure for sinus drainage was an anterior wall approach above the canine fossa, which was maintained patent for irrigation procedures. Then came the Caldwell-Luc procedure, which combined the anterior wall approach with an intranasal antrostomy, and after removal of the infected mucosa, the intranasal incision was closed. Intranasal endoscopic sinus surgery is currently performed primarily for treating infected maxillary sinuses (Tange, 1991).

3.7. FRONTAL SINUS

3.7.1. Anatomy and Historical Background

Volcher Coiter of Holland, a pupil of Fallopius and Eustachius, is said to be the first to describe the frontal sinus (Libersa et al., 1981). Berengario da Carpi (da Carpi, 1523) described the frontal bone region as having “two tables within which there is a notable vacuity so as to not weigh down the body.” However, it was da Vinci, in 1489, who first recognized its existence and illustrated its morphology (da Vinci, 1489; see also Imperatori, 1941).

Development of the frontal sinus is initiated in the fourth fetal month, when the entire nasofrontal area is represented by the frontal recess (Van Alyea, 1941), and it is the last paranasal sinus to develop (Scuderi et al., 1993). The usually paired frontal sinuses have several possible origins, each of which influences the relationship of this sinus to the lateral nasal wall and its drainage pattern within the middle meatus (Van Alyea, 1946a). In a study of 100 adult specimens and fifteen late-term fetuses, Kasper (1936) found the most common origin of the frontal sinus to be pits or furrows originating within the frontal recess that are considered rudimentary anterior ethmoid cells (described previously as frontal recess cells). These additional furrows are not to be confused with the previously described furrows that become the meatus. Kasper (1936) described these nasofrontal structures within the frontal recess as frontal pits because of their dimple-like appearance. The anatomy of this region is challenging because there is neither a clear developmental pattern nor any constancy in the differentiation of these frontal pits. An

individual may have as many as four pits to a total absence of pit formation. When there is no pit formation, the frontal recess remains a simple blind outgrowth from the middle meatus. The variability in pit formation influences frontal sinus formation and determines the specific pattern of sinus drainage. For example, the more lateral the pit is from the ethmoid infundibulum, the more lateral the frontal sinus and its communication with the nasal chamber is (Kasper, 1936). Various developmental patterns are possible when all four pits are present because each pit has the potential to become a frontal sinus (Schaeffer, 1916a). If the most anterior pit (i.e., pit 1) migrates in a ventral direction it may pneumatize the agger nasi bone becoming an agger nasi cell with the second most anterior pit (i.e., pit 2) migrating anterosuperiorly and becoming the frontal sinus. The terms agger nasi (i.e., referring to the mound of bone) and agger nasi cell (i.e., referring to the pneumatization of the agger nasi bone) are not interchangeable, since each represents a distinct anatomic entity. Moreover, a markedly pneumatized agger nasi cell could have potential pathophysiologic consequences in frontal sinus drainage (Talbot, 1996). Figure 3-28 demonstrates the relationship between the frontal sinus and its drainage tract with the agger nasi cell. Since the roof of the agger nasi cell is the floor of the frontal sinus and the posterior wall of the agger nasi cell is the anterior border of the frontal sinus drainage tract, a markedly inflated cell could interrupt its normal drainage and ventilation (Talbot, 1996). Brunner (et al., 1996) have implicated the agger nasi cell in the pathogenesis of frontoethmoid sinus pain and chronic frontal sinusitis by narrowing of the frontal sinus outflow tract. By the end of the second year of life, one of the anterior ethmoid cells will migrate upwards into the frontal bone to form the frontal sinus (Shea,

Figure 3-28. A 2-dimensional computer tomography reconstruction shows the topographical relationship of the frontal sinus (*FS*) and the agger nasi cell (*ANC*). Note that the roof of the ANC forms part of the floor of the FS.



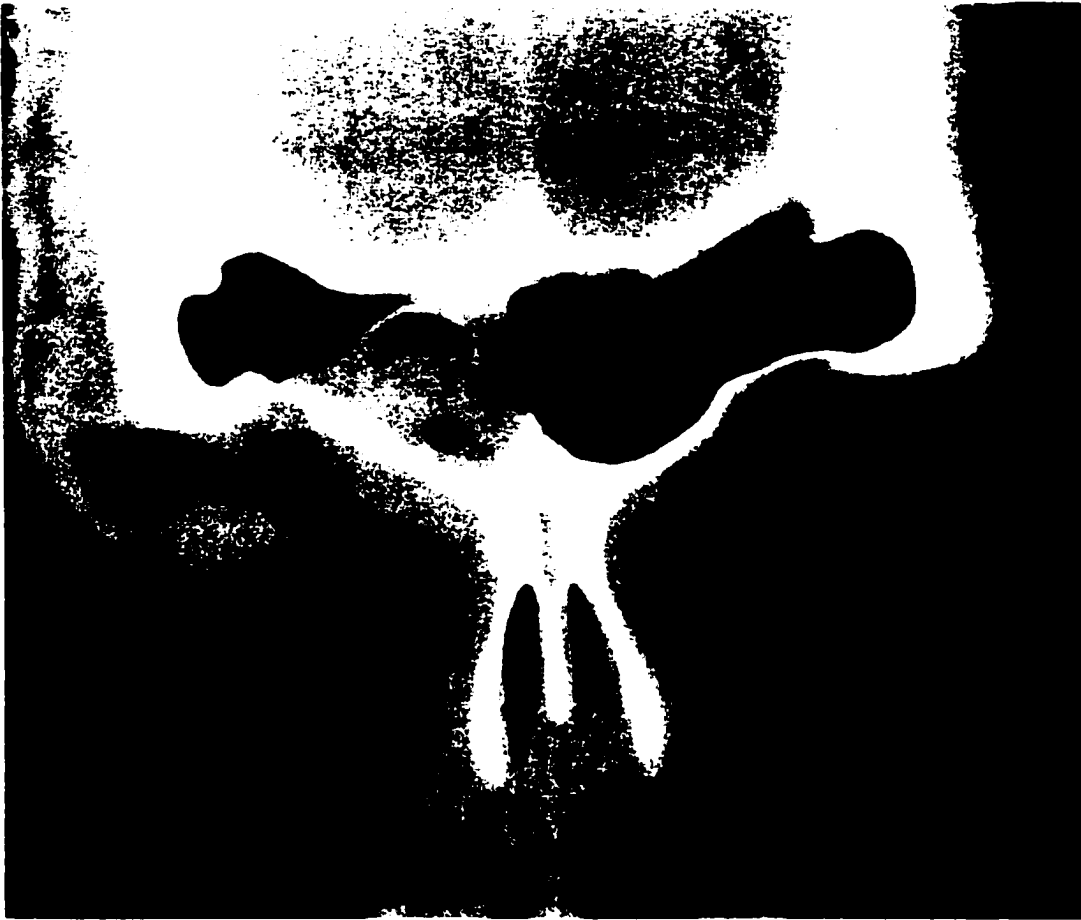
3-28

1936). If no anterior ethmoid air cells develop in the frontal recess, ethmoid air cell extension from the ethmoid infundibulum can then create a frontal sinus (Brown, 1941).

The following is a summary of the possible developmental patterns of the frontal sinus. A frontal sinus can result from a direct outgrowth from the frontal recess if no frontal pits are present; from one of the frontal pits within the frontal recess when present; and as a direct outgrowth from the ventral portion of the ethmoid infundibulum by direct extension or from one of its cellular outgrowths (Schaeffer, 1916c). There also can be combinations of the possible patterns of development resulting in duplicate and even triplicate sinuses on one side (Schaeffer, 1912c).

At birth, the sinus has little clinical relevance, and it is often indistinguishable from the anterior ethmoid cells. Davis (1918) tracked the postnatal development of the frontal sinus of 160 crania in persons ranging from birth to 16 years of age and noted that an evagination into the vertical portion of the frontal bone occurred during the second year. At three years of age, the frontal sinus was observed 3.8 mm above nasion (i.e., a craniometric point defined as the junction between the nasal and frontal bones at the midline) and continued its vertical growth trajectory at an average annual rate of 1.5 mm, until the fifteenth year. Final growth was completed before the twentieth year (Van Alyea, 1951). Although as many as three sinuses have been reported in the literature (Schaeffer, 1912c) (Figure 3-29), adult frontal sinuses generally consist of a pair which are asymmetric (Mosher, 1904). Tilley (1896) illustrated the diversity of frontal sinus morphology, and he discredited the use of prominences of the superciliary ridges as a guide in determining the presence and extent of the sinuses behind them. The potential for the diverse growth patterns of the frontal sinus is so highly variable that each

Figure 3-29. The frontal cell is visible within the right frontal sinus. There is an air-fluid level within the frontal cell. (Courtesy Timothy L. Smith, MD, MPH, Medical College of Wisconsin, Milwaukee, WI)



3-29

configuration is considered unique (Schaeffer, 1916b). Forensic identification of postmortem skeletal material based on the radiography of frontal sinus morphology has been used successfully in criminal investigations (for historical review see Ubelaker, 1985). Shapiro and Schorr (1980) attempted to explain the vast differences observed in pneumatization patterns of the frontal bone and concluded three factors may be ultimately responsible: 1) craniofacial configuration; 2) thickness of the frontal bone; and 3) hormonal growth factors. Urken (et al., 1987a) attempted to evaluate whether an overly “large” frontal sinus may actually be abnormally inflated based on linear and derived area measurements as predictors of its “normal” variation. This led to a follow-up study in which Urken (et al., 1987b) proposed three new categories of excessive pneumatization which they termed *hypersinus*, *pneumosinus dilatans*, and *pneumocele* based on aeration and bony changes of the sinus walls.

3.7.2. Clinical Implications

The adult frontal sinus, when viewed in a transverse section, has been classically described as pyramidal shaped (Mosher, 1904). The base, or floor of the pyramid is the orbital nasal portion of the splanchnocranium; the apex extends outwards a variable distance over the orbit; the anterior wall is subcutaneous; and the posterior wall is cerebral. The adult frontal sinus has been measured as 28 mm high, 27 mm wide, and 17 mm long (Maresh, 1940). This is a representative average, with the actual size and configuration reflecting the origin of the cavity and the superior development into the squama of the frontal bone (Hollingshead, 1968). The anterior, or outer table of the

frontal sinus at its inferior aspect in the midsagittal plane, is approximately twice as thick as the posterior, or inner table. The sinus is compartmentalized further by intrasinus septae and margined by irregular bone. The loss of definition of the scalloped border, or the intrasinus septae, on plain film radiographs indicates chronic infection (Wigh, 1950).

Conflicting terminology has caused confusion in descriptions of the nasal cavity. While anatomists have concentrated on the frontal ostium (i.e., the “discharge” point), surgeons have concerned themselves with the treatment of frontal sinus disease and the so-called nasofrontal duct (Hartmann, 1900). Historically, the communication of this sinus with the nasal cavity has been described as a distinct nasofrontal duct, although others prefer the term frontal recess. The term nasofrontal duct, which is used to describe the communication of the frontal sinus through the middle meatus and into the nasal cavity, is anatomically and developmentally incorrect. To confuse the issue even further, the terms frontal recess, frontal infundibulum, and nasofrontal duct have also been used interchangeably, when in reality they represent different anatomic structures (Stammberger et al., 1995). Conceptually, drainage of the frontal sinus has been likened to an hourglass with the upper portion being the ostium (varying 2 mm to 10 mm in diameter), and the frontal recess representing the lower portion beneath the neck. However, the term frontal recess, introduced by Killian (1895), is based on the prenatal observation of a space that is the continuation of the ascending branch of the first primary interturbinal furrow, with the descending branch becoming the ethmoid infundibulum.

The frontal sinus and the agger nasi cells are formed by pneumatization superiorly and anteriorly from the frontal recess region (Stammberger, 1991). Cells may develop in

the frontal bone adjacent to the frontal sinus, a phenomena that Zuckerkandl (1893) called the *bullae frontalis*. The frontal infundibulum was defined by Killian (1895) as the superior opening of the frontal sinus drainage tract. The nasofrontal duct, as defined by Lang (1989), is any mucosal lined bony passage greater than 3 mm in length. The developmental variability of the frontal sinus leads to the multiple observed drainage patterns, which can be further complicated by the highly variable pneumatization of the adjacent ethmoid air cells and by the position of the uncinate process. As an example, Lothrop (1898) reported a direct communication between the frontal sinus and ethmoid infundibulum in 47% of 125 cadaver specimens, whereas Van Alyea (1946) reported a 12.5% incidence in 112 cadavers.

Serial computer tomography (CT) scans are necessary to demonstrate the sinus anatomy in order to gain access to the frontal sinus via the nasal cavity. In following air cells superiorly into the frontal sinus it is important to dissect as far anteriorly as possible. The position of the anterior ethmoidal artery forms an extremely important anatomic landmark in frontal sinus surgery by helping to identify the frontal recess and preventing an intracranial injury. The vessel runs in a bony canal along the roof of the ethmoid labyrinth to form the posterior border of the frontal recess. Accordingly, surgery above the level of the canal must be anteriorly to enter the frontal sinus. Surgery posteriorly to it would violate the ethmoidal roof resulting in a dural injury.

Accessing the frontal sinus through the nose may be hazardous because one of the visualized openings may not be the primary drainage of the frontal sinus and may lead to an intracranial injury by violating the floor of the anterior cranial fossa. Moreover, scarring from previous surgery or pathologic conditions, can make identification of the

frontal recess impossible. This may require trephining the frontal sinus and transilluminating its floor by placement of a light source in the sinus, or the threading a probe through its ostium into the nasal cavity to guide further surgery. Intraoperative visualization has been aided by CT-guided visualization of the sinus and its outflow tract by electromagnetic and infrared navigational devices (see Table 3-5 for clinical anatomic concerns).

Table 3-5 Important Anatomical Relationships and Their Surgical Implications

Middle turbinate marks the junction of the roof of nasal cavity and ethmoidal labyrinth

Surgery is performed laterally to avoid cribriform plate injury

Middle turbinate slopes downward along its posterior course

To resect, scissors must be inclined downward; posterior tip of middle turbinate and superior turbinate lie in the plane of the face of the sphenoid.

Middle turbinate resection

Superior portion maintained as a landmark; posterior tip may be a source of bleeding and should be electrocauterized.

The nasolacrimal duct runs downward at the anterior border of the attachment of the middle and inferior turbinates.

Inferior or middle meatus antrostomies must not be carried too far anteriorly to avoid duct injury.

The nasofrontal duct drains into the infundibulum or frontal recess cells.

It cannot be safely enlarged and the frontal sinus entered intranasally in every case.

The natural ostium of the maxillary sinus is generally present 1 to 2 cm beyond the anterior attachment of the middle turbinate.

Dissection anteriorly may injure the nasolacrimal duct; dissection superiorly will penetrate the orbit.

Table 3-5 (continued)

Fovea ethmoidalis is generally at a higher level than the cribriform plate.

Thickness, yellow color, and sensitivity of bone are not reliable indicators; the higher the fovea, the weaker its medial wall and the more susceptible to fracture and perforation, with intracranial entry.

Posterior ethmoidal cells may extend behind the sphenoid face

Dissection behind may produce optic nerve injury or CSF leak.

Posterior ethmoidal cells may present superior to sphenoid sinus.

Dissection may produce CSF leak.

Developmental abnormalities of anterior ethmoidal cells exist.

Hypoplasia of the uncinate process may lead to orbital injury on infundibulotomy; hyperplasia of agger nasi cells may block frontal recess, or impinge on nasolacrimal duct, making it vulnerable to surgical injury.

Ethmoidal labyrinth is placed superior as well as lateral to the middle turbinate in its posterior aspect.

Failure to follow cells upward may result in orbital injury.

Narrow ethmoid variant (the ethmoid may not widen posteriorly in a small number of cases).

Lateral dissection in a posterior cell may produce optic nerve injury.

The lamina papyracea lies superiorly in the plane of the membranous middle meatus.

Middle meatus antrostomy must be made on the upper border of the inferior turbinate (Supratubinal) to prevent orbital injury.

Table 3-5 (continued)

Sphenoid ostium lies about 7 cm and 30 degrees from the nares.

Never blindly perforate into sinus; always cannulate transnasally or transseptally.

Sphenoid ostium is 8 mm below cribriform plate.

Dissection superiorly carries the risk of intracranial injury; attempted entry should be medially and inferiorly.

Sphenoid ostium widening should be performed selectively.

Superior widening (danger of cerebrospinal fluid (CSF) leak); inferior widening (danger of sphenopalatine artery injury).

Sphenoid sinus walls may be dehiscent laterally.

Instrumentation laterally may cause internal carotid artery injury.

Sphenoid sinus may be partially encircled by medially displaced internal carotid arteries.

Dissection or fracture superiorly may cause arterial injury.

Adapted from Lawson (1994).

3.8. SPHENOID SINUS

3.8.1. Anatomy and Historical Background

In his 1521 work, *Commentaria*, Giacomo Berengario da Carpi was the first to describe the sphenoid sinuses (Berengario da Carpi, 1521). However, it was not until 1862 when Tillaux (1862) suggested that this sinus was part of the paranasal sinus complex. For almost a hundred years the sphenoid sinus has been described as the neglected sinus because it was “so far off and so isolated,” as compared to the other paranasal sinuses (Mosher, 1903, pg. 177, see also Gibson, 1908 and Fujii et al., 1979). Its more distant topographical location and its decreased involvement with pathological processes have contributed to this delinquency (Reino, 2000). Difficulty in visualization with traditional imaging techniques and limited instrumentation before the advent of endoscopic and computerized navigational approaches did not permit the accessibility available to the other sinuses. Consequently, it is only recently that the sphenoid sinus has received the same attention as the other sinuses.

While Mosher (1903) simply described the sphenoid body as quadrilateral, Dixon (1937) characterized the sphenoid sinus as the most variable cuboidal sinus of all the paranasal sinuses. Zuckerkandl (1882) divided the bony borders of the sinus into superior, inferior, anterior, posterior, and lateral walls.

The *superior wall* is intracranial and consists of the root of the small wing of the sphenoid, the planum sphenoidale (with the optic foramen at each lateral angle), and the sella turcica. A portion of the frontal lobe (with the olfactory lobe), the optic chiasm, and

the hypophysis cerebri lie upon the superior surface of the sphenoid sinus (Gibson, 1908). The superior wall is thin, with the sella turcica and the osseous wall of the optic canal, often projecting into the sphenoid sinus (Hajek, 1926). This explains the occurrence of disturbances of vision with various disease processes of the sphenoid sinus. Zuckerkandl (1892) reported the absence of this wall and Sieur and Jacob (1901) described it as being so thin that the dura could not be removed without its disruption.

Formed by the bony portion of the carotid canal, the *lateral wall* is also intracranial, adjacent to the cavernous sinus. The lateral walls of these venous sinuses contain the following structures from superior to inferior: the oculomotor nerve (*CN III*); the trochlear nerve (*CN IV*); and the ophthalmic and maxillary divisions of the trigeminal nerve (*CN V¹* and *CN V²*). Also contained within each cavernous sinus is the *internal carotid artery* with its sympathetic plexus and the abducent nerve (*CN VI*). The walls of the internal carotid artery canal are thin and project as prominences within the sphenoid cavity. The relationship between the sphenoid sinus and the cavernous sinus is important because it permits extension of destructive processes of the sphenoid sinus into the cranial cavity. The topographico-anatomic relationships are so delicate in this region that it prompted Mosher to comment:

“Therefore, when you curette the external surface of the sphenoid as advised by Grünwald you are treading on thin ice because sometimes the ophthalmic and internal carotid arteries project into the sinus that they would be in danger from such curetting” (Mosher, 1903, pg. 182).

The *posterior wall* lies in the coronal plane and is also intracranial. The basilar artery and the medulla oblongata and pons sit upon the clival surface. The occipital venous sinus is another sinus that is topographically related to the sphenoid.

Consequently, three venous sinuses abut the anterosuperior, lateral, and posterosuperior sides of the sphenoid: the coronary, cavernous, and occipital, respectively.

The *inferior wall* forms the roof of the nose and nasopharynx, however, the latter configuration is dependent upon the extent of development of the sphenoid sinus in the sagittal plane. The thickness varies widely with the extent of pneumatization of the sphenoid sinus (Hajek, 1926). With expansion of the sphenoid sinus into the greater wing of the sphenoid, the pterygoid canal can project as a ridge in the angle between the inferior and the lateral walls (Zuckerlandl, 1893). In most cases, the bony walls are too thick to be punctured easily for removal of the overlying thick mucous membrane (Mosher, 1903). The soft-tissue membrane thins out as it turns superiorly onto the anterior face of the sphenoid.

The *anterior wall* lies in the frontal plane and contains the sphenoid ostium. The ostium may appear large in a macerated skull, but with the mucous membrane covering intact may be narrow. It can vary in diameter from the size of a "pinhead" to several millimeters (Hajek, 1926). This wall can be divided into two parts: an outer which abuts the posterior ethmoid cells; and an inner which is free and forms the posterior roof and posterior wall of the nose. The bony nasal septum of the nose forms a median partition on the face of the sphenoid bone. The anterior wall is important clinically because it permits access into the sinus cavity.

Growth of the usually paired sphenoid sinuses is initiated during the third month of intrauterine development (Dixon, 1937; Van Alyea, 1941). These two sinuses generally develop asymmetrically with one sinus encroaching upon and limiting the growth of the other. The bony partition between the two sinuses has been incorrectly

called the “median septum.” Congdon (1920) suggested the more appropriate term “intersinus septum” because the partition is frequently found more lateral than medial, and is the accepted term today. Complete and partial septation of the sinuses is a frequent occurrence, with no clear pattern of division emerging in a number of studies (e.g., Congdon, 1920). The variety of encroachment patterns, the pneumatization of contiguous structures, and the irregularities of its septa are all considered normal variants (Van Alyea, 1941).

The sphenoid sinus begins development as an evagination of the nasal mucosa into the posterior portion of the cartilaginous nasal capsule. The inferoposterior expansion forms a pouchlike cavity in the cartilage, the wall of which is called the sphenoid conchae, or Bertini’s ossicles (Van Alyea, 1941). At birth, the pyramidal shaped paired ossicles which are in contact with the medial pterygoid laminae and help to form the roof of the nasal cavity, begin to ossify. At the time of birth, the sphenoid sinus is primarily an evagination of the sphenoethmoid recess, with essentially no further growth until age 3 years. At this time, the sphenoid conchae become attached to the presphenoid and the cavity develops into the definitive sphenoid sinus (Van Gilse, 1922). The sinus later begins to pneumatize the sphenoid bone and by the seventh year extends posteriorly towards the sella turcica (Van Gilse, 1926). Based on the prenatal development of the sphenoid bone (e.g., the anterior to posterior arrangement of its ossifications centers), Congdon (1920) identified four patterns of sphenoid sinus pneumatization: conchal; presphenoid; basisphenoid; and occipitosphenoid (i.e., the basilar part of the occipital bone). Congdon (1920), after study of 181 specimens, classified 5% as conchal, 4.5% between conchal and presphenoid types, 23.5%

presphenoid, and the remaining 67% included basisphenoid and occipitosphenoid types. The relative incidence of the types of sphenoidal pneumatization reported varies with different investigators. Hammer and Radberg (1961) found a conchal type in 2.5% of cases, a presellar type (presphenoid) in 11%, a postsellar type (basisphenoid) in 59% and mixed types in 27%. In the most common developmental type, the postsellar, the sinus has extended posteriorly toward the sella turcica by age 7 years. Development may continue into adulthood to involve the basisphenoid. However, the extent of pneumatization varies widely producing recesses in the sphenoid rostrum, the lesser wing of the sphenoid, and the orbital processes (Sluder, 1909; Cope, 1917; Peele, 1957). Pneumatization of the pterygoid processes has been reported in 25% to 40% and the anterior clinoid process in 13% of adults (Scuderi et al., 1993). Donald (1995) reported the occurrence of a septal recess, called the sphenovomerine bulla, by pneumatization of the vomer. The tendency to pneumatize contiguous bony structures is not restricted to human development and is also seen in CT-based investigations of the sinus anatomy of the great apes (Márquez et al., 1999, Figure 3-30).

The average adult sinus measures 20 mm in height, 23 mm in length, and 17 mm in width (Van Alyea, 1951). The volume varies from 0.1 to 30 mL, with the average ranging from 5 to 7.5 mL (Dixon, 1937; Van Alyea, 1951). As the sinus expands, vessels and nerves adjacent to the lateral aspect of the body of the sphenoid bone form indentations in the walls of the sinus. Van Alyea (1951) found projection of the internal carotid artery into the lateral wall in 65 specimens (n=100), with the projection being pronounced in 53 of them (Figures 3-31 – 3-35). Based on a study of 1600 skulls,

Figure 3-30. a: An axial scan of adult chimpanzee (*Pan troglodytes* catalogue no. 51382 Division of Anthropology, American Museum of Natural History) showing invasion of the sphenoid sinus proper into the lateral pterygoid plate (small white arrowhead). **B:** An axial scan of an adult gorilla (*Gorilla gorilla gorilla* catalogue no. 72895 Department of Mammalogy, American Museum of Natural History) demonstrating the sphenoid sinus (*white asterisk*) having invaded and pneumatized the pterygoid plates (*white arrows*).



Figure 3-30

Figure 3-31. A: Parasagittal section through the sphenoid and posterior ethmoid sinuses. The lateral wall of these sinuses has been removed to expose the cavernous sinus and optic nerve. B: The proximity of the optic nerve and internal carotid artery to the lateral wall of the sphenoid and posterior ethmoid sinuses is illustrated.

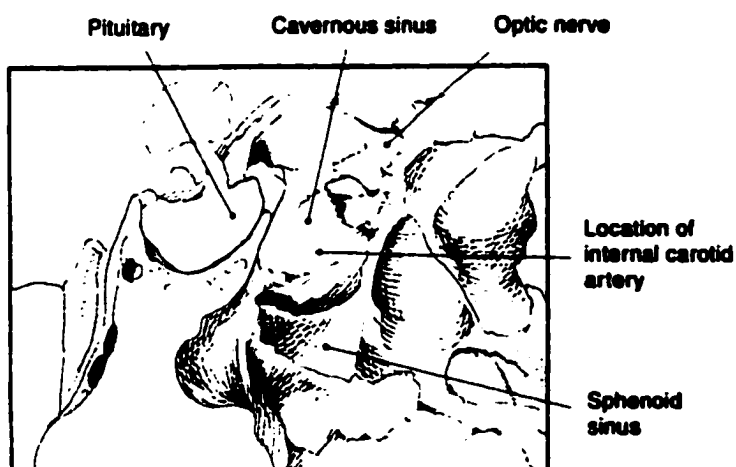
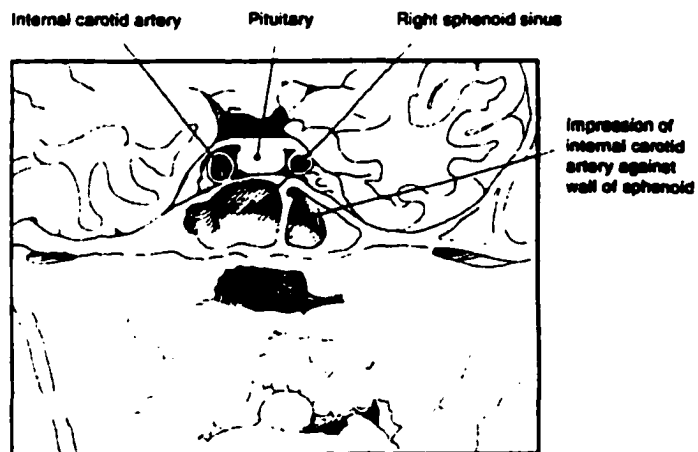
3-31A**3-31B**

Figure 3-32. A: A coronal section of a human cadaver that is contiguous with the section seen in Figure 3-35 C, which is at the level of the posterior sphenoid sinus. **B:** The diagram of A demonstrating the close relationship of the sphenoid sinus to important neurovascular structures. **C:** A CT scan of specimen A. The arrows point to the internal carotid.

3-32A



3-32B



3-32C



Figure 3-33. Lateral wall of left sphenoid sinus as visualized with a 25° endoscope. The optic nerve (*A*) is crossing horizontally the internal carotid artery (*B*).



3-33

Dixon (1937) found that the optic nerve was present as an indentation in the sinus wall in 8% of the specimens, and the vidian nerve in 7% (Figure 3-34). The primary septum was found in the midline in only one fourth of the subjects. Generally, the septum is asymmetric, with most of its bony wall coursing to one side and sometimes exhibiting an “S” or “C” shape.

3.8.2. Clinical Anatomy

The sphenoid sinus drains by a single ostium into the sphenoethmoid recess. Clinically, the ostium is 2 to 3 mm in diameter and may be round, or elliptical (Dixon, 1937; Van Alyea, 1951). The sinus depends on mucociliary flow for drainage as the ostium is located 10 to 15 mm above the floor of the sinus, or 8 mm beneath the posterior border of the cribriform plate (range 1 to 15 mm), and 5 mm lateral to the nasal septum (Dixon, 1937). Pneumatization of the posterior aspect of the middle turbinate may make visualization of this ostium difficult. The importance of its identification in surgery has led to several studies measuring the clinical distances (Figures 3-21 and 3-24 and Table 3-6).

One of the most important relationships is that of the optic nerve and its bony canal to the sphenoid sinus. Onodi (1908) catalogued 38 distinct morphological relationships between the optic canal and structures comprising the nasal complex. He corroborated the study of Berger and Tyrmann (1886) in which posterior ethmoid air cells were found extending so far posteriorly that the anterior wall of the sphenoid sinus lied behind the optic canal. The posterior ethmoid air cells have the tendency to develop

Figure 3-34. A: A coronal section of a human cadaver exposing the posterior wall of the maxillary sinuses. **B:** The residual maxillary cavity is shown along diagrammatically with the adjacent posterior ethmoid cells. Note the fovea ethmoidalis is properly identified.

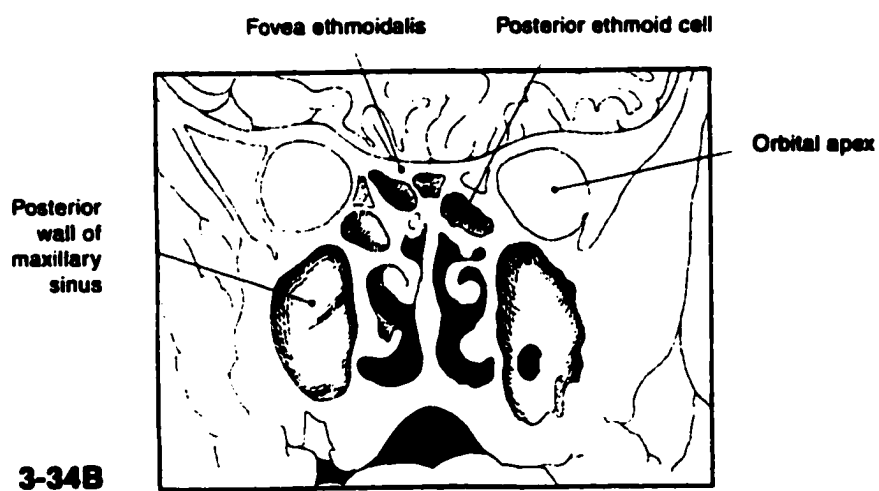
3-34A

Figure 3-34. (continued) C: The posterior surface of the specimen in **A** is immediately dorsal to the maxillary sinus or at the plane of the pterygopalatine space. **D:** Diagram of the dorsal surface of the anterior wall of the sphenoid sinus. Note the relationship of the nerves to the sinus wall. **E:** CT scan of the specimen in Figures 3-8 shows the remnant of the pterygoid plates and the convergence of the posterior ethmoids (Figure 3-8A) and the sphenoid sinus (Figure 3-8C).

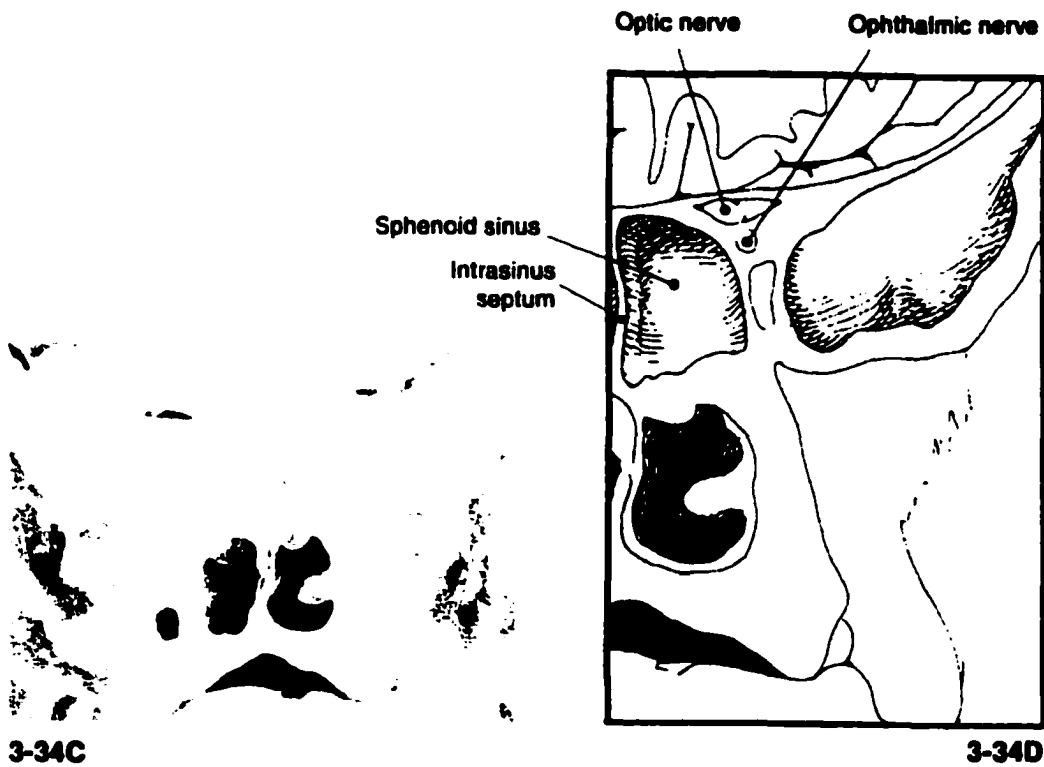


Table 3-6 Distances in sphenoid sinus

	Distance from anterior nasal spine	Distance from anterior nasal rim
Sphenoid ostium	7 cm	—
Pituitary fossa	8.5 cm	—
Inferior face of sphenoid	—	5.7 cm
Posterior wall of sphenoid sinus	—	7.6 cm
	Dixon (1937) in living subjects	Mosher (1929) in cadavers

laterally and superiorly around the sphenoid sinus. The extension has been recorded laterally and posteriorly 1.5 cm beyond the anterior wall of the sphenoid sinus (Onodi, 1908). In recognition of Onodi's anatomic contribution regarding the migratory tendency of these posterior ethmoid air cells, they have been eponymically designated *Onodi cells*.

Understanding the extensive variations documented by Onodi requires knowledge of the pre- and postnatal development of the different portions of the sphenoid base (i.e., the presphenoid, the orbitosphenoid, and the basisphenoid). The appearance of the sphenoid turbinate, the development of the ethmoid air cells, and the centers of ossification of the sphenoid are all related morphologically. These relationships have a direct effect on the optic nerve and contiguous structures.

The thinness of the bony walls of the sphenoid is an important consideration clinically for they may separate the sinus from the dura by 1.0 mm (Ritter, 1978), 0.5 mm (Mosher, 1903), 0.25 mm (Gibson, 1908), or only by the intervening mucosa (Fujii et al., 1979). The presence of bony dehiscences may result in orbital and intracranial disturbances from disease in the sphenoid sinus. Berger and Tyrmann (1886) were early to recognize the importance of this clinical barrier. Several workers have subsequently documented and classified the nature of these bony dehiscences. Hyrtl (1869) reported the presence of dehiscences in the lamina papyracea of the ethmoid bone and also in the lateral wall of the sphenoid sinus which communicated with the middle cranial fossa. Zuckerkandl (1893) and Hajek (1926) also observed dehiscence of the intersinus septum which may result in disease in one side affecting the optic nerve on the contralateral side. Dehiscence of the sella floor is very rare (Zuckerkandl, 1893), and dehiscence of the lateral wall over the internal carotid artery is also uncommon.

The sphenoid sinus may undergo further enlargement by absorption of its bony walls with age. Gaps that develop may result in the mucous membrane lying directly against the dura mater (Fujii et al., 1979). The optic canals may vary in size from four to 6.5 mm, and in shape from the usually circular configuration to various degrees of ovalness. White (1924) found that the smaller the optic canal, the more extensive the pneumatization around it, therefore the greater possibility for nerve involvement with disease in the sphenoid sinus. White (1924) concluded that both the shape and size of the canals were dependent largely upon the amount of pneumatization surrounding them.

Of the many sinus surgical procedures done today, the sphenoethmoidectomy operation is considered one of the more complex. Schaefer (1998) reminds us of the comments offered by the surgeon Harris Peyton Mosher when referring to the ethmoidectomy procedure: "one of the easiest operations with which to kill a patient." To be performed safely and effectively, the sphenoethmoidectomy operation requires a detailed knowledge of the anatomy of the paranasal sinuses. When surgical procedures were performed during the early twentieth century, they usually involved an external approach. The intranasal sphenoethmoidectomy operation was first reported by Yankauer (1921), at the Mount Sinai Hospital, New York. However, the inherent danger of this procedure resulted in very little endonasal sinus surgery being performed until the introduction of the endoscope to the United States from Europe in 1986. It had already been in use for over a decade in Europe. With the advent of more sophisticated cross-sectional imaging techniques and refinements in instrumentation, the

sphenoethmoidectomy operation is considered an essential procedure for surgeons well grounded in the intricate anatomy of the nose and paranasal sinuses.

3.9. DISCUSSION

The detailed anatomy of the nose and paranasal sinuses has gained tremendous clinical importance because of the current trend to minimally invasive (intranasal) surgery for the treatment of sinonasal disease. A knowledge of their morphology and relationship to each other and the orbit and brain gained by traditional dissection studies has been greatly expanded by modern radiologic imaging modalities which permit insight into visualization and structural integration of both their osseous and soft tissue components. Their strategic location in relation to vital craniofacial structures demands a precise knowledge of their anatomy for the safe performance of surgical procedures. The accurately and defined description of sinus size and structure in different human geographic regional populations may implicate their physiologic and biological role in the climatic adaptation of different ecological settings. The ability to delineate precisely the nasal complex 3-dimensionally facilitates comparative anatomical study and allows greater insight into mechanisms of evolutionary change.

CHAPTER 4

CLIMATE AND THE NASAL COMPLEX: INVESTIGATION OF *MACACA FASCICULARIS* AND *MACACA MULATTA*

4.1 INTRODUCTION

The nasal complex provides several vital functions. For example, it is the entry portal of the upper respiratory tract. As such, all of its constituent components must be included in any comprehensive study examining respiratory adaptation to climate. In this study, groups of *Macaca fascicularis* and *Macaca mulatta* inhabiting lowland and highland habitats respectively were to test the hypothesis that climate affects morphology.

The study will use a sample of dry crania of *Macaca fascicularis* and *Macaca mulatta*. Each cranium will provide measurement data on various aspects of the nasal cavity, maxillary sinus, and other craniofacial landmarks. Linear distances were obtained using traditional anthropometric measurements. Volume measures were obtained using a new seed-filling method (Márquez et al., 1995).

It is hypothesized that there will be significant differences in nasal complex morphology for macaques inhabiting different climates. Isolation and identification of the specific regions of the nasal complex involved in adaptive solutions to environmental challenges was identified and results may contribute to knowledge about the function of the various components of the nasal complex. These results may lead to a better understanding of the inter-relationships amongst these components. The macaque differences within the nasal complex may provide baseline knowledge for a fuller understanding of the adaptive evolutionary nature of the upper respiratory system.

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**THE HUMAN NASAL COMPLEX: A STUDY OF ITS ANATOMY, FUNCTION AND
EVOLUTION BY CT, COMPARATIVE
AND
MORPHOMETRIC METHODS**

**By
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4.2. A HISTORY OF RESEARCH INTO THE BONY NASAL COMPLEX

Indices of the nasal region (e.g., nasal index defined as $[\text{maximum nasal breadth/nasal height}] * 100$) have been widely used in anthropology for distinguishing the various human races since the eighteenth century (e.g., Blumenbach, 1775 and Topinard, 1878). Racial differences could be accounted for by the fact that, when anatomically modern humans migrated to other geographic areas of the world, physiologic adaptations arose in response to local climatic conditions. Such adaptations could be manifested in the osteological composition of the nasal region. One of the earliest studies to demonstrate a relationship between the nasal index and climatic factors of multiregional populations was published by Thomson and Buxton (1923). Their study was not the first to call attention to the association of climate and the bony nasal morphology. That distinction falls to the American anthropologist Ales Hrdlicka whose first publication on the craniology of the Eskimo suggested that the narrow nasal aperture of these early North Americans was importantly related to the effects of the Arctic cold (Hrdlicka, 1910). He did not, however, discuss the functional significance of this narrowing. Osteological changes of the nasal region may reflect adjustments and accommodation of respiratory mucosa, the primary modifier of inspired air. In an effort to explain such adaptational characteristics of the bony nasal profile, the correlational method has often been used in anthropological studies which have linked nasal morphology variation with climate (e.g., Thomson and Buxton, 1923; Davies, 1932; Weiner, 1954; Wolpoff, 1968). For example, Endler (1986) suggested that this method demonstrates natural selection by establishing an association between the variation in a single trait, or set of traits, and specific environments. Workers who have explained the apparent correlation between the nasal index of various human populations and climate as an adaptive response to climatic variability include Davies (1932); Weiner (1954); Crognier (1981); and Beals et al., (1984). It has been shown that populations from hot moist climates generally have a

larger nasal index than populations from cold dry climates (Thomson and Buxton 1923; Davies, 1932). For example, the Eskimo's nasal profile fits into this pattern with their rather low nasal index (i.e., a narrow and high nasal skeletal aperture). Weiner (1954) suggested that the critical variable operating on nasal shape (i.e., the nasal index) was not temperature/relative humidity but instead was absolute humidity. According to Weiner, correlations among the nasal index and temperature and relative humidity were not as high as the correlation between the nasal index and absolute humidity. From this finding, he concluded that absolute humidity was the operative critical factor in determining nose form.

The means by which the relationships between the morphologic state of cranial structures and the nature of their adaptive solution to their particular environment has been investigated is craniometric analysis (e.g., Atchley & Hall, 1991). Climate is an example of an environmental factor which is thought to be a major selective force that affects nasal variation as represented by the breadth and height of the bony nasal aperture (Boaz, 1997). However, the relationship between climatic variation and the human nasal index has been challenged as an indication of natural selection in humans (St. Hoyme and Iscan, 1989). Traditionally, the height and breadth of the piriform aperture has been used since it is through this triangular shape that the nasal cavity is involved in the inspiration and expiration of air (e.g., Thomson and Buxton, 1923; Wolpoff, 1968; Franciscus and Trinkaus, 1988). Many investigators hold to the premise that environmental factors which affect craniofacial dimensions would also affect the primary entry portal of the upper respiratory system, the piriform aperture. Examples of related craniofacial adaptations include masticatory apparatus adjustments due to differences in diet (Albrecht, 1978) and foreshortening of the splanchnocranium caused by brain expansion (Le Gros Clark, 1962). Bergland (1963) noted that the size and shape of the nasopharyngeal cavity is largely determined by the bony nasopharynx. However, little attention has been paid to the internal naris (choanae), even though the nasal cavity communicates with the

nasopharynx via this portal (see Figure 4-1a). Its potential importance as a functional determinant warrants measurement of this region. In addition, previous studies have not included measurements of the maxillary sinus which also contributes a significant dimension to nasal complex configuration (see Figure 4-1b). Choanal dimensions and maxillary sinus volumes must be factored into any morphometric analyses to ensure all possible structures are accounted for which may be under the influence of selection. This would allow for investigation of whether selection may have also been acting differentially on regions of the upper respiratory system.

Glanville (1969) has suggested that there is a direct relationship between nasal shape, prognathism and the shape of the maxillary dental arch. He found strong correlations between nasal height and the length of the cranial base, and between nasal breadth and the distance which separates the upper canines. Such relationships can lead to inferences about functional relationships as Laitman and colleagues (e.g., 1977; Laitman et al., 1978, 1979, 1982, 1996) have raised in regard to cranial base flexure and positional descent of the larynx. If both the nasal shape and maxillary dental arch-prognathism complex are subject to direct selection by environmental stress, then, by extension, comparing these results with nasal complex dimensions could uncover functional relationships for these accessory cavities of the nose relating to climate.

Figure 4-1a. Inferior view of *M. fascicularis* skull showing relative size of internal nares, or choanae (*Ch*).

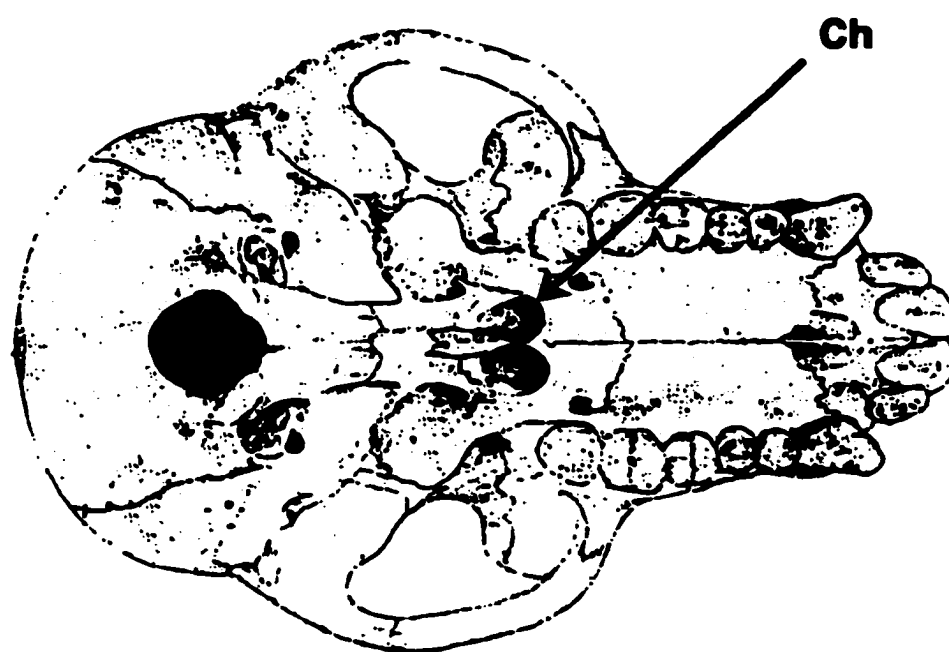


Fig. 4-1a.

Figure 4-1b. Frontal view of same skull as in 4-1a showing relationship of right maxillary sinus (*MS*) with nasal cavity.

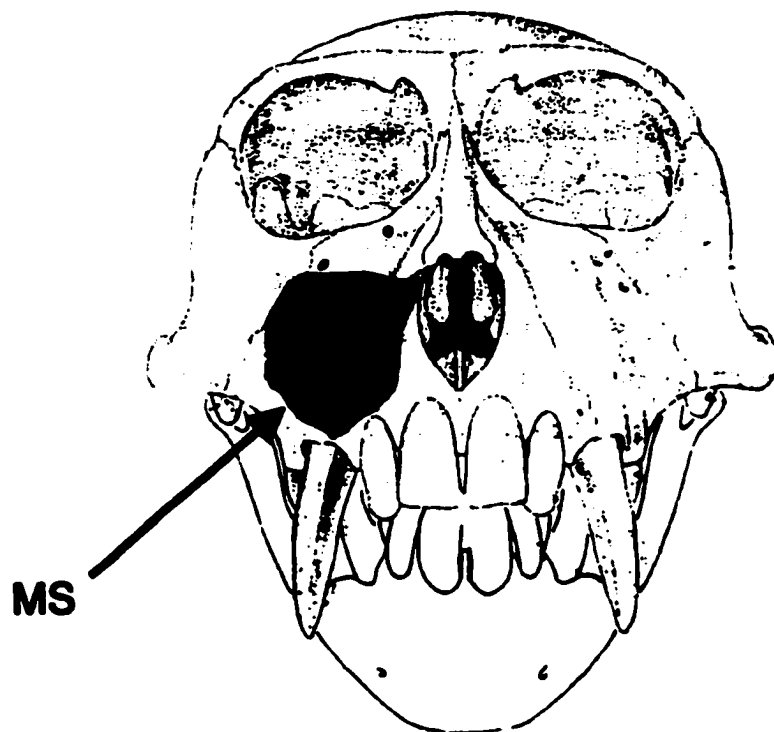


Fig. 4-1b.

4.3. THE NASAL COMPLEX: ANATOMY & PHYSIOLOGY

4.3.1. Anatomy

The external nose is a cartilaginous structure which channels inspired air. As discussed in previous chapters the nasal complex is involved in olfaction and the filtering of particulate matter (e.g., bacteria, dust, etc.). However, its role as the “porte d’entrée” of the upper respiratory tract necessitates detailed study of its functional importance in respiration. Although the dynamics of some features of the upper respiratory system have been reported before (e.g., Laitman et al., 1982; 1988), the relationship between paranasal sinuses and nasal cavity structures still remains unclear. Knowledge of the unique anatomy of the nasal complex should be integral to a fuller understanding of the functioning of the entire upper respiratory system.

4.3.2. Physiology

A properly functioning respiratory system requires that inspired air reaching the trachea and bronchi be 100% humidified and be at or near a core body temperature of 37° Celsius (Negus, 1952, 1958; Taylor, 1981). Thus, two key functions of the nose are to condition the inspired air by supplying water, and to regulate the air temperature via its respiratory mucosal linings (Negus, 1952, 1957b). Consequently, the nose requires a large surface area to provide attachment for the mucosal lining in order to meet these demands imposed by the respiratory system, otherwise cold-or heat-induced respiratory damage would develop. A large surface area is afforded by the nasal septum, consisting of an anterior cartilaginous and a bony posterior part, which separates the nasal cavities into two compartments. Division of the nasal cavity via its septum has the effect of nearly doubling the surface area for its mucosal lining (Marshall and Attia, 1987). The mucosal

surface is further augmented by the presence of three paired bony sheets known as the nasal turbinates (Hillenius, 1992). Hillenius (1994) has suggested that the complex turbinate system, which originated with the therapsid ancestors of mammals, relates to elevated ventilation rates and the evolution of endothermy.

4.4. EVOLUTION AND FUNCTION OF THE NASAL COMPLEX

Aspects of skeletal nasal morphology have been important features in the description and analysis of both extant and fossil material (e.g., Conroy et al., 1978; Ward and Pilbeam, 1983; Brown et al., 1985; Ward & Brown, 1986; Johanson et al., 1987). Of particular interest has been the paranasal sinuses, which Negus (1957a, 1958) reported to be a characteristic cranial feature of placental mammals, and the maxillary sinus, in particular, which may be a primitive eutherian trait. Paranasal sinuses are such a prominent feature of the modern human face that their presence may be a paleontological marker for our own species, *Homo sapiens* (broadly defined by Stringer et al., 1979). This potential phylogenetic marker may explain why workers have traditionally described them when examining fossil material even though their taxonomic valence has not been fully documented (e.g., Weidenreich, 1941; Leakey, 1951; Tillier, 1975; Ward and Brown, 1986; Wood, 1991; Márquez et al., 2001). A phylogenetic reconstruction based on sinus anatomy was attempted by Begun (1992) where he utilized maxillary sinus morphology in conjunction with other facial features to assist in characterizing the hypothetical common ancestor of the living great apes. Another study was the examination of the maxillary sinuses of fossil catarrhines by Rae (1999) where he carefully describes the phylogenetic consequences of maxillary sinus presence, or absence, and size in different taxa. One preliminary conclusion reached is that cercopithecoids may have lost the maxillary sinus early in their evolution, but Rae concludes that additional work is necessary on the detailed morphology of the sinuses in fossil catarrhines in order to reconstruct their evolutionary

pathways. Despite their prevalence, there is neither a satisfactory explanation for the existence of paranasal sinuses nor has there been a satisfactory attempt at correlating their morphology with function.

A number of studies have shown that all of the paranasal sinuses originate as mucosal evaginations from the nasal fossa, with which communications remain throughout life (e.g., Libersa et al., 1981; Som, 1984; and Rice and Schaefer, 1993). To date, however, the paranasal sinuses remain a mystery with regard to ontogenetic pattern, comparative function, and disease processes. Nevertheless, many theories, arguably dating back to Galen (Nemours, 1931) have been advanced to explain their relationship to differing functions (see discussion of proposed functions for the paranasal sinuses in chapter 3).

4.5. HYPOTHESES, SPECIFIC AIMS, METHODS & MATERIALS

4.5.1. Hypotheses

- 1) Climatic conditions (temperature and humidity) affect the craniofacial dimensions of the nasal complex in *Macaca fascicularis* and *Macaca mulatta*.
- 2) Dental measures can predict maxillary sinus size in *Macaca fascicularis* and *Macaca mulatta*.

4.5.2. Specific Aims

Specific Aim 1.

To assess via linear and volumetric measurements craniofacial proportions of lowland and highland macaque groups and determine if they are correlated with climate.

Specific Aim 2.

To determine whether dental measures can predict maxillary sinus size with the use of a regression.

4.5.3. Methods

4.5.3.1. *Choice of animal model*

Macaques, rather than humans, have been selected as our model for studying the relationship between the nasal region and climate in primates. The reason is that the recency of migratory human populations may preclude using them as reliable models to test the long-term relationship of climate to nasal morphology. Certain macaque groups, to the contrary, have been suggested to be inhabitants of different climates for extensive periods of time (Delson, 1980). Although macaques and humans have a number of morphological differences in their upper respiratory configuration - such as the macaque larynx being positioned higher in the neck (Laitman and Reidenberg, 1993), or that they exhibit only one of the four paranasal sinuses (i.e., maxillary sinus) - they do have many similarities. For example, my gross dissection of *Macaca fascicularis* (n=31) and *Macaca mulatta* (n=11) revealed similar internal nasal morphology in their turbinate system and maxillary sinus configuration (Márquez et al., 1996b)(see Figure 4-2). Additional similarities between macaques and modern humans is in their epithelial structure (Harkema, 1981), their similar patterns in the direction of their mucociliary movement within the nasal cavity (Lucas, 1933) and that they are considered microsmatic primates.

Figure 4-2a. Right lateral view of nasal cavity wall of *Macaca fascicularis* showing tongue (*TG*), hard palate (*HP*), inferior turbinate (*IT*), middle turbinate (*MT*).



Fig. 4-2a

Figure 4-2b. Right lateral view of nasal cavity wall of *Macaca fascicularis* whose middle turbinate (*MT*) is reflected exposing the medial wall of the maxillary sinus (*MS*).



Fig. 4-2b

Figure 4-2c. Right lateral view of nasal cavity wall of *Macaca fascicularis*. The middle turbinate (*MT*) has been removed revealing the internal morphology of the maxillary sinus (*MS*).



Fig. 4-2c

4.5.3.2. Choice of Old World monkey species

Macaca mulatta (the rhesus monkey) will serve as the primary focus of the study because they live at both low and high altitudes (Fooden, 2000). Although *M. mulatta* may lack the geographic distribution of humans, they can be found in quite diverse climatic habitats. For example, *Macaca mulatta* ranges from Paktia, Afganistan (Puget, 1971), through much of India (Frick, 1969), and into Indochina (Van Peenen et al., 1969). Of all the macaques, *M. mulatta* occupies the widest range of habitats: from sea level to 3000 m in the mountainous areas of Afganistan (Kullmann, 1970), 3050 m in Nepal (Richie et al., 1978), and even up to 4,300 m in the temperate forests of the Himalayas in northern Pakistan (Haltenorth 1975). Seasonal variations may be extensive in these high altitude environments, with their 3 month wet seasons (averaging 38cm of rain), warm dry springs, and freezing winters averaging 6.5 cm of snow (Roberts, 1977). Temperatures vary from below freezing to above 50°C. Rhesus macaques from Afganistan, Pakistan, Kashmir, Nepal, Kumaon in India, and the Himalayas will comprise the highland sample. The lowland sample will be rhesus macaques from northern areas of India (e.g., Uttar Pradesh, Punjab and Bhuta). The selection process is based on the historical records of capture for each of the specimens examined at their respective museum collections.

A possible complication of relying solely on *M. mulatta*, however, is that a lowland population may migrate from a highland area, thereby confounding the analysis. As a result, *Macaca fascicularis* (also known as the cynomolgus, crab-eating, longtail and kra macaque), a natural lowland dweller, has been chosen as an additional comparator. *M. fascicularis* has a wide range of distribution in Southeast Asia across 30° of latitude and 35° of longitude (Fooden, 1993; see also Fooden, 1995). *M. fascicularis* has been reported to live in primary forest, disturbed forest, and secondary forest, as well as in riverine and lowland coastal forest (Medway, 1970).

M. fascicularis seems a good choice for comparison as it is a species very closely akin to *M. mulatta*. Indeed, there is still controversy on whether *M. fascicularis* is a subspecies of *M. mulatta* or a distinct species. At one time *M. fascicularis* was considered conspecific with *M. mulatta* based on a phenotypically intermediate *M. fascicularis* population from Indochina (Fooden, 1964). However, it is now thought that these animals do not represent a single intergrading species, but rather two separate species whose ranges came into secondary contact, thereby resulting in their hybridization (Fooden 1971). Fooden (1980) does, however, place *M. fascicularis* and *M. mulatta* into a single species group that also includes *M. fuscata*, and *M. cyclopis*. Unfortunately, morphological, chromosomal, allozyme, and mtDNA based studies are in disagreement about the relationships among these four taxa (compare for example Cronin et al., 1980, Hayasaka et al., 1988, Melnick and Hoelzer 1993, and Disotell pers. comm.). For example, Chiarelli (1962) reports that *M. mulatta* and *M. fascicularis* exhibit similar amounts of lengthening of the X chromosome, whereas Paszter (1976) states that they cannot be differentiated chromosomally by the G (Giemsa) banding technique. Other studies have shown a high degree of similarity in the proteins between these two species (Weiss, et al., 1973). In addition, *M. mulatta* and *M. fascicularis* share similar facial dimensions which make these two species prime candidates for a comparative morphological study. Due to their great craniofacial similarity, differences between aspects of their nasal complex should reflect climatic and not species differences. However, the confounding effects of masticatory adaptations to dietary regimes may contribute to differences in craniofacial morphology between these two taxa and thus may affect nasal complex variation in an incidental rather than a causal manner. So in effect, masticatory compensatory response to dietary staples could potentially indirectly affect nasal complex morphology with differences reflecting an architectural instead of a thermoregulatory basis. To ensure that the interpretation for the differences in nasal complex components will be of a respiratory rather than a biomechanical adaptation

multiple regression statistical treatments will be implemented. This statistical technique allows one to select an independent variable (i.e., a nasal complex component) and regress a set of dependent variables simultaneously. The groups of dependent variables to be studied will include the most likely masticatory dependent variables (i.e. zygoma and maxilla height), respiratory variables (i.e., choanal and nasal breadth), and neutral variables (i.e., external auditory meatus and foramen magnum length). This line of investigation will identify intimate relationships among variables, potentially eliminate the possible explanation of nasal complex differences attributed to biomechanical rather than climatic influences, and support the bivariate linear regression treatment of the sample data.

In addition to being a useful comparator for *M. mulatta*, the use of *M. fascicularis* also brings a number of other benefits. For example, aspects of its basic biology are becoming well known since the species is used extensively as an animal model in medical research, especially with regard to the otologic region and upper respiratory tract. Indeed, members of our laboratory have great familiarity with this species (e.g., Eden, Laitman, Gannon, 1988, middle ear aeration; Gannon, Eden, Laitman, 1994, compartments and functions of palatal muscles).

The null hypothesis of this study is that nasal complex anatomy will not reflect climatic differences whereas the alternative hypothesis implies a significant correlation between variations in nasal complex and climate. The secondary hypothesis will test a presumed axiom from work of previous investigators that have reported the existence of a strong relationship between fully erupted molar teeth and adult final maxillary sinus form (e.g., Keith, 1902; Underwood, 1910).

4.5.3.3. *Specific methodology*

Linear measurements of craniofacial and dental parameters and volumetric measures of the maxillary sinus and endocranial capacity of dry crania were determined by using the following methods:

1) standard craniometric techniques, 2) a seed-filling technique, and 3) CT-imaging with two- and three-dimensional reconstruction and reformatting techniques.

1) 69 craniodental linear measurements were taken from which 3 indices were derived (see tables 1-4). Skull length (prosthion-opisthocranium) was obtained with a spreading caliper, all other linear measures with a digital sliding caliper, endocranial and maxillary sinus volumes via a seed-filling technique (see below). As an added precaution and to safeguard from errors stemming from bias several colleagues measured independently all linear and volume measures a total of three times with scores being averaged before statistical treatment. The selection criteria for these measurements were based on the following: a) they have previously been shown to reflect “patterns” of craniofacial morphology, and b) they are traditional measures and thus allow for direct comparison to previous studies.

2) A recent protocol for establishing maxillary sinus and nasal cavity volumes for *Macaca fascicularis* (Márquez, Gannon, and Laitman, 1995) has been developed as a way to test some of the current approaches of craniometric analysis. A shortcoming of these approaches relates to the difficulty in obtaining accurate volumetric measurements. Volume measurements on these macaque groups was obtained by the use of oil rapeseeds. These seeds were chosen due to their small size and their superior packing qualities. Filling the sinuses required that all communicating portals to the nasal cavity be clearly identified and subsequently sealed with cotton or modeling clay (inert materials which do not damage the specimens upon removal). With each cranium positioned on its side, the seeds were then introduced into the maxillary sinus via a funnel placed either through the choana or piriform aperture. Continual gentle tapping of the cranium was done throughout the filling process in order to ensure that the seeds packed and settled. Any seeds projecting through the opening of the medial wall of the maxillary sinus were leveled off and removed through the piriform aperture. Transillumination was required to confirm the complete filling of the sinus. Crania were weighed before and after seed-

filling so the difference obtained represented the weight of the seeds alone. This procedure was repeated three times for each cranium. Data for weight (in grams) was then transformed to a volumetric measurement (in milliliters) by linear regression. The reference regression line was created by use of weights for nine known volumes of seeds (5ml to 45ml at 5ml intervals), whereby each observation was measured and recorded twice by using two different shaped graduated cylinders. Endocranial volumes were similarly obtained by filling the cranium with seeds through the foramen magnum. Endocranial volumes were taken in order to standardize measures to body/skull size differences. The linear regression equations used for weight to volume transformations were generated in each of the collection sites where the seeds were utilized in order to reduce measurement error from the effects of humidity (see Albrecht, 1983). As the outer coverings of the rapeseeds are of an organic nature humidity factors would affect expansion parameters of the seeds. Generating the linear regression equation on the day, and in the environment, in which volume determinations were conducted, ensures reduction in the source of measurement error.

The oil rapeseed filling method used here requires inspection of the material in order to ensure that all foramina, fissures, and internal nasal morphologies are intact. Once approved the skull is catalogued and weighed on a scale with an accuracy to 0.01 gm. An additional method of determining volumes was employed using plain film radiography. The X-ray method requires 2 separate plain radiographs per individual: a frontal view to assess the width of the maxillary sinus, and a lateral view to assess the anteroposterior length and height of the maxillary sinus (see Figure 4-3).

TABLE 1 CRANIOFACIAL LINEAR MEASUREMENTS

- 1) BIZYGOMATIC BREADTH
- 2) SUPERIOR BIZYGOMAXILLARE BREADTH
- 3) INFERIOR BIZYGOMAXILLARE BREADTH
- 4) INF ZYGOMAXILL PT TO MIDPT GLENOID TUBERCLE - LEFT
- 5) INF ZYGOMAXILL PT TO MIDPT GLENOID TUBERCLE - RIGHT
- 6) INFERIOR ZYGOMAXILLARE PT TO INION - LEFT
- 7) INFERIOR ZYGOMAXILLARE PT TO INION - RIGHT
- 8) PROTHION TO INFERIOR ZYGOMAXILLARE PT - LEFT
- 9) PROTHION TO INFERIOR ZYGOMAXILLARE PT - RIGHT
- 10) PROTHION TO HORMION
- 11) PROTHION TO STAPHYLION
- 12) PROTHION TO ALVEOLAR SPINE
- 13) PROTHION TO SPHENOBASION
- 14) PROTHION TO BASION
- 15) PROTHION TO NASION
- 16) PROTHION TO OPISTHION
- 17) STAPHYLION TO HORMION
- 18) STAPHYLION TO SPHENOBASION
- 19) STAPHYLION TO BASION
- 20) INTER CANINE BREADTH
- 21) ECTOMOLAR BREADTH
- 22) ENDOMOLAR BREADTH
- 23) CHOANAL HEIGHT - LEFT
- 24) CHOANAL HEIGHT - RIGHT
- 25) CHOANAL WIDTH - LEFT
- 26) CHOANAL WIDTH - RIGHT
- 27) ORBITAL HEIGHT - LEFT
- 28) ORBITAL HEIGHT - RIGHT
- 29) ORBITAL WIDTH - LEFT
- 30) ORBITAL WIDTH - RIGHT
- 31) NASAL HEIGHT
- 32) NASAL BREADTH
- 33) APERTURE HEIGHT
- 34) NASION -ALVEOLARE (IDS)
- 35) GLABELLA-OPISTHOCRANION
- 36) BASION-NASION
- 37) AVEOLARE-OPISTHOCRANION
- 38) PROTHION-OPISTHOCRANION
- 39) PROTHION-MAXILLOPALATAL SUTURE
- 40) BASION-HORMION
- 41) INTERNAL PALATAL LENGTH

TABLE 2 UPPER DENTAL MEASUREMENTS

- 42) MESIAL-DISTAL M3 LEFT
- 43) BUCCAL-LINGUAL M3 LEFT
- 44) INF-SUP LENGTH M3 LEFT
- 45) MESIAL-DISTAL M3 RIGHT
- 46) BUCCAL-LINGUAL M3 RIGHT
- 47) INF-SUP LENGTH M3 RIGHT
- 48) MESIAL-DISTAL M2 LEFT
- 49) BUCCAL-LINGUAL M2 LEFT
- 50) INF-SUP LENGTH M2 LEFT
- 51) MESIAL-DISTAL M2 RIGHT
- 52) BUCCAL-LINGUAL M2 RIGHT
- 53) INF-SUP LENGTH M2 RIGHT
- 54) MESIAL-DISTAL M1 LEFT
- 55) BUCCAL-LINGUAL M1 LEFT
- 56) INF-SUP LENGTH M1 LEFT
- 57) MESIAL-DISTAL M1 RIGHT
- 58) BUCCAL-LINGUAL M1 RIGHT
- 59) INF-SUP LENGTH M1 RIGHT
- 60) MESIAL-DISTAL M1, M2, M3 -L
- 61) MESIAL-DISTAL M1, M2, M3 -R
- 62) MESIAL-DISTAL M1 and M2 -L
- 63) MESIAL-DISTAL M1 and M2 -R

TABLE 3 VOLUME MEASUREMENTS

- 64) MAXILLARY SINUS LEFT
- 65) MAXILLARY SINUS RIGHT
- 66) ENDOCRANIAL CAPACITY

TABLE 4 DERIVED INDICES

- 67) NASAL INDEX = (Nasal breadth/nasal height) * 100
- 68) UPPER FACIAL INDEX = (pros-nas/bz)* 100
- 69) PALATAL INDEX = (endomolar breadth/ pros-staph length) * 100

Figure 4-3a. Frontal view X-ray of *Macaca fascicularis* above and *Macaca mulatta* below. Note the difficulty in demarcating the bony borders of the maxillary sinus.

Figure 4-3b. Schematic drawing of a frontal view X-ray showing how to obtain the two dimensions of height (1) and width (2) of the maxillary sinus.

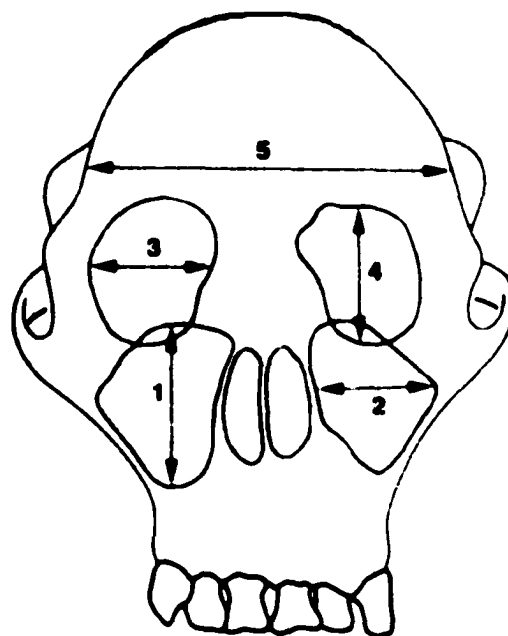
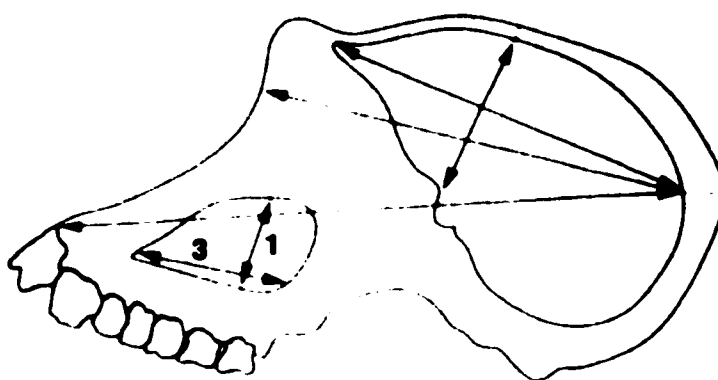
**Fig. 4-3a****Fig. 4-3b**

Figure 4-3c. Lateral view X-ray of same specimens as in figure 4-3a.

Figure 4-3d. Schematic drawing of figure 4-3c depicting how measures of height (*l*) and length (*3*) of the maxillary sinus are attained. Note that height (*l*) derived from the lateral view can corroborate the same dimensional measure from the frontal view.

**Fig. 4-3c****Fig. 4-3d**

Then, treating the maxillary sinus as a prism shaped object and then following the calculation of Aust and Helmius (1974) the surface area is estimated. The use of an oil rapeseed filling method is preferable due to the packing qualities of seed, thereby allowing the mass of the seeds to follow the contours of the irregular three-dimensional shape of the maxillary sinus. Volumetric measures provide baseline data for these macaques, and allows assessment of whether the oil rapeseed method provides a more accurate estimate of nasal complex dimensions compared to that obtained by CT imaging (see below).

Volumetric measurements taken are listed in table 3.

3) This phase of the study will employ the use of the relatively new imaging opportunities made available through computer tomography (CT). CT-imaging allowed visualization of internal nasal structures to an extent not previously possible. In order to analyze the morphology of the sinuses from the CT images segmentation of the structures from the volume data set was undertaken (Udupa and Herman, 1991). Segmentation refers to the extraction of the voxels comprising the individual structures (see Spoor et al., 1999). The nasal cavity and maxillary sinus are defined traditionally based on anatomical landmarks (see Cave, 1967, 1973). Instead of developing an analogous strategy for identifying the landmarks in the CT image, physical isolation of the structures was required before scanning. The nasal cavity and maxillary sinus region was enclosed by sealing the choanae, incisive foramen, the medial wall of the maxillary sinus, the pterygomaxillary fissure and the piriform aperture with clay (see Figure 4-4). The enclosed cavity was then segmented by thresholding the voxels of low intensity (air) from the high intensity (bone and clay) enclosing structures. The burden of the segmentation process is on physically sealing the openings with clay and not on the image processing strategies. In order to scale and orient the CT image to the physical specimen, small capsules filled with copper sulphate (a highly detectable marker for CT scans) was placed at distinct, non-coplanar, osteometric points on the cranium.

1.0 mm coronal slice scans of *Macaca fascicularis* and *Macaca mulatta* crania (samples from AMNH only) were taken using a 9800 HiSpeed Advantage General Electric CT-scanning machine in the department of Radiology at The Mount Sinai Hospital.

Figure 4-4 a and b. (a) A two-dimensional coronal CT scan reconstruction of a *M. mulatta* cranium showing internal nasal structures. This, and all subsequent reconstructions, have been generated by VoxelView. All are of the same cranium. Areas of white density reflect (besides dentition) the clay (*Cl*) used to seal portals (see text). (b) Same reconstructed cranium as in (a) but showing a transverse plane from an inferior view; the clay indicated by arrow covers the incisive foramen (*If*), dash arrow covers the pterygomaxillary fissure (*Pm*), and arrowhead covers the choanae (*Ch*).



Fig. 4-4a

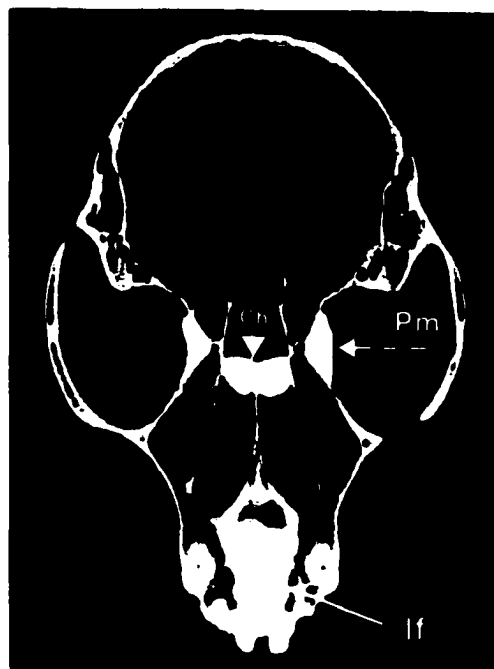


Fig. 4-4 b

The computerized tomograms were digitized and subsequently transferred to a Silicon Graphics Indigo 2-XZ Workstation and then analyzed with software that allows for 3-dimensional image analyses. These volume microscopy workbench computer packages include VoxelView, VoxelMath, and VoxelAnimator programs. VoxelView is a comprehensive volume rendering application program that permits 3-dimensional reconstruction of CT scan data. In addition, it allows for specified measures to be made of discrete components thereby isolating internal anatomical structures outside the surrounding area (e.g., turbinates, nasal cavity, maxillary sinus). The volumes calculated from the CT image were compared to the volumes calculated from the seed filling method. This component of the study provided assessments of maxillary sinus and nasal cavity volumes and thus can provide a quantitative baseline understanding of the contributing role of sinus to nasal cavity volume.

4.5.3.4. *Methodological Details*

There are a variety of methods regarding size standardization for morphological measurements, and each has been debated (e.g., Martin, 1993). However, size standardization utilizing brain size has been historically studied, used, and evaluated by a number of investigators (e.g., Bauchot and Stephan, 1969; Martin, 1993). Size standardization for volumetric measurements to be used in this study consists of dividing the nasal cavity and maxillary sinus volumes, respectively, by endocranial volume for each specimen. Taking the cube root of each of these ratios converts the volumetric data to linear data. In addition, standardization of the linear measurements listed in tables 1 and 2 will be done by dividing each measurement by the cube root of endocranial volume for each specimen. This allows each raw linear measurement to be standardized as a function of brain size per individual. By standardizing linear and volumetric measurements in this

way both sets of measurements will have uniform units and thus can be compared statistically. Other possible standardizations were explored by extensively plotting the unadjusted data (Marcus, 1990) and evaluating alternate standardization methods in terms of recent suggestions in the literature (Jungers, et al., 1995).

In measuring two samples for a number of variables one can use the Hotelling T^2 statistic to determine whether the set of means for one group differs significantly from that of the other group (Tabachnick and Fidell, 1983). If they do differ significantly, it would reflect the differential effects of the alternative treatments that the two independent samples received namely different climatic conditions. The T^2 test is a special case of multivariate analysis of variance just as the Student t-test is a special case of univariate analysis of variance in which two groups comprise the independent variable. Since the T^2 test assesses the dependent variables simultaneously, it may be difficult to discern which variables contribute most to a significant difference between the two groups. As the number of variables increases the explanatory power diminishes for any given variable. For this reason a bivariate analysis was also be conducted to determine whether relationships are present.

Student t-tests provides pair wise contrasts, and discerns which dependent variable(s) contribute most to a significant difference between the two groups for the particular morphological feature. Test for significance will be at the 0.05 level. However, a Bonferoni inequality calculation was required since this procedure is an adjustment of the probability level for the evaluation of most simultaneous tests. The adjustment takes into account the number of contrast made, usually estimated as level of significance 0.05 divided by number of contrasts, in order to protect against falsely accepting a significant statistical difference between samples when none exist (Sokal and Rolf, 1981). However, it is possible to have a significant multivariate test despite insignificant univariate tests. This is attributed to the accumulation of the evidence from the individual variables on the overall test. Alternatively, an insignificant multivariate test can occur when some univariate

tests are significant because the evidence of a difference provided by the significant variables is swamped by the evidence of no difference provided by the other variables (Manly, 1994). Consequently, a principal component analysis (PCA) was also applied to the data in the form of a correlation matrix. The importance of applying a principal component analysis is in the identification of factors, underlying a set of variables, which finds linear combinations accounting for a relatively large amount of the total variation. PCA, in effect, reduces the number of variables to principal components of a descending order of importance with regard to explaining the variation. If the data contains such information, then each variable, by looking at its loading or eigenvalue, can be studied for its relative contribution to each component (Neff and Marcus, 1980). Should data from the study show significant differences based on climate, the hypothesis that climate affects nasal morphology will be supported. To the contrary, if significant differences are not shown, the effect of climate to nasal morphology will not be substantiated. The Hotelling T^2 test will be carried out using one of the readily available spreadsheet programs that permits matrix inversion, such as LOTUS 123 (Lotus Development Corporation, 1992). Student t-test will be carried out using EXCEL for windows spreadsheet microsoft program. PCA will be carried out using Statistical Analysis System (SAS) for personal computer.

4.5.4. Materials

Crania of adult male *M. fascicularis* (n=35) and *M. mulatta* (n=34) were selected from osteological collections housed in different museums. Samples of specimens that were assessed, studied, and measured are from the departments of Anthropology and Mammalogy at The American Museum of Natural History in New York (AMNH), The Museum of Comparative Zoology (The Agassiz Museum) in Harvard University (MCZ), division of Primatology at The National Museum of Natural History in Washington, D C.

(NMNH), and department of Mammalogy at the British Museum (Natural History), London in England (BMNH) (see table 5). The confounding factors of sexual dimorphism and age are controlled for by using male adult samples (determined by upper molar eruption patterns). As mentioned previously, all specimens were chosen based on the presence of the variables to be studied and the intact nature of all portals.

Table 5. Species sample grouped by collection source. (see Appendix A for raw data. Specimens and catalogue numbers in Appendix A).

TAXON	AMNH	MCZ	NMNH	BMNH	Totals
<i>M. mulatta</i>	11	5	6	12	34
<i>M. fascicularis</i>	12	17	6	0	35

4.6. STATISTICAL ANALYSIS

The Shapiro-Wilk statistic (i.e., W-statistic) was used to test for normality since it is appropriate for samples under 2000 (Cody and Smith, 1997). Normality tests were performed on various forms of the data including raw and log transformed. The results of showed that no *p*-values of less than 0.01 were found thus demonstrating that all measures fell within the range of normal distribution.

4.7. QUALITATIVE RESULTS

CT scans analyzed with the use of VoxelView provided a comprehensive image of the morphology of the maxillary sinus by generating 2- and 3-dimensional reconstructions. Figure 4-5a depicts the reconstruction of a 2-dimensional coronal slice image of *Macaca mulatta* showing maxillary sinus (*ms*), nasal cavity (*nc*), endocranial cavity (*ec*), and clay (*cl*). Figure 4-5b shows a 3-dimensional reconstruction of figure 4-5a structures yielding volumes of 1.4 mL and 1.5 mL for left and right maxillary sinus volumes respectively (see table 6 for quantitative volumes derived from CT). A total reconstruction of the cranium was generated and viewed at any orientation by taking the points of intersection of a particular plane with the full series of coronal CT-scans (see figure 4-6). The VoxelView volume rendering program yielded a parasagittal 3-dimensional reconstructed image as seen in figure 4-7, which allows a visualization of the bony contours of the right maxillary sinus. Figure 4-8a shows an entire reconstructed cranium with the left maxillary sinus highlighted in color, and an isolated maxillary sinus extracted from this same cranium is seen in figure 4-8b (see also Figure 4-9).

Table 6. Maxillary sinus volumes of *Macaca fascicularis* (Mf) derived from CT.

	Species	AMNH Cat. #	Left MS	Right MS
1)	Mf	3056	2.7449	3.0389
2)	Mf	99.1/3030	2.8792	3.1421
3)	Mf	99/3062	3.2576	3.3197
4)	Mf	102765	1.8732	2.4231
5)	Mf	103648	2.3588	2.2679
6)	Mf	106283	3.2546	3.3128
7)	Mf	106566	2.8872	2.3221
8)	Mf	106568	2.7821	2.9241
9)	Mf	106569	2.7982	2.8533
10)	Mf	107099	3.3338	2.4913
11)	Mf	187215	3.1987	3.0932
12)	Mf	175460	2.9124	2.5121

Figure 4-5 a) A two-dimensional transverse slice showing internal structures of nasal cavity (*nc*), maxillary sinus (*ms*), endocranial cavity (*cc*), and the high density detection of the clay (*cl*) used to seal the pterygomaxillary fissure.



Fig. 4-5a

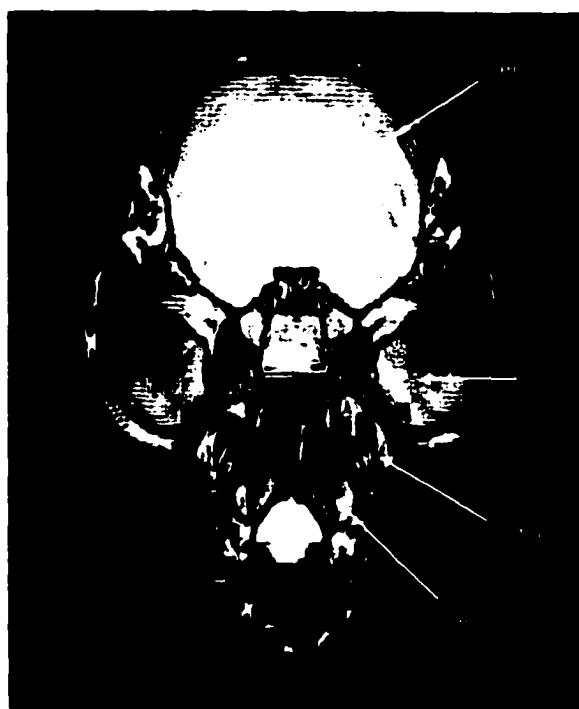


Fig. 4-5b

Figure 4-6. Three-dimensional reconstruction of the entire *M. mulatta* cranium. The clay (C) used to seal the nasal aperture can be seen in this figure.



Fig. 4-6

Figure 4-7 a) A parasagittal view of a three-dimensional reconstruction of *M. mulatta* showing the relationship of the right maxillary sinus (*MS*) and its contiguous structures. Note the floor of the sinus in (a) covers most of the molar dentition. **b)** A three-dimensional reconstruction of the same specimen from another parasagittal perspective showing the left maxillary sinus. Note the difference in the relative position of the anterior portion of the sinus and the canine seen in (b – indicated by white arrow) as compared with (a).

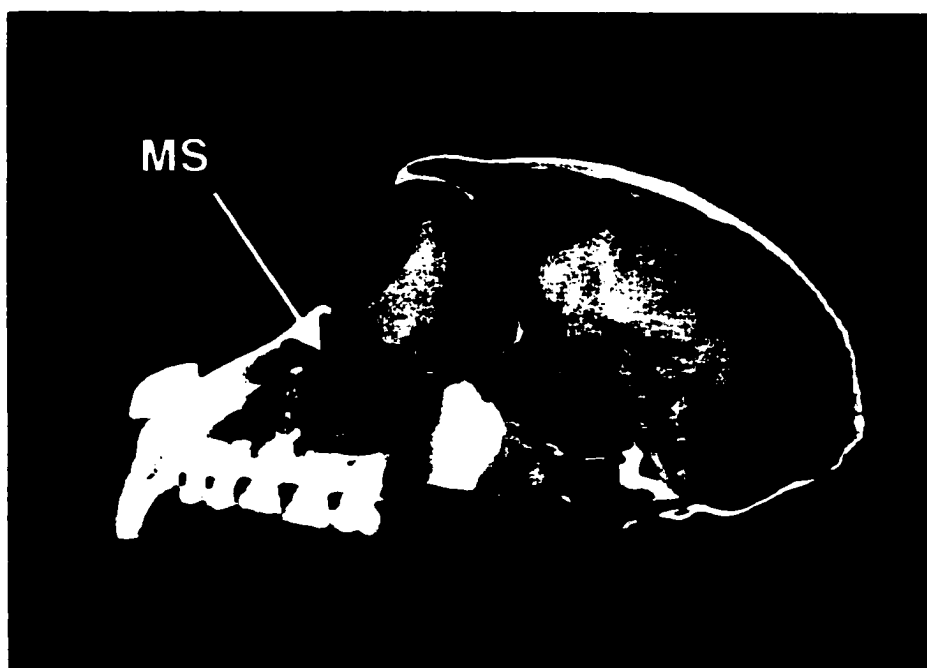


Fig. 4-7a



Fig. 4-7b

Figure 4-8 a) The left maxillary sinus of *M. mulatta* has been highlighted in black in this reconstruction (a) and extracted from the cranium (b).

Figure 4-9. The three dimensional space of the maxillary sinus of *M. fascicularis* has been digitized and graphically represented both *insitu* and extracted in parasagittal view. Identification of the maxillary sinus in this manner both affords the opportunity to visualize the detailed morphology of the sinus to its contiguous craniodental structures *insitu* and in isolated form.



Fig. 4-8a

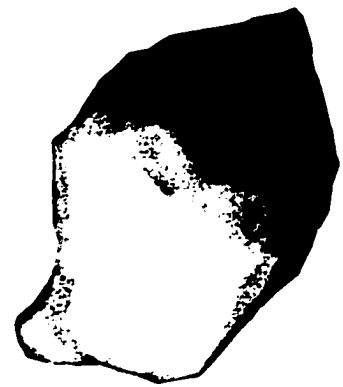


Fig. 4-8b



Fig. 4-9

4.8. QUANTITATIVE RESULTS

Results from CT to derive maxillary sinus volume determinations are listed in table 6. Volume differences derived from CT and seed-filling methods were evaluated using Student t-tests and were found not to be statistically significant. Results from the traditional approach of conventional X-rays show that it was not reliable in obtaining maxillary sinus volumes due to the inability to define with precision its borders, and thus ensure confidence in either accuracy or reproducibility. Analysis of variance (ANOVA) was performed to estimate measurement error of the seed-filling method. For the left maxillary sinus Σ Mean Squares within groups = 0.048, $p = 0.99$ and right maxillary sinus Σ Mean Squares within groups = 0.039, $p = 0.99$. Reproducibility was excellent based upon small standard deviations, low variances, and high correlations between repeated measures for the same individual.

Principal component analysis (PCA) reveals that the first three components accounted for 64% of total variance for *M. fascicularis* (see table 7) and 77% for *M. mulatta* (see table 8). The loadings of the variables for *M. fascicularis* and *M. mulatta* were of homogeneous contribution with the maxillary sinus volume being one of the lower loadings. PCA plots for both taxa are shown in figures 4-10 and 4-11. Results from the bivariate linear regression analysis between the dependent variable of maxillary sinus volume and 30 linear measurements show 8 measures to be statistically significantly correlated for *M. fascicularis*, and 4 for *M. mulatta*; while 3 of these measures are common to both taxa. Selected bivariate linear regression plots including r^2 and p values are shown in figures 4-12 to 4-19.

Table 7 **PCA for *Macaca fascicularis***

The FACTOR Procedure
Initial Factor Method: Principal Components

Eigenvalues of the Correlation Matrix: Total = 44 Average = 1

	Eigenvalue	Difference	Proportion	Cumulative
1	19.6711799	14.0227712	0.4471	0.4471
2	5.6484087	2.5139975	0.1284	0.5754
3	3.1344113	0.1926699	0.0712	0.6467
4	2.9417414	0.3026891	0.0669	0.7135
5	2.6390523	0.9895743	0.0600	0.7735
6	1.6494780	0.0391560	0.0375	0.8110
7	1.6103220	0.5719689	0.0366	0.8476
8	1.0383531	0.0712120	0.0236	0.8712
9	0.9671412	0.0461616	0.0220	0.8932
10	0.9209796	0.2542935	0.0209	0.9141
11	0.6666861	0.0827120	0.0152	0.9293
12	0.5839741	0.1510176	0.0133	0.9425
13	0.4329565	0.0716223	0.0098	0.9524
14	0.3613341	0.0474443	0.0082	0.9606
15	0.3138898	0.0581901	0.0071	0.9677
16	0.2556998	0.0144893	0.0058	0.9735
17	0.2412105	0.0458177	0.0055	0.9790
18	0.1953928	0.0617310	0.0044	0.9835
19	0.1336618	0.0128016	0.0030	0.9865
20	0.1208602	0.0177672	0.0027	0.9892
21	0.1030929	0.0147854	0.0023	0.9916
22	0.0883075	0.0208391	0.0020	0.9936
23	0.0674685	0.0067521	0.0015	0.9951
24	0.0607164	0.0152023	0.0014	0.9965
25	0.0455140	0.0126038	0.0010	0.9975
26	0.0329103	0.0068219	0.0007	0.9983
27	0.0260883	0.0024880	0.0006	0.9989
28	0.0236003	0.0013484	0.0005	0.9994
29	0.0222519	0.0189349	0.0005	0.9999
30	0.0033170	0.0033170	0.0001	1.0000
31	0.0000000	0.0000000	0.0000	1.0000
32	0.0000000	0.0000000	0.0000	1.0000
33	0.0000000	0.0000000	0.0000	1.0000
34	0.0000000	0.0000000	0.0000	1.0000
35	0.0000000	0.0000000	0.0000	1.0000
36	0.0000000	0.0000000	0.0000	1.0000
37	0.0000000	0.0000000	0.0000	1.0000
38	0.0000000	0.0000000	0.0000	1.0000
39	0.0000000	0.0000000	0.0000	1.0000
40	0.0000000	0.0000000	0.0000	1.0000
41	0.0000000	0.0000000	0.0000	1.0000
42	0.0000000	0.0000000	0.0000	1.0000

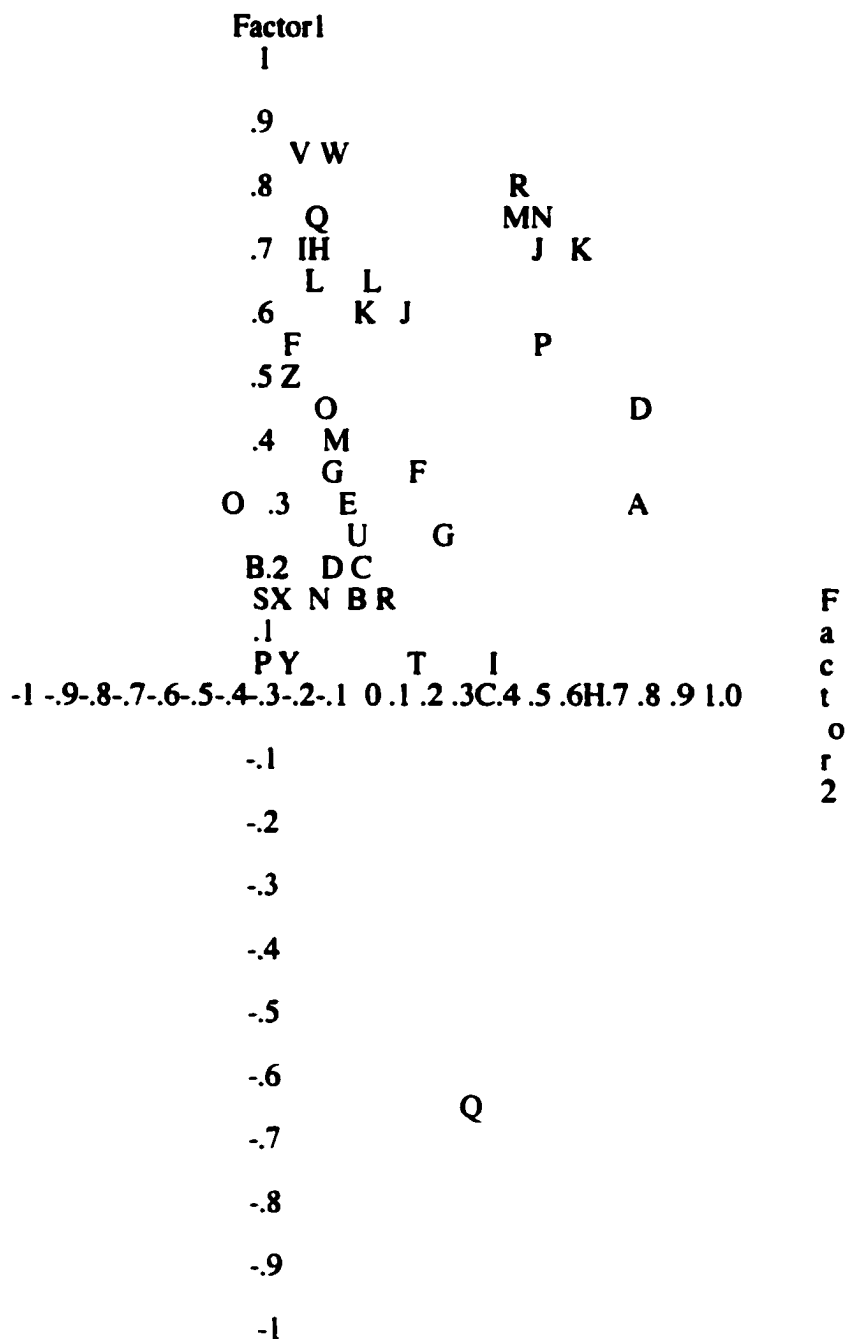
Table 8 **PCA for *Macaca mulatta***

The FACTOR Procedure
Initial Factor Method: Principal Components

Eigenvalues of the Correlation Matrix: Total = 44 Average = 1

	Eigenvalue	Difference	Proportion	Cumulative
1	25.8681313	21.6296810	0.5879	0.5879
2	4.2384503	0.6486491	0.0963	0.6842
3	3.5898012	1.1572906	0.0816	0.7658
4	2.4325106	0.7118009	0.0553	0.8211
5	1.7207097	0.1842208	0.0391	0.8602
6	1.5364889	0.4382430	0.0349	0.8951
7	1.0982459	0.1265192	0.0250	0.9201
8	0.9717268	0.3100512	0.0221	0.9422
9	0.6616756	0.0472333	0.0150	0.9572
10	0.6144423	0.1925691	0.0140	0.9712
11	0.4218732	0.1559835	0.0096	0.9808
12	0.2658897	0.0471359	0.0060	0.9868
13	0.2187538	0.0294162	0.0050	0.9918
14	0.1893376	0.0857408	0.0043	0.9961
15	0.1035967	0.0352301	0.0024	0.9984
16	0.0683667	0.0683667	0.0016	1.0000
17	0.0000000	0.0000000	0.0000	1.0000
18	0.0000000	0.0000000	0.0000	1.0000
19	0.0000000	0.0000000	0.0000	1.0000
20	0.0000000	0.0000000	0.0000	1.0000
21	0.0000000	0.0000000	0.0000	1.0000
22	0.0000000	0.0000000	0.0000	1.0000
23	0.0000000	0.0000000	0.0000	1.0000
24	0.0000000	0.0000000	0.0000	1.0000
25	0.0000000	0.0000000	0.0000	1.0000
26	0.0000000	0.0000000	0.0000	1.0000
27	0.0000000	0.0000000	0.0000	1.0000
28	0.0000000	0.0000000	0.0000	1.0000
29	0.0000000	0.0000000	0.0000	1.0000
30	0.0000000	0.0000000	0.0000	1.0000
31	0.0000000	0.0000000	0.0000	1.0000
32	0.0000000	0.0000000	0.0000	1.0000
33	0.0000000	0.0000000	0.0000	1.0000
34	0.0000000	0.0000000	0.0000	1.0000
35	0.0000000	0.0000000	0.0000	1.0000
36	0.0000000	0.0000000	0.0000	1.0000
37	0.0000000	0.0000000	0.0000	1.0000
38	0.0000000	0.0000000	0.0000	1.0000
39	0.0000000	0.0000000	0.0000	1.0000
40	0.0000000	0.0000000	0.0000	1.0000
41	0.0000000	0.0000000	0.0000	1.0000
42	0.0000000	0.0000000	0.0000	1.0000

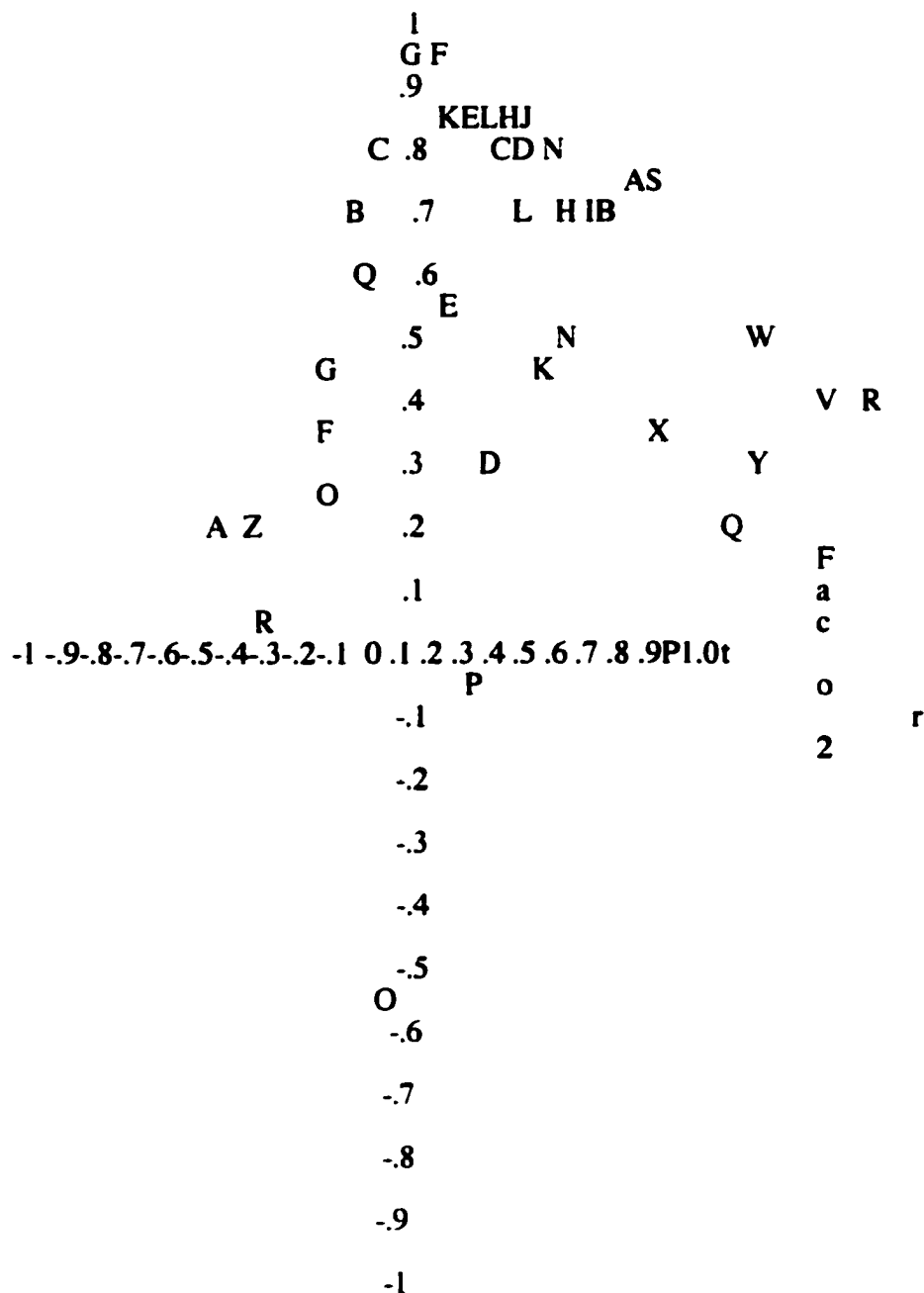
PCA for *Macaca fascicularis* The FACTOR Procedure - Rotation Method:
 Varimax - Plot of Factor Pattern for Factor1 and Factor2



Bizygomatic=A Superior_b=B Inferior_b=C inf_max_mi=D inf_max_mi=D
 inf_maxill=F inf_maxill=G prosthion_=H prosthion_=I prosthion_=J prosthion_=K
 prosthion_=L prosthion_=M prosthion_=N prosthion_=O staphylion=P staphylion=Q
 staphylion=R inter_cani=S ectomolar_=T endomolar_=U choanal_he=V
 choanal_he=W choanal_wi=X choanal_wi=Y orbital_he=Z orbital_he=Z orbital_wi=B
 orbital_wi=C nasal_heig=D nasal_brea=E aperture_h=F nasion_alv=G glabella_o=H
 basion_nas=I

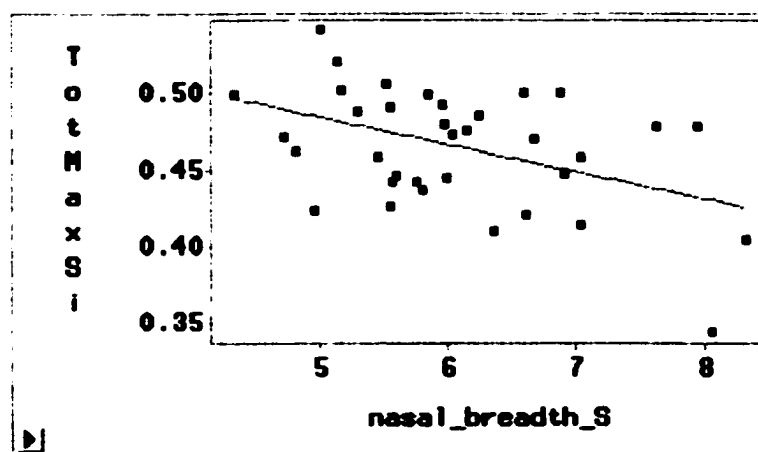
Figure 4-10

PCA for *Macaca mulatta* The FACTOR Procedure - Rotation Method: Varimax
Plot of Factor Pattern for Factor1 and Factor2
Factor1



Bizygomatic=A Superior_b=B Inferior_b=C inf_max_mi=D inf_max_mi=E
 inf_maxill=F inf_maxill=G prosthion_=H prosthion_=I prosthion_=D prosthion_=K
 prosthion_=L prosthion_=L prosthion_=N prosthion_=O staphylion=P staphylion=Q
 staphylion=R inter_cani=S ectomolar_=E endomolar_=L choanal_he=V choanal_he=W
 choanal_wi=X choanal_wi=Y orbital_he=Z orbital_he=A orbital_wi=Borbital_wi=C
 nasal_heig=D nasal_brea=E aperture_h=F nasion_alv=G glabella_o=H basion_nas=H

Figure 4-11



Macaca fascicularis

$$\text{TotMaxSinusCubeRt\_S} = \text{nasal\_breadth\_S}$$

$$\text{TotMaxSinusCubeRt\_S} = \text{Model Equation} \\ 0.5766 - 0.0180 \text{ nasal\_breadth\_S}$$

Parametric Regression Fit				
Curve	Degree(Polynomial)	DF	Mean Square	Error Mean Square
	1	1	0.0105	33 0.0013

Parametric Regression Fit

R-Square	F Stat	Pr > F
0.1960	8.04	0.0077

Summary of Fit

Mean of Response	0.4673	R-Square	0.1960
Root MSE	0.0361	Adj R-Sq	0.1716

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Stat	Pr > F
Model	1	0.0105	0.0105	8.04	0.0077
Error	33	0.0431	0.0013	.	.
C Total	34	0.0535	.	.	.

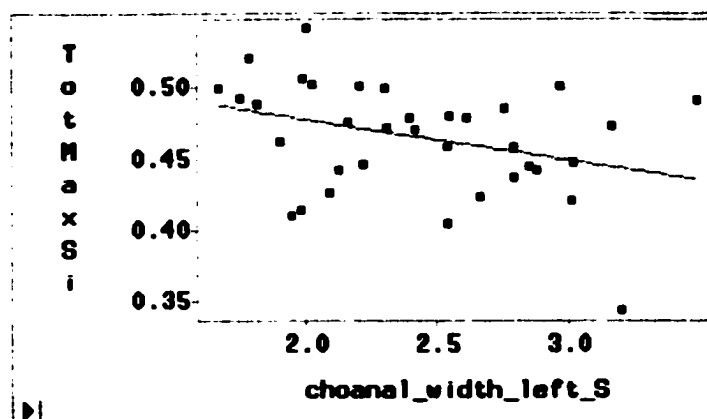
Type III Tests

Source	DF	Sum of Squares	Mean Square	F Stat	Pr > F
nasal_breadth_S	1	0.0105	0.0105	8.04	0.0077

Parameter Estimates

Variable	DF	Estimate	Std Error	t Stat	Pr > t	Tolerance	Var Inflation
Intercept	1	0.5766	0.0390	14.77	<.0001	.	0.0000
nasal_breadth_S	1	-0.0180	0.0063	-2.84	0.0077	1.0000	1.0000

Figure 4-12



Macaca fascicularis

TotMaxSinusCubeRt_S = choanal_width_left_S

TotMaxSinusCubeRt_S = Model Equation
0.5373 - 0.0289 choanal_width_left_S

Parametric Regression Fit					
Curve	Degree(Polynomial)	Model	Error	DF	Mean Square
	1		0.0063	33	0.0014

Parametric Regression Fit

R-Square F Stat Pr > F
0.1185 4.44 0.0429

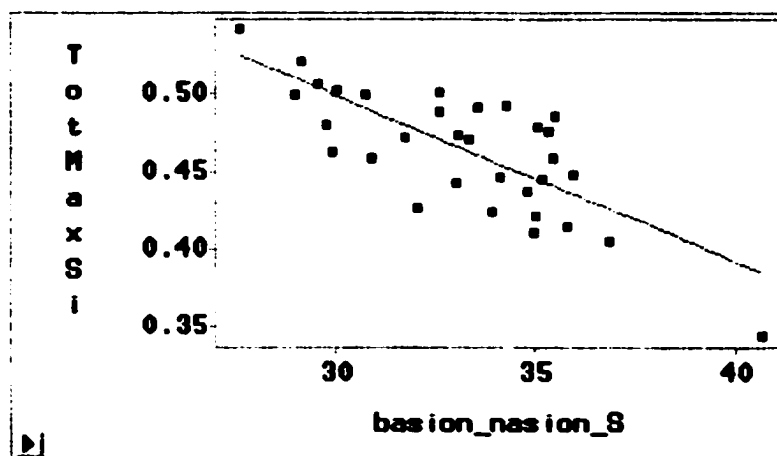
Summary of Fit

Mean of Response 0.4673 R-Square 0.1185
Root MSE 0.0378 Adj R-Sq 0.0918

Analysis of Variance					
Source	DF	Sum of Squares	Mean Square	F Stat	Pr > F
Model	1	0.0063	0.0063	4.44	0.0429
Error	33	0.0472	0.0014		
C Total	34	0.0535			

Type III Tests					
Source	DF	Sum of Squares	Mean Square	F Stat	Pr > F
choanal_width_left_S	1	0.0063	0.0063	4.44	0.0429

Figure 4-13



Macaca fascicularis

$$\text{TotMaxSinusCubeRt\_S} = \text{basion\_nasion\_S}$$

$$\text{TotMaxSinusCubeRt\_S} = \text{Model Equation} \\ 0.8228 - 0.0107 \text{ basion\_nasion\_S}$$

Parametric Regression Fit

Curve	Model	Error
Degree(Polynomial)	DF	Mean Square
1	1	0.0287
	32	0.0007

Parametric Regression Fit

R-Square	F Stat	Pr > F
0.5513	39.32	<.0001

Summary of Fit

Mean of Response	0.4662	R-Square	0.5513
Root MSE	0.0270	Adj R-Sq	0.5373

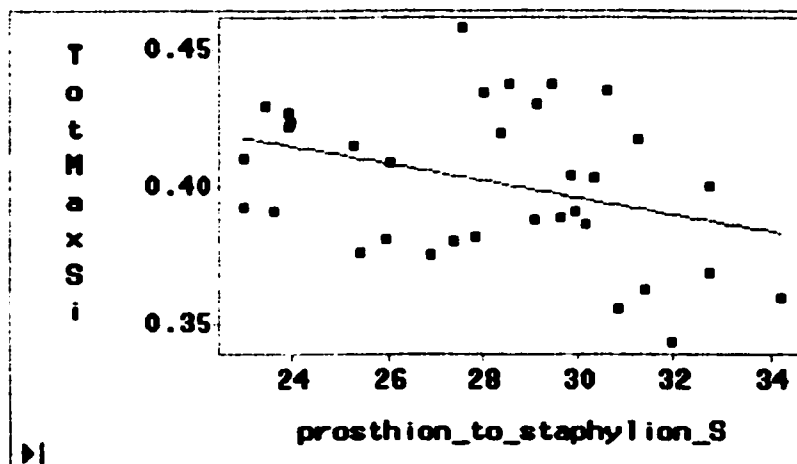
Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Stat	Pr > F
Model	1	0.0287	0.0287	39.32	<.0001
Error	32	0.0234	0.0007		
C Total	33	0.0521			

Type III Tests

Source	DF	Sum of Squares	Mean Square	F Stat	Pr > F
basion_nasion_S	1	0.0287	0.0287	39.32	<.0001

Figure 4-14



Macaca mulatta

TotMaxSinusCubeRt_S = prosthion_to_staphylion_S
 Response Distribution: Normal
 Link Function: Identity

Model Equation
 TotMaxSinusCubeRt_S = 0.4904 - 0.0031
 prosthion_to_staphylion_S

Parametric Regression Fit

Curve	Model	Error		
Degree(Polynomial)	DF	Mean Square	DF	Mean Square
1	1	0.0032	32	0.0007

Parametric Regression Fit

R-Square	F Stat	Pr > F
0.1262	4.62	0.0393

Summary of Fit

Mean of Response	0.4020	R-Square	0.1262
Root MSE	0.0265	Adj R-Sq	0.0989

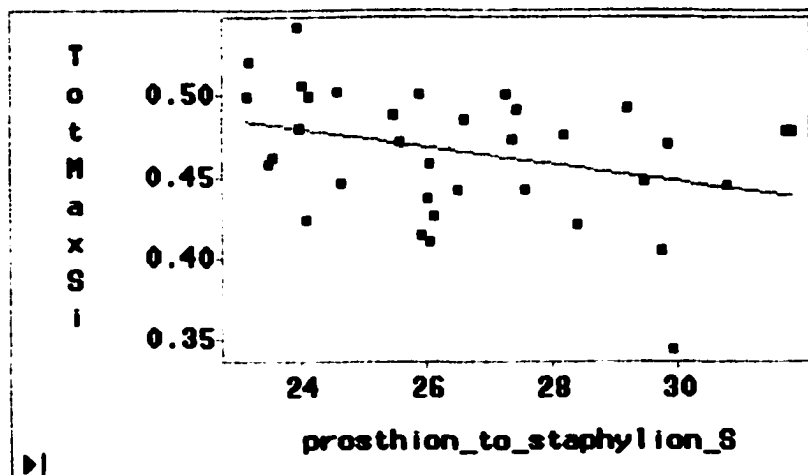
Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Stat	Pr > F
Model	1	0.0032	0.0032	4.62	0.0393
Error	32	0.0225	0.0007		
C Total	33	0.0257			

Type III Tests

Source	DF	Sum of Squares	Mean Square	F Stat	Pr > F
prosthion_to_staphylion_S1		0.0032	0.0032	4.62	0.0393

Figure 4-15



Macaca fascicularis

$$\text{TotMaxSinusCubeRt\_S} = \text{prosthion\_to\_staphyilion\_S}$$

Model Equation

$$\text{TotMaxSinusCubeRt\_S} = 0.6099 - 0.0054 \text{ prosthion\_to\_staphyilion\_S}$$

Parametric Regression Fit					
Curve	Degree(Polynomial)	Model	Error	DF	Mean Square
	1			1	0.0062
				33	0.0014

Parametric Regression Fit

R-Square	F Stat	Pr > F
0.1150	4.29	0.0463

Summary of Fit

Mean of Response	0.4673	R-Square	0.1150
Root MSE	0.0379	Adj R-Sq	0.0882

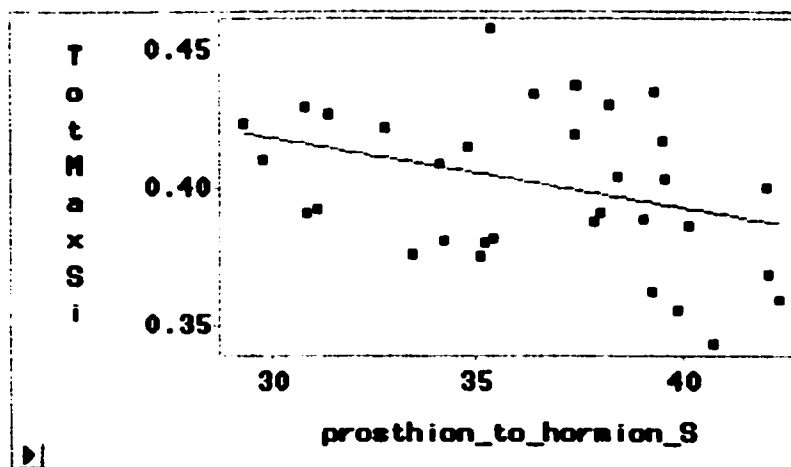
Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Stat	Pr > F
Model	1	0.0062	0.0062	4.29	0.0463
Error	33	0.0474	0.0014		
C Total	34	0.0535			

Type III Tests

Source	DF	Sum of Squares	Mean Square	F Stat	Pr > F
prosthion_to staphyilion_S _	1	0.0062	0.0062	4.29	0.0463

Figure 4-16



Macaca mulatta

$$\text{TotMaxSinusCubeRt\_S} = \text{prosthion\_to\_hormion\_S}$$

Model Equation

$$\text{TotMaxSinusCubeRt\_S} = 0.4959 - 0.0026 \text{ prosthion\_to\_hormion\_S}$$

Parametric Regression Fit					
Curve	Degree(Polynomial)	Model	Error	DF	Mean Square
1	1	0.0030	32	0.0007	

Parametric Regression Fit

R-Square	F Stat	Pr > F
0.1170	4.24	0.0477

Summary of Fit

Mean of Response	0.4020	R-Square	0.1170
Root MSE	0.0266	Adj R-Sq	0.0894

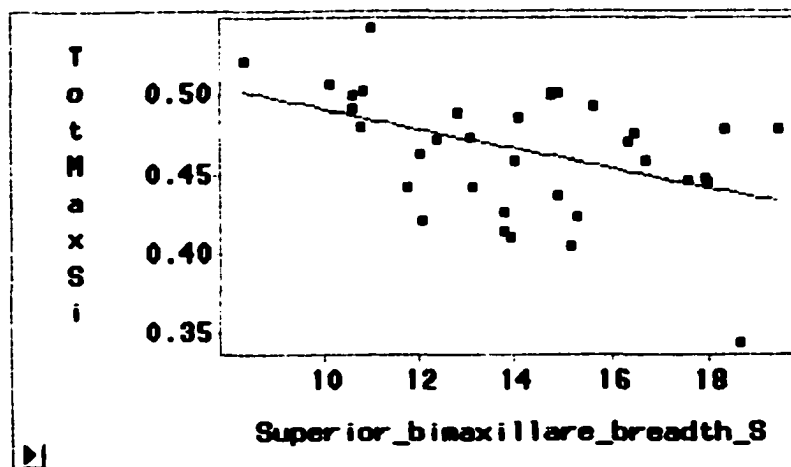
Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Stat	Pr > F
Model	1	0.0030	0.0030	4.24	0.0477
Error	32	0.0227	0.0007		
C Total	33	0.0257			

Type III Tests

Source	DF	Sum of Squares	Mean Square	F Stat	Pr > F
prosthion_to_hormion_S	1	0.0030	0.0030	4.24	0.0477

Figure 4-17



Macaca fascicularis

$$\text{TotMaxSinusCubeRt\_S} = \text{Superior\_bimaxillare\_breadth\_S}$$

Model Equation

$$\text{TotMaxSinusCubeRt\_S} = 0.5538 - 0.0061$$

Model Equation
Superior_bimaxillare_breadth_S

Parametric Regression Fit

Curve	Model	Error	
Degree(Polynomial)	DF	Mean Square	DF Mean Square
1	1	0.0098	33 0.0013

Parametric Regression Fit

R-Square	F Stat	Pr > F
0.1836	7.42	0.0102

Summary of Fit

Mean of Response	0.4673	R-Square	0.1836
Root MSE	0.0364	Adj R-Sq	0.1589

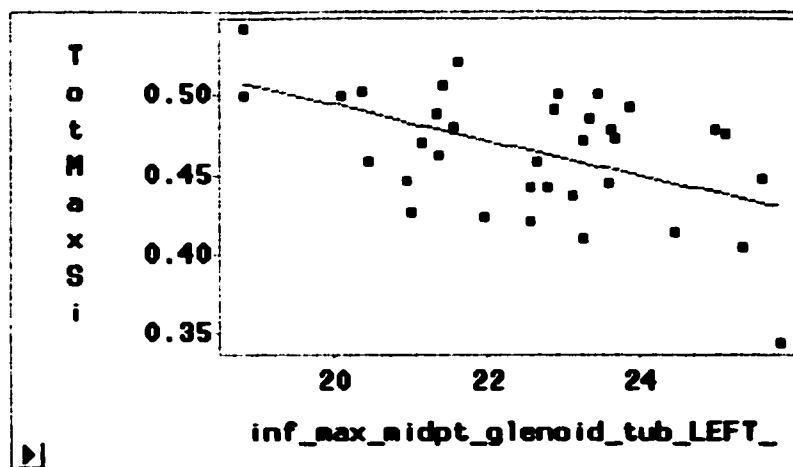
Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Stat	Pr > F
Model	1	0.0098	0.0098	7.42	0.0102
Error	33	0.0437	0.0013		
C Total	34	0.0535			

Type III Tests

Source	DF	Sum of Squares	Mean Square	F Stat	Pr > F
Sup._bimaxillare_breadth_S	1	0.0098	0.0098	7.42	0.0102

Figure 4-18



Macaca fascicularis

TotMaxSinusCubeRt_S = inf_max_midpt_glenoid_tub_LEFT_S

Model Equation

TotMaxSinusCubeRt_S = 0.7181 - 0.0111

Model Equation

inf_max_midpt_glenoid_tub_LEFT_S

Parametric Regression Fit

Curve	Degree(Polynomial)	Model	DF	Error	Mean Square	DF	Mean Square
	1		1	0.0134		33	0.0012

Parametric Regression Fit

R-Square	F Stat	Pr > F
0.2500	11.00	0.0022

Summary of Fit

Mean of Response	0.4673	R-Square	0.2500
Root MSE	0.0349	Adj R-Sq	0.2273

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Stat	Pr > F
Model	1	0.0134	0.0134	11.00	0.0022
Error	33	0.0402	0.0012		
C Total	34	0.0535			

Type III Tests

Source	DF	Sum of Squares	Mean Square	F Stat	Pr > F
inf_max_midpt_glenoid_tub_LEFT_S	1	0.0134	0.0134	11.00	0.0022

Figure 4-19

In order to explain statistically the greatest amount of variance in maxillary sinus morphology, several of the most likely sets of variables were entered into tests for multiple regression. When a subset of splanchnocranial and neurocranial variables were regressed against total maxillary sinus volume Basion-Hormion is shown to be statistically significant only for *M. fascicularis* (Table 9). Regressing a subset of only splanchnocranial variables (i.e., staphylion to hormion, choanal width, and endomolar breadth) against total maxillary sinus volume show statistical significance for both taxa (Table 10). In another set (i.e., nasal breadth, nasal height, prosthion to staphylion, prosthion to nasion) revealed statistical significance for *M. fascicularis* when regressed against maxillary sinus volume (Table 11). Another set included aperture height, staphylion to hormion and basion to nasion and when regressed against maxillary sinus volume it was shown that *M. fascicularis* was the only taxa that showed a significant r^2 value. When a combination of choanal dimensions were entered and regressed against maxillary sinus volume it was *Macaca mulatta* that resulted with a statistical significant r^2 value.

Table 9 Multiple regression result for *Macaca fascicularis*

TotMaxSinusCubeRt_S		=	nasal_breadth_S		nasal_height_S
Model Equation					
TotMaxSinusCubeRt_S		=	0.5940	-	0.0166 nasal_breadth_S -
			0.0011	nasal_height_S	
Summary of Fit					
Mean of Response		0.4673	R-Square	0.1987	
Root MSE		0.0366	Adj R-Sq	0.1487	
Analysis of Variance					
Source	DF	Sum of Squares	Mean Square	F Stat	Pr > F
Model	2	0.0106	0.0053	3.97	0.0289

Figure 4-20

Table 10 Multiple regression result for *Macaca fascicularis*

TotMaxSinusCubeRt_S = nasal_breadth_S nasal_height_S
 prosthion_to_staphylion_S prosthion_to_alveolar_spine_S prosthion_to_basion_S
 prosthion_to_nasion_S

Model Equation
 TotMaxSinusCubeRt_S = 0.6128 - 0.0149
 - 0.0135 prosthion_to_alveolar_spine_S +
 0.0142 nasal_breadth_S - 0.0155 nasal_height_S +
 0.0004 prosthion_to_basion_S +
 0.0190 prosthion_to_nasion_S
 0.0048 prosthion_to_staphylion_S

Summary of Fit
 Mean of Response 0.4673 R-Square 0.5042
 Root MSE 0.0308 Adj R-Sq 0.3979

Analysis of Variance					
Source	DF	Sum of Squares	Mean Square	F Stat	Pr > F
Model	6	0.0270	0.0045	4.74	0.0019
Error	28	0.0266	0.0009	.	.

Table 11 Multiple regression result for *Macaca fascicularis*

TotMaxSinusCubeRt_S = prosthion_to_staphylion_S
 prosthion_to_alveolar_spine_S prosthion_to_basion_S prosthion_to_nasion_S
 Basion_Hormion_S nasion_alveolar_IDS_S

Model Equation
 TotMaxSinusCubeRt_S = 0.6595 + 0.0168 + 0.0176
 prosthion_to_nasion_S - prosthion_to_staphylion_S - 0.0184
 prosthion_to_alveolar_spine_S 0.0279 Basion_Hormion_S -
 0.0159+ 0.0045 prosthion_to_basion_S nasion_alveolar_IDS_S

Summary of Fit
 Mean of Response 0.4660 R-Square 0.5054
 Root MSE 0.0308 Adj R-Sq 0.3955

Analysis of Variance					
Source	DF	Sum of Squares	Mean Square	F Stat	Pr > F
Model	6	0.0261	0.0044	4.60	0.0024
Error	27	0.0256	0.0009	.	.

Table 12 Multiple regression result for *Macaca fascicularis*

TotMaxSinusCubeRt_S = aperture_height_S basion_nasion_S
staphylion_to_hormion_S

Model Equation
TotMaxSinusCubeRt_S = 0.8057 + 0.0033 aperture_height_S -

Model Equation
0.0123 basion_nasion_S + 0.0044 staphylion_to_hormion_S

Summary of Fit
Mean of Response 0.4662 R-Square 0.5662
Root MSE 0.0274 Adj R-Sq 0.5228

Analysis of Variance					
Source	DF	Sum of Squares	Mean Square	F Stat	Pr > F
Model	3	0.0295	0.0098	13.05	<.0001
Error	30	0.0226	0.0008	.	.
C Total	33	0.0521	.	.	.

Table 13 Multiple regression result for *Macaca mulatta*

nasal_breadth_S = TotMaxSinusCubeRt_S choanal_width_left_S
staphylion_to_hormion_S endomolar_breadth_S

Model Equation
nasal_breadth_S = 0.8302 + 2.1685 TotMaxSinusCubeRt_S
+ 0.3632 endomolar_breadth_S

Model Equation
+ 0.2411 choanal_width_left_S + 0.0705 staphylion_to_hormion_S

Summary of Fit
Mean of Response 7.6342 R-Square 0.3507
Root MSE 0.9687 Adj R-Sq 0.2579

Analysis of Variance					
Source	DF	Sum of Squares	Mean Square	F Stat	Pr > F
Model	4	14.1926	3.5481	3.78	0.0140
Error	28	26.2764	0.9384	.	.
C Total	32	40.4690	.	.	.

Table 14 Multiple regression result for *Macaca fascicularis*

nasal_breadth_S = TotMaxSinusCubeRt_S choanal_width_left_S					
staphylion_to_hormion_S endomolar_breadth_S					
Model Equation					
nasal_breadth_S =	1.0770	-	4.4988	TotMaxSinusCubeRt_S	
+	0.4144	endomolar_breadth_S			
Model Equation					
-	0.3029	choanal_width_left_S	+	0.3887	staphylion_to_hormion_S
Summary of Fit					
Mean of Response	6.0858	R-Square	0.4884		
Root MSE	0.7448	Adj R-Sq	0.4202		
Analysis of Variance					
Source	DF	Sum of Squares	Mean Square	F Stat	Pr > F
Model	4	15.8841	3.9710	7.16	0.0004
Error	30	16.6402	0.5547	.	.
C Total	34	32.5244	.	.	.

Student t-tests for a number of craniofacial variables are listed below.

Table 15 The TTEST Procedure for maxillary sinus volumes

Statistics									
Variable	Species	Lower CL		Upper CL		Lower CL		Upper CL	
		N	Mean	Mean	Mean	Std Dev	Std Dev	Std Dev	Std Err
TotMaxSinusCubeRt_S	F	35	0.4536	0.4673	0.4809	0.0321	0.0397	0.052	0.0067
TotMaxSinusCubeRt_S	M	34	0.3922	0.402	0.4117	0.0225	0.0279	0.0367	0.0048
TotMaxSinusCubeRt_S	Diff (1-2)		0.0488	0.0653	0.0818	0.0294	0.0344	0.0414	0.0083

T-Tests						
Variable	Method	Variances	DF	t Value	Pr > t	
TotMaxSinusCubeRt_S	Pooled	Equal	67	7.89	<.0001	
TotMaxSinusCubeRt_S	Satterthwaite	Unequal	61.1	7.93	<.0001	

Equality of Variances						
Variable	Method	Num DF	Den DF	F Value	Pr > F	
TotMaxSinusCubeRt_S	Folded F	34	33	2.02	0.0457	

Table 16 The TTEST Procedure for nasal breadth

Statistics									
Variable	Species	Lower CL		Upper CL		Lower CL		Upper CL	
		N	Mean	Mean	Mean	Std Dev	Std Dev	Std Dev	Std Err
nasal_breadth_S	F	35	5.7499	6.0858	6.4218	0.7911	0.9781	1.2815	0.1653
nasal_breadth_S	M	34	7.2514	7.6379	8.0243	0.8934	1.1076	1.4579	0.19
nasal_breadth_S	Diff (1-2)		-2.054	-1.552	-1.05	0.8932	1.0439	1.2563	0.2514

Table 16 – continued -

Variable	Method	Variances	DF	t Value	Pr > t
nasal_breadth_S	Pooled	Equal	67	-6.17	<.0001
nasal_breadth_S	Satterthwaite	Unequal	65.5	-6.16	<.0001

Equality of Variances

Variable	Method	Num DF	Den DF	F Value	Pr > F
nasal_breadth_S	Folded F	33	34	1.28	0.4742

Table 17 The TTEST Procedure for nasal height

Statistics

Variable	Species	Lower CL		Upper CL		Lower CL		Upper CL	
		N	Mean	Mean	Mean	Std Dev	Std Dev	Std Dev	Std Err
nasal_height_S	F	35	23.797	24.612	25.427	1.9193	2.3728	3.1088	0.4011
nasal_height_S	M	34	25.191	26.107	27.024	2.1194	2.6277	3.4587	0.4506
nasal_height_S	Diff (1-2)		-2.698	-1.495	-0.293	2.1404	2.5016	3.0105	0.6024

T-Tests

Variable	Method	Variances	DF	t Value	Pr > t
nasal_height_S	Pooled	Equal	67	-2.48	0.0156
nasal_height_S	Satterthwaite	Unequal	65.9	-2.48	0.0158

Equality of Variances

Variable	Method	Num DF	Den DF	F Value	Pr > F
nasal_height_S	Folded F	33	34	1.23	0.5568

Table 18 The TTEST Procedure for nasal index

Statistics									
Variable	Species	Lower CL		Upper CL		Lower CL		Upper CL	
		N	Mean	Mean	Mean	Std Dev	Std Dev	Std Dev	Std Err
Nasal_Index	F	35	23.619	24.76	25.9	2.6846	3.319	4.3486	0.561
Nasal_Index	M	34	27.986	29.331	30.677	3.1107	3.8566	5.0764	0.6614
Nasal_Index	Diff (1-2)		-6.299	-4.572	-2.844	3.075	3.5939	4.3251	0.8654

T-Tests						
Variable	Method	Variances	DF	t Value	Pr > t	
Nasal_Index	Pooled	Equal	67	-5.28	<.0001	
Nasal_Index	Satterthwaite	Unequal	64.9	-5.27	<.0001	

Equality of Variances						
Variable	Method	Num DF	Den DF	F Value	Pr > F	
Nasal_Index	Folded F	33	34	1.35	0.3880	

Table 19 The TTEST Procedure for maxillo-alveolar index

Statistics									
Variable	Species	Lower CL		Upper CL		Lower CL		Upper CL	
		N	Mean	Mean	Mean	Std Dev	Std Dev	Std Dev	Std Err
MaxilloAlveolar_Index	F	35	66.304	68.421	70.538	4.9847	6.1625	8.0741	1.0417
MaxilloAlveolar_Index	M	30	61.291	63.413	65.536	4.527	5.6843	7.6415	1.0378
MaxilloAlveolar_Index	Diff (1-2)		2.0511	5.008	7.9649	5.0658	5.9471	7.2027	1.4797

T-Tests						
Variable	Method	Variances	DF	t Value	Pr > t	
MaxilloAlveolar_Index	Pooled	Equal	63	3.38	0.0012	

Table 19 – continued -

MaxilloAlveolar_Index	Satterthwaite	Unequal	62.6	3.41	0.0012

Equality of Variances

Variable	Method	Num DF	Den DF	F Value	Pr > F
MaxilloAlveolar_Index	Folded F	34	29	1.18	0.6616

Table 20 The TTEST Procedure for palatal index

Statistics

Variable	Species	Lower CL		Upper CL		Lower CL		Upper CL		Std Dev	Std Err
		N	Mean	Mean	Mean	Mean	Std Dev	Std Dev	Std Dev		
Palatal_Index	F	35	37.234	39.245	41.256	4.7346	5.8533	7.6691	0.9894		
Palatal_Index	M	34	43.947	44.737	45.527	1.8255	2.2633	2.9791	0.3881		
Palatal_Index	Diff (1-2)		-7.637	-5.492	-3.347	3.8178	4.462	5.3698	1.0744		

T-Tests

Variable	Method	Variances	DF	t Value	Pr > t
Palatal_Index	Pooled	Equal	67	-5.11	<.0001
Palatal_Index	Satterthwaite	Unequal	44.2	-5.17	<.0001

Equality of Variances

Variable	Method	Num DF	Den DF	F Value	Pr > F
Palatal_Index	Folded F	34	33	6.69	<.0001

Table 21 The TTEST Procedure for bizygomatic breadth

Statistics									
Variable	Species	Lower CL N	Mean	Upper CL Mean	Lower CL Mean	Std Dev	Upper CL Std Dev	Std Dev	Std Err
Bizygomatic ic_ Breadth_S	F	35	42.014	43.216	44.419	2.8317	3.5008	4.5868	0.5917
Bizygomatic ic_ Breadth_S	M	31	46.575	48.476	50.377	4.1407	5.1816	6.9261	0.9306
Bizygomatic ic_ Breadth_S	Diff (1-2)		-7.413	-5.26	-3.107	3.7266	4.3699	5.2838	1.0778

T-Tests

Variable	Method	Variances	DF	t Value	Pr > t
Bizygomatic_Breadth_S	Pooled	Equal	64	-4.88	<.0001
Bizygomatic_Breadth_S	Satterthwaite	Unequal	51.7	-4.77	<.0001

Equality of Variances

Variable	Method	Num DF	Den DF	F Value	Pr > F
Bizygomatic_Breadth_S	Folded F	30	34	2.19	0.0282

Table 22 The TTEST Procedure for prosthion to nasion

Statistics									
Variable	Species	Lower CL N	Mean	Upper CL Mean	Lower CL Mean	Std Dev	Upper CL Std Dev	Std Dev	Std Err
prosthion _to_ nasion_S	F	35	28.556	29.468	30.38	2.1478	2.6553	3.4789	0.4488
prosthion _to_ nasion_S	M	33	29.361	30.61	31.858	2.8307	3.5199	4.6557	0.6127
prosthion _to_ nasion_S	Diff (1-2)		-2.645	-1.141	0.3628	2.6536	3.1047	3.7421	0.7533

Table 22 –continued –

T-Tests						
Variable	Method	Variances	DF	t Value	Pr > t	
prosthion_to_nasion_S	Pooled	Equal	66	-1.51	0.1346	
prosthion_to_nasion_S	Satterthwaite	Unequal	59.4	-1.50	0.1382	

Equality of Variances

Variable	Method	Num DF	Den DF	F Value	Pr > F	
prosthion_to_nasion_S	Folded F	32	34	1.76	0.1087	

Table 23 The TTEST Procedure prosthion to opisthocranion

Statistics									
Variable	Species	Lower CL		Upper CL		Lower CL		Upper CL	
		N	Mean	Mean	Mean	Std Dev	Std Dev	Std Dev	Std Err
Prosthion_ F		35	53.083	54.673	56.263	3.7448	4.6297	6.0658	0.7826
Opisthiocr anion_S									
Prosthion_ M		25	56.13	59.617	63.104	6.5962	8.4476	11.752	1.6895
Opisthiocr anion_S									
Prosthion_ Diff (1-2)			-8.345	-4.944	-1.543	5.4923	6.488	7.928	1.699
Opisthiocr anion_S									

T-Tests

Variable	Method	Variances	DF	t Value	Pr > t	
Prosthion_Opisthiocranion_S	Pooled	Equal	58	-2.91	0.0051	
Prosthion_Opisthiocranion_S	Satterthwaite	Unequal	34.3	-2.66	0.0119	

Equality of Variances

Variable	Method	Num DF	Den DF	F Value	Pr > F	
Prosthion_Opisthiocranion_S	Folded F	24	34	3.33	0.0014	

Table 24 The TTEST Procedure for superior bimaxillary breadth

Statistics									
Variable	Species	Lower CL		Upper CL		Lower CL		Upper CL	
		N	Mean	Mean	Mean	Std Dev	Std Dev	Std Dev	Std Err
Superior_ bimaxillar e_breadth_ S	F	35	13.166	14.119	15.072	2.2435	2.7737	3.634	0.4688
Superior_ bimaxillar e_breadth_ S	M	33	16.749	17.818	18.887	2.4237	3.0139	3.9864	0.5246
Superior_ bimaxillar e_breadth_ S	Diff (1-2)		-5.1	-3.699	-2.298	2.4723	2.8926	3.4865	0.7019

T-Tests						
Variable	Method	Variances	DF	t Value	Pr > t	
Superior_bimaxillare_breadth_S	Pooled	Equal	66	-5.27	<.0001	
Superior_bimaxillare_breadth_S	Satterthwaite	Unequal	64.7	-5.26	<.0001	

Equality of Variances						
Variable	Method	Num DF	Den DF	F Value	Pr > F	
Superior_bimaxillare_breadth_S	Folded F	32	34	1.18	0.6334	

Table 25 The TTEST Procedure for inferior bimaxillary breadth

Statistics									
Variable	Species	Lower CL		Upper CL		Lower CL		Upper CL	
		N	Mean	Mean	Mean	Std Dev	Std Dev	Std Dev	Std Err
Inferior_ bimaxillar e_breadth_ S	F	35	26.426	27.348	28.27	2.1713	2.6844	3.5171	0.4537
Inferior_ bimaxillar e_breadth_ S	M	32	31.226	32.596	33.967	3.0476	3.8014	5.0539	0.672

Table 25 – continued –

Inferior_ Diff (1-2)	-6.843	-5.248	-3.653	2.7876	3.2652	3.9417	0.7986
bimaxillar							
e_breadth_							
S							

T-Tests

Variable	Method	Variances	DF	t Value	Pr > t
Inferior_bimaxillare_breadth_S	Pooled	Equal	65	-6.57	<.0001
Inferior_bimaxillare_breadth_S	Satterthwaite	Unequal	55.2	-6.47	<.0001

Equality of Variances

Variable	Method	Num DF	Den DF	F Value	Pr > F
Inferior_bimaxillare_breadth_S	Folded F	31	34	2.01	0.0497

Table 26 The TTEST Procedure for left choanal height**Statistics**

Variable	Species	Lower CL N	Upper CL Mean	Lower CL Mean	Upper CL Mean	Lower CL Std Dev	Upper CL Std Dev	Lower CL Std Dev	Upper CL Std Dev	Std Err
choanal_ height_ left_S	F	35	6.5703	7.0359	7.5014	1.0962	1.3552	1.7756	0.2291	
choanal_ height_ left_S	M	33	7.0634	7.3907	7.7181	0.7424	0.9231	1.221	0.1607	
choanal_ height_ left_S	Diff (1-2)		-0.92	-0.355	0.2099	0.9965	1.1659	1.4052	0.2829	

T-Tests

Variable	Method	Variances	DF	t Value	Pr > t
choanal_height_left_S	Pooled	Equal	66	-1.25	0.2141
choanal_height_left_S	Satterthwaite	Unequal	60.2	-1.27	0.2096

Equality of Variances

Variable	Method	Num DF	Den DF	F Value	Pr > F
choanal_height_left_S	Folded F	34	32	2.16	0.0315

Table 27 The TTEST Procedure for right choanal height

Statistics									
Variable	Species	Lower CL		Upper CL		Lower CL		Upper CL	
		N	Mean	Mean	Mean	Std Dev	Std Dev	Std Dev	Std Err
choanal_height_right_S	F	35	6.4741	6.9599	7.4457	1.1439	1.4142	1.8528	0.239
choanal_height_right_S	M	31	7.1191	7.4549	7.7908	0.7316	0.9155	1.2237	0.1644
choanal_height_right_S	Diff (1-2)		-1.089	-0.495	0.0994	1.0288	1.2064	1.4586	0.2975

T-Tests

Variable	Method	Variances	DF	t Value	Pr > t
choanal_height_right_S	Pooled	Equal	64	-1.66	0.1010
choanal_height_right_S	Satterthwaite	Unequal	58.9	-1.71	0.0932

Equality of Variances

Variable	Method	Num DF	Den DF	F Value	Pr > F
choanal_height_right_S	Folded F	34	30	2.39	0.0177

Table 28 The TTEST Procedure for left choanal width

Statistics									
Variable	Species	Lower CL		Upper CL		Lower CL		Upper CL	
		N	Mean	Mean	Mean	Std Dev	Std Dev	Std Dev	Std Err
choanal_width_left_S	F	35	2.2624	2.425	2.5875	0.3828	0.4732	0.62	0.08
choanal_width_left_S	M	33	3.0479	3.2486	3.4493	0.4552	0.5661	0.7487	0.0985
choanal_width_left_S	Diff (1-2)		-1.076	-0.824	-0.572	0.4447	0.5203	0.6271	0.1262

Table 28 – continued -

T-Tests					
Variable	Method	Variances	DF	t Value	Pr > t
choanal_width_left_S	Pooled	Equal	66	-6.52	<.0001
choanal_width_left_S	Satterthwaite	Unequal	62.5	-6.49	<.0001

Equality of Variances

Variable	Method	Num DF	Den DF	F Value	Pr > F
choanal_width_left_S	Folded F	32	34	1.43	0.3061

Table 29 The TTEST Procedure for right choanal width

Statistics

Variable	Species	Lower CL		Upper CL		Lower CL		Upper CL	
		N	Mean	Mean	Mean	Std Dev	Std Dev	Std Dev	Std Err
choanal_width_right_S	F	35	2.3549	2.5125	2.67	0.371	0.4587	0.601	0.0775
choanal_width_right_S	M	30	3.1689	3.3557	3.5426	0.3985	0.5004	0.6727	0.0914
choanal_width_right_S	Diff (1-2)		-1.081	-0.843	-0.605	0.4074	0.4783	0.5793	0.119

T-Tests

Variable	Method	Variances	DF	t Value	Pr > t
choanal_width_right_S	Pooled	Equal	63	-7.09	<.0001
choanal_width_right_S	Satterthwaite	Unequal	59.5	-7.04	<.0001

Equality of Variances

Variable	Method	Num DF	Den DF	F Value	Pr > F
choanal_width_right_S	Folded F	29	34	1.19	0.6216

Table 30 The TTEST Procedure intercanine breadth

Statistics									
Variable	Species	Lower CL		Upper CL		Lower CL		Upper CL	
		N	Mean	Mean	Mean	Std Dev	Std Dev	Std Dev	Std Err
inter_	F	35	10.514	11.037	11.559	1.2301	1.5208	1.9925	0.2571
canine_									
breadth_	S								
inter_	M	34	10.336	10.995	11.654	1.5244	1.89	2.4877	0.3241
canine_									
breadth_	S								
inter_	Diff (1-2)		-0.781	0.0417	0.8648	1.4653	1.7126	2.061	0.4124
canine_									
breadth_	S								

T-Tests						
Variable	Method	Variances	DF	t Value	Pr > t	
inter_canine_breadth_S	Pooled	Equal	67	0.10	0.9198	
inter_canine_breadth_S	Satterthwaite	Unequal	63.3	0.10	0.9200	

Equality of Variances						
Variable	Method	Num DF	Den DF	F Value	Pr > F	
inter_canine_breadth_S	Folded F	33	34	1.54	0.2125	

Table 31 The TTEST Procedure for ectomolar breadth

Statistics									
Variable	Species	Lower CL		Upper CL		Lower CL		Upper CL	
		N	Mean	Mean	Mean	Std Dev	Std Dev	Std Dev	Std Err
ectomolar	F	35	18.823	19.354	19.885	1.2498	1.5451	2.0244	0.2612
breadth									
S									
ectomolar	M	34	21.505	22.297	23.089	1.8308	2.2698	2.9877	0.3893
breadth									
S									
ectomolar	Diff (1-2)		-3.874	-2.943	-2.012	1.6567	1.9362	2.3302	0.4662
breadth									
S									

Table 31 – continued -**T-Tests**

Variable	Method	Variances	DF	t Value	Pr > t
ectomolar_breadth_S	Pooled	Equal	67	-6.31	<.0001
ectomolar_breadth_S	Satterthwaite	Unequal	58	-6.28	<.0001

Equality of Variances

Variable	Method	Num DF	Den DF	F Value	Pr > F
ectomolar_breadth_S	Folded F	33	34	2.16	0.0286

Table 32 The TTEST Procedure for endomolar breadth**Statistics**

Variable	Species	Lower CL		Upper CL		Lower CL		Upper CL	
		N	Mean	Mean	Mean	Std Dev	Std Dev	Std Dev	Std Err
endomolar_breadth_S	F	35	10.729	11.142	11.555	0.9729	1.2028	1.576	0.2033
endomolar_breadth_S	M	34	12.075	12.57	13.064	1.1432	1.4173	1.8656	0.2431
endomolar_breadth_S	Diff (1-2)		-2.058	-1.427	-0.796	1.1233	1.3129	1.58	0.3161

T-Tests

Variable	Method	Variances	DF	t Value	Pr > t
endomolar_breadth_S	Pooled	Equal	67	-4.51	<.0001
endomolar_breadth_S	Satterthwaite	Unequal	64.6	-4.50	<.0001

Equality of Variances

Variable	Method	Num DF	Den DF	F Value	Pr > F
endomolar_breadth_S	Folded F	33	34	1.39	0.3457

Table 33 The TTEST Procedure for aperture height

Statistics									
Variable	Species	Lower CL N	Upper CL Mean	Lower CL Mean	Upper CL Mean	Std Dev	Std Dev	Std Dev	Std Err
aperture_	F	35	8.9709	9.4225	9.874	1.0633	1.3145	1.7223	0.2222
height_S									
aperture_	M	34	11.117	11.49	11.863	0.8619	1.0685	1.4065	0.1833
height_S									
aperture_	Diff (1-2)		-2.644	-2.067	-1.491	1.0265	1.1997	1.4438	0.2889
height_S									

T-Tests

Variable	Method	Variances	DF	t Value	Pr > t
aperture_height_S	Pooled	Equal	67	-7.16	<.0001
aperture_height_S	Satterthwaite	Unequal	65	-7.18	<.0001

Equality of Variances

Variable	Method	Num DF	Den DF	F Value	Pr > F
aperture_height_S	Folded F	34	33	1.51	0.2368

Table 34 The TTEST Procedure for basion to nasion

Statistics									
Variable	Species	Lower CL N	Upper CL Mean	Lower CL Mean	Upper CL Mean	Std Dev	Std Dev	Std Dev	Std Err
basion_	F	34	32.292	33.252	34.212	2.2188	2.7508	3.6209	0.4718
nasion_S									
basion_	M	34	35.612	37.723	39.834	4.8802	6.0505	7.9641	1.0376
nasion_S									
basion_	Diff (1-2)		-6.746	-4.471	-2.195	4.0168	4.6998	5.6646	1.1399
nasion_S									

Table 34 – continued -

T-Tests						
Variable	Method	Variances	DF	t Value	Pr > t	
basion_nasion_S	Pooled	Equal	66	-3.92	0.0002	
basion_nasion_S	Satterthwaite	Unequal	46.1	-3.92	0.0003	

Equality of Variances

Variable	Method	Num DF	Den DF	F Value	Pr > F	
basion_nasion_S	Folded F	33	33	4.84	<.0001	

Table 35 The TTEST Procedure for prosthion to staphylion

Statistics

Variable	Species	Lower CL		Upper CL		Lower CL		Upper CL	
		N	Mean	Mean	Mean	Std Dev	Std Dev	Std Dev	Std Err
prosthion_ F to_ staphylion _S		35	25.774	26.638	27.501	2.0335	2.514	3.2938	0.4249
prosthion_ M to_ staphylion _S		34	27.031	28.131	29.231	2.5431	3.153	4.1502	0.5407
prosthion_ Diff (1-2) to_ staphylion _S			-2.862	-1.494	-0.125	2.4357	2.8467	3.4259	0.6855

T-Tests

Variable	Method	Variances	DF	t Value	Pr > t	
prosthion_to_staphylion_S	Pooled	Equal	67	-2.18	0.0329	
prosthion_to_staphylion_S	Satterthwaite	Unequal	63	-2.17	0.0336	

Equality of Variances

Variable	Method	Num DF	Den DF	F Value	Pr > F	
prosthion_to_staphylion_S	Folded F	33	34	1.57	0.1941	

Table 36 The TTEST Procedure for staphylion to hormion

Statistics									
Variable	Species	Lower CL	Upper CL	Lower CL	Upper CL	Std Dev	Std Dev	Std Dev	Std Err
		N	Mean	Mean	Mean				
staphylion_F		35	8.0797	8.305	8.5303	0.5305	0.6558	0.8592	0.1108
n_to_hormion_S									
staphylion_M		34	7.6956	8.4805	9.2655	1.8145	2.2497	2.9612	0.3858
n_to_hormion_S									
staphylion_Diff (1-2)			-0.967	-0.176	0.6159	1.4088	1.6465	1.9815	0.3965
n_to_hormion_S									

T-Tests						
Variable	Method	Variances	DF	t Value	Pr > t	
staphylion_to_hormion_S	Pooled	Equal	67	-0.44	0.6594	
staphylion_to_hormion_S	Satterthwaite	Unequal	38.4	-0.44	0.6644	

Equality of Variances						
Variable	Method	Num DF	Den DF	F Value	Pr > F	
staphylion_to_hormion_S	Folded F	33	34	11.77	<.0001	

4.9. DISCUSSION

4.9.1. Statistical results

The traditional approach to investigating maxillary sinus morphology has been based upon linear measures derived from plain radiographic films. Volumes have, in turn, been mathematically derived from such linear measures. Reliance upon plain film radiography has, however, exhibited some weaknesses. For example, the margins of the maxillary sinus cannot be identified clearly, thus precluding precise determination of

landmarks. Accordingly, dimensional measures are by necessity estimates, and volumetric measures based upon these are estimates as well. An additional problem is that use of conventional radiographs requires two separate views per individual, (an A-P for width and lateral for length and height). This procedure thus increases the error potential for now compounded estimates.

Data from this study has shown that the seed filling method, although labor intensive, provides a reliable and reproducible means for obtaining volumetric data. This is partly due to the size and packing qualities of the seeds, which allow them to follow the contours of the three-dimensional shape of the maxillary sinus. Another advantage of the seed filling method is that it has the ability to provide volumes for very irregular spaces, such as the nasal cavity proper with its turbinates.

CT-imaging markedly increases visualization of maxillary sinuses and internal nasal structures as compared to conventional X-ray. Assisted by VoxelView, CT-imaging also provides multiplanar two-dimensional visualizations which can be generated and viewed at any orientation by taking the points of intersection of a particular plane with the full series of coronal CT-scans. A three-dimensional reconstruction of the cranium can also be generated and viewed at any orientation by taking a variable number of points of intersection of the transverse and sagittal planes with the full series of coronal CT-scans. These various slice perspectives allowed appreciation of the sinus region in a manner not previously possible revealing, for example, intricacies of the irregular sinus walls not visible in plain films due to overlapping bone.

This initial phase of this work has shown that traditional measures, i.e., plain film radiography, for assessing dimensions or volumes of the nasal complex would not be optimum for this study. Both seed filling and reconstructed CT-imaging do appear appropriate for providing both reliable and reproducible volumetric measures, and CT-imaging, in addition, affords views and details of morphology previously unavailable.

Bivariate plots using maxillary sinus volume (MSV) as the dependent variable for all regressions offered differing results. The fact that the bivariate regression analysis indicated only 3 measures to be statistically significant for both *M. mulatta* and *M. fascicularis* was somewhat surprising given their close craniofacial similarity and, as has been suggested by molecular evidence, their shared phylogenetic history. Although the regression formula between MSV and nasal breadth for *M. fascicularis* is significant the r^2 value accounts about 20% of the variance leaving the other 80% of the variance to unknown factors. Similarly, MSV regressed against choanal width reveals a significant relationship but again with a low r^2 value of 0.11.

One of the more interesting findings was a significant r^2 regression score for the measure of prosthion to staphylion which essentially represents the length of the nasal cavity floor and by extension an indicator to the air conditioning process of the nasal region. This measure was significant for both taxa with r^2 values of 0.13 for *M. mulatta* and 0.12 for *M. fascicularis*. When prosthion to hormion, which is basically the previous measure extended from staphylion to hormion (this measure thus incorporates nasal cavity floor and choanal region), *M. mulatta* continues to show a significant r^2 value of 0.12 whereas *M. fascicularis* does not demonstrate a significant association to this measure. This may mean that choanal dimensions are not as critical as the nasal cavity proper when it comes to a respiratory prerequisite.

One measure that has been traditionally linked to biomechanical, or masticatory regimes was the measure of inferior bimaxillary suture to midpoint of glenoid tubercle. *M. fascicularis* was the taxa that showed a r^2 value of 0.25. On the other hand, a measure that may show mixed signal for thermoregulation or biomechanical adaptation is the superior bimaxillary suture. This measure was significant for *M. fascicularis* but had a somewhat low r^2 value of 0.18.

Bivariate plots for all dental linear measures against MSV were not statistically significant. Moreover, when height, width, and length were multiplied (and then the cube root was taken), in order to derive a volumetric surrogate for the molar tooth, no significant linear regression score was revealed. When the volumetric estimate for all three molars were regressed against MSV no significant r^2 value appeared. Thus, no single dental measure, or combination of measures, could be reliably used to predict MSV for any of the taxa in this study.

Perhaps the most important observations arise from multiple regression analyses, which are useful in indicating specific relationships. When a number of splanchnocranial variable sets were regressed against maxillary sinus volume, measures representing the respiratory portion of the nasal region (i.e., aperture height and choanal region) was revealed to be statistically significant for the *M. fascicularis* with a relatively high r^2 value of 0.57 while no significance was found for *M. mulatta*. When a subset of variables that include the nasal cavity floor were entered in the multiple regression analysis and combined with nasal height *M. fascicularis* was significant with an r^2 value of 0.50. What these significant r^2 scores may be indicating is that *M. fascicularis* is more dependent upon the nasal cavity proper with respect to either air conditioning or heat dissipation. *M. mulatta* had a significant r^2 score of 0.35 when nasal cavity floor width and length (endomolar breadth and staphylion to hornion respectively) were entered in the multiple regression analysis. Here, *M. mulatta* is putting more of an emphasis on choanal dimensions in conjunction with nasal cavity proportions. It appears that nasal breadth and prosthion to staphylion are covarying with maxillary sinus size in the same direction as reflected by their negative slope for each respected taxa. This suggests that nasal breadth, for *M. mulatta*, and prosthion to staphylion for *M. fascicularis*, are the strongest predictors of maxillary sinus size.

The student t-tests analysis of the study revealed many differences between the two groups especially in nasal complex components. For example, nasal breadths were found to be smaller in the lowland group when compared to the highland *M. mulatta* group. *M. fascicularis* exhibited larger paranasal sinuses than the highland macaque group. Indices of upper face (i.e., maxilloalveolar index), nasal index, and palatal index (a measure that incorporates the floor of nasal cavity) were found to be statistically significant between the two groups. Aside from nasal complex differences between the two groups of macaques, they also differed in a number of other craniofacial parameters. Such measures as include the length of cranium and both superior and inferior bimaxillary breadths, and bizygomatic breadth.

A major observation from multiple regression results is that both of these measures (nasal breadth – a part of the entry portal of the upper respiratory tract, and prosthion to staphylion – the height of the internal nares) relate to aspects of nasal complex structures rather than to other regions of the cranium. This suggests a tight functional coupling of one moiety of the nasal complex (e.g., aperture breadth) with another (e.g., maxillary sinus volume). Indeed, what these covarying relationships may give insight into are functional units within the nasal complex proper involving both splanchnocranial bones derived from membranous development and the more conservative endochondral bones. Change in these “functional units” may, in turn, relate to particular climatic or environmental influences. While further studies are needed to decipher the specific effects of differing environments upon the nasal complex, these results strongly suggest the interdependence of the maxillary sinus with other parts of the complex. Such ties strongly support a functional role for the sinuses in nasal complex/upper respiratory functions.

4.9.2. Implications of climatic factors on the nasal complex

The hypothesis offered that climate affects sinus size and other nasal complex components was indeed borne out by this study. The lowland *M. fascicularis* group exhibited larger paranasal sinuses but smaller nasal breadths than the highland *M. mulatta* group. They also differed significantly and extensively in a number of other parameters. The functional meaning of these are more complicated and will be discussed in the next chapter. One possible explanation is that differences found here may reflect genetic distinctiveness of the two taxa. As discussed earlier, there is a long history of debate as to whether these two groups constitute separate species as I have done here, or merely subspecies of a population of *M. mulatta*. As the differences seem so large between groups and as the respiratory system is so central to an animal's existence it appears unlikely that they are both members of the same species but, in turn, each may be moving along its own individual trajectory. So while climate may well affect nasal morphology a precise answer to the question will require a comparison of intraspecific lowland and highland groups of these, or other species. It was not possible to compare the two subgroups of *M. mulatta* because the low altitude population was not robust enough. An excellent test of these findings, however would be to examine a larger such sample to see if they were more similar to other *M. mulatta* or to the *M. fascicularis* group.

A major important difference from previous studies was the incorporation of new measures of the upper respiratory tract structures (e.g., maxillary sinus, nasal cavity, choanal dimensions), and the use of new techniques to measure them allowed for a more complete examination of the functional adaptation of the nasal complex. Thus, the value of this study was that it showed that selection could target any component of the nasal complex. Studies restricting their analysis to only classic external parameters may find

no significant differences among species studied when in fact they may be adapting to their environments differently.

Another avenue of concentration regarded the relationship between dentition and maxillary sinus size. Although not all dental measures were taken for each specimen more than 600 measures were obtained and analyzed with respect to maxillary sinus size. It was found that no reliable dental measure could be used to predict MSV for any of the taxa in this study. The fact that no combination of molar volumes showed significant relationships with MSV was surprising given that some researchers have previously proposed a strong relationship between fully erupted molar teeth and adult maxillary sinus form. Unquestionably, the floor of the maxillary sinus is related at least anatomically to the adult upper and posterior dentition. However, dentition has a robust functional relationship with dietary constraints but not to respiration and/or the paranasal sinuses. Clearly, the maxillary sinus, as a key component of the nasal complex, suggests it plays a primary functional role in respiration and perhaps a secondary, incidental structural support role within the dental arcade.

This study demonstrated the importance of including all components of the nasal complex, which may be subject to selection at different rates and magnitudes. This study also stressed the importance of treating the nasal complex as a functional integrated unit and not as independently distinct anatomic entities.

CHAPTER 5

THE NASAL COMPLEX IN HUMAN EVOLUTION: COMPARATIVE EXAMINATION OF NEANDERTHALS, ARCHAIC *HOMO SAPIENS* AND MODERN HUMANS

5.1. INTRODUCTION

The Neanderthals are the best known and most extensively studied group of extinct humans, yet paleoanthropologists still debate the morphological specializations that help to define their clade. In recent years, Schwartz and Tattersall (1996) proposed three newly recognized apomorphies within the Neanderthal nasal region that separate them from modern humans. Franciscus (1999), however, questioned the taxonomic validity of all three character states. This difference of interpretation led to the extensive re-examination of the nasal region of both modern and extinct humans in this chapter.

There are three primary objectives to this chapter. The first is to clarify the descriptions of the unique nasal features proposed by Schwartz and Tattersall (1996). The second is to evaluate the criticisms offered by Franciscus (1999). The third objective is to report the findings of a qualitative and quantitative comparative examination of the nasal complex of a “classic” Neanderthal – Gibraltar 1, an archaic *Homo sapiens* – Kabwe, and a multiregional group of modern humans. A

brief commentary is offered on the possible functional roles for the apparent nasal specializations of Neanderthals. The examination of regionally distinct modern human populations (n=1,205), available Neanderthal data, and an archaic *Homo sapiens* was undertaken in order to better understand and thus clarify some of the issues related to the comparative midfacial anatomy of Neanderthals and recent modern humans.

5.2. BACKGROUND

In the summer of 1856, two limestone quarrymen cleared out a six foot thick section of clay matrix from the inside of a small cave situated about 45 feet above the Düssel River within the township of Haan, Germany. Cutting into the clay with their picks and shovels, the workers unknowingly uncovered a calotte and other skeletal elements of a peculiar looking human (Eggerath, 1996). Named after the valley, or “thal” in German, from whence it came, the Neanderthal fossil became the type specimen of a newly recognized extinct human species, *Homo neanderthalensis* (King, 1864). Since King’s taxonomic assessment of the Haan human, numerous other fossils found throughout Europe and the Middle East have been attributed to this species, including those previously discovered from Engis in 1830 and Gibraltar in 1848. The large number of known specimens that constitute the Neanderthal sample, comprised of both cranial and postcranial elements at various developmental stages, have broadened our understanding of the ranges of morphological variability expressed among these ancient humans through time. Analyses of these remains have allowed us to make inferences about many of the physiological parameters (Laitman et al., 1996) and neurological capabilities (Lieberman, 1998) within the Neanderthal hypodigm, especially those pertaining to the upper respiratory tract

region. More recently, important advances in ancient nuclear and mitochondrial DNA analyses (Krings et al., 1999; Scholz et al., 1999) have provided firm genetic support for what William King had proposed more than a century earlier – that Neanderthals are taxonomically distinct from modern humans. Although considerable evidence has been offered suggesting that Neanderthals are a closely related but separate species from humans, many anthropologists continue to question the validity of *Homo neanderthalensis* (see discussion in Stringer and Gamble, 1993; Duarte et al., 1999).

In a recent article on Late Pleistocene hominin nasal anatomy, Schwartz and Tattersall (1996) offered further insights into the morphological delineation of Neanderthals from modern humans that were not previously recognized by researchers. They qualitatively examined archaic and modern human crania and reported that Neanderthals possess three autapomorphic bony features of the nasal region: 1) an internal nasal margin bearing a well-developed and vertically oriented medial projection, 2) a swelling of the lateral nasal cavity wall into the capacious posterior nasal cavity, and 3) the lack of an ossified roof over the lacrimal groove. Reviewing this work, Franciscus (1999) objected to all three of these apomorphies. Franciscus stated that Schwartz and Tattersall relied on damaged or incomplete fossils when making their anatomical assessment, failed to consider primary and secondary spatial consequences when describing nasal traits, and failed to consider ranges of variation in these traits in both fossil and modern humans. Franciscus concluded that these purported bony autapomorphic features are nothing more than shared derived characters, which he also observed in some archaic *Homo* fossils and many modern human populations.

5.3. CHARACTER 1: AN INTERNAL MARGIN BEARING A WELL-DEVELOPED AND VERTICALLY ORIENTED MEDIAL PROJECTION

Schwartz and Tattersall (1996) used Gibraltar 1 as their prime example of the three autapomorphies because all three characters are well illustrated in this fossil although many other Neanderthals exhibit character 1. The authors described this character as a rim of raised bone that projects from the anterior nasal aperture (on both sides) just within its anterior edge that forms an internal secondary margin. The rim travels almost halfway up the inner nasal wall, where it expands and becomes “a wide, bluntly pointed mass that protrudes medially into the nasal cavity... fades superiorly into a low ridge that continues to frame the nasal cavity...and the vertical portion is bounded by an open lacrimal groove” (Schwartz and Tattersall (1996, pg. 10852). The vertical portion is usually fully present only in adults.

Personal observations regarding this character (Figure 5-1) reveal that located within the piriform aperture of Gibraltar 1 is an internal secondary crest of bone situated posterior to the anterior rim of the nasal fossa. This secondary internal crest originates from the floor of the nasal aperture near the anterior nasal spine, where it begins to course in a lateral direction, forming a prenasal fossa. Upon reaching the lateral border of the piriform aperture, the internal secondary crest rises superiorly in the coronal plane, where it melds into a medially projected process, or medial projection (hereafter termed MP). Visualizing the MP as pyramidal in shape, its base is confluent with the lateral wall of the nasal cavity, while the apex projects medially towards the midline. The inferior portion of the base is continuous with the

Figure 5-1 a) The Gibraltar 1 external nasal aperture depicts the basic anatomy of the medial projection showing how it can be described as pyramidal in shape with an apex that projects medially towards the midline of the nasal aperture. Also, the prenasal fossa and secondary internal nasal crest are clearly visible. Notice that the medial projection and prenasal fossa in Gibraltar 1 are expressed bilaterally. **b)** The second close-up of the nasal region in Gibraltar 1 shows that the inferior border of the MP base is continuous with the secondary internal crest. This character alone negates inclusion of Gibraltar 1 into Gower's Stage 5 category as argued by Franciscus (1999). Furthermore, this picture points out that the superior base of the MP extends superiorly beyond the demarcation of the inferior orbital rim. (Photograph courtesy of Dr. Kenneth Mowbray, AMNH)

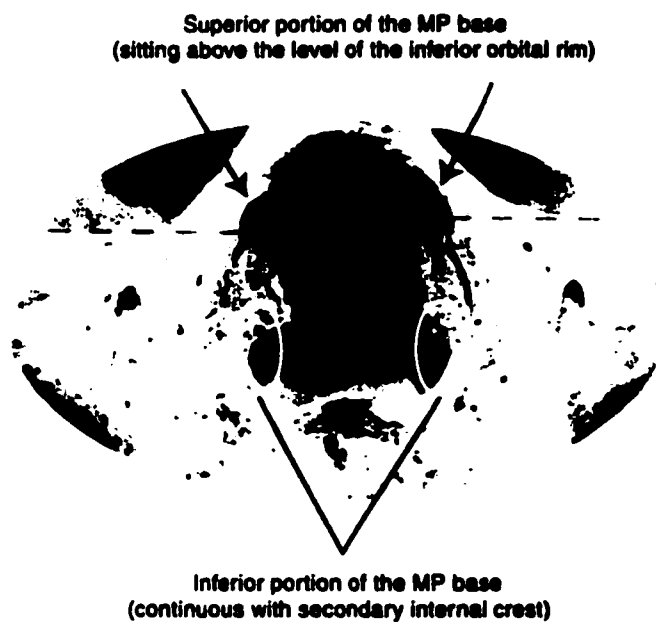


Figure 5-1a

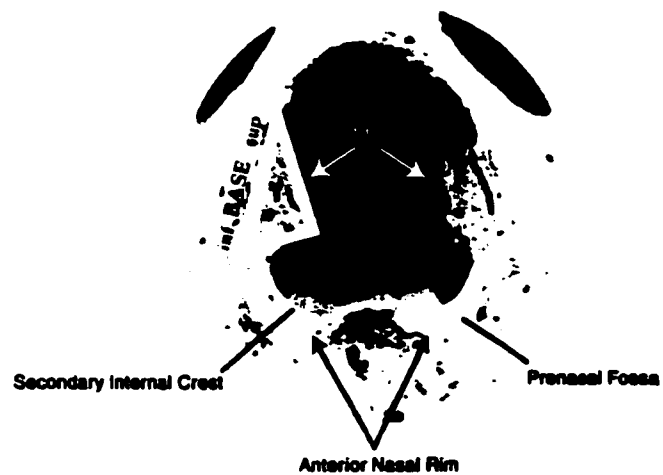


Figure 5-1b

internal secondary crest, while its superior portion continues to rise towards the orbit. Most of the posterior side of the base broadens in the parasagittal plane, particularly its superior portion, as it becomes confluent with the lateral wall of the piriform aperture. When viewing Gibraltar 1 from an anteroposterior perspective (in the Frankfurt Horizontal plane), the most superior portion of the MP base follows along the lateral internal portion of the frontal process of the maxilla, where it continues to rise well above the level of the inferior orbital rim (see Figure 5-1).

Franciscus (1999) contends that Schwartz and Tattersall (1996), by not using conventional terminology, incorrectly identified the internal margin and the medial projection. Schwartz and Tattersall, though, never intended the internal nasal margin and medial projection to be considered as separate characters: “[t]he ‘internal nasal margin,’ *with its* remarkable medial projection, does not, however, appear to be the only peculiarity of the Neanderthal nasal region” (p. 10852, my emphasis). In atomizing character 1 and assessing each part separately, Franciscus (1999, see table 1) argued that Gower’s (1923) terminology of nasal anatomy, which he claims is the nomenclature most widely used today to describe nasal cristae morphology, can be appropriately used to describe the Neanderthal nasal region. In doing so, Franciscus (1999) alleged that the internal nasal margin – his first feature dissected from character 1 – in Gibraltar 1 is actually a crista turbinalis which is the “Stage 5” condition as defined by Gower (1923) (also see Arsuaga et al., 1997). According to Gower (1923, pg. 34), this condition must exhibit a small angle between the crista spinalis and medial palatal suture, it must show a discontinuous rim of bone, and it must lack a prenasal fossa. Gower also stated (1923,

pg.35) that the crest of the crista turbinalis must terminate superiorly near the anterior end of the inferior turbinate.

My examination of the Neanderthal fossil revealed this is not the case. Rather, examination of the Gibraltar I nasal region reveals that the “Stage 5” distinction advocated by Franciscus is unwarranted since this Neanderthal exhibits a continuous crest of bone (my secondary internal crest), which merges with the MP (see Figure 5-1). In addition, this continuous secondary crest also contributes to the formation of a prenasal fossa, which according to Gower (1923) should not be present in a “Stage 5” condition. Interestingly, McCown and Keith (1937, pg. 262) also noted the presence of the internal secondary crest and the prenasal fossa in Gibraltar I, but they apparently opted not to follow Gower’s (1923) nomenclature (e.g., McCown and Keith “inner ridge” instead of “crista spinalis” and “paraseptal fossa” instead of “fossa prenasalis”). The presence of a continuous rim of bone and a prenasal fossa suggests that Gibraltar I either does not exhibit a “Stage 5” nasal cristae morphology, or lacks a crista turbinalis altogether. A prenasal fossa is not considered a unique feature in and of itself as a number of extant human specimens from different global regions have exhibited this feature (see Figure 5-2). What is unique is the intimate relation that the prenasal fossa has with the topographic position and the medial orientation of the MP coronally. For example, when specimens are viewed from a frontal view it may appear that these two structures are confluent and that the anterior attachment of the inferior turbinate appears to have a medial orientation in the coronal plane except when specimens are positioned in an oblique view (see Figure 5-3). This is because photographs are pictures of 3-dimensional objects

Figure 5-2. Cranium from a sub-Saharan population (Cat. No. 99/99102 AMNH) demonstrating the prenasal fossa morphology as indicated by black arrow. (Photo by the author)



Figure 5-2

Figure 5-3. a) Oblique view of sub-Saharan cranium (Cat. No. 99/9978 AMNH) showing prenasal fossa morphology and the anterior attachment of inferior turbinate (*black arrow*). (Photo by the author)

b) Similar view of a European specimen (Cat. No. 67/768102 AMNH) with inferior turbinate broken off but with the remaining morphology clearly showing the posterior orientation of the remnant turbinate (*black arrow*). (Photo by the author)



Figure 5-3a



Figure 5-3b

and are represented 2-dimensionally, without the aid of markers, depth perception becomes difficult. The reality is that anterior attachment of the inferior turbinate is the beginning of a posterior course that is angled sharply back. This is revealed when a 3-dimensional reconstruction of a CT scan of a live subject (i.e., the author's) is shown in a similarly oblique view (see Figure 5-4).

Unfortunately, due to poor nasal cavity preservation in Neanderthals, it is unclear whether the MP has a definite anatomical relationship with the inferior turbinate. Until more fossils with better preserved nasal regions become available to examine, one is left with two possibilities to help explain the morphology observed in Gibraltar 1. First, is that the MP represents a continuation of the crista spinalis, crista turbinalis or a combination of the two; and second, is that the secondary internal crest, which is continuous with the MP, is its own unique anatomical structure. In either case, the terminology devised by Gower (1923) is inadequate to describe the variation in morphology seen in Neanderthals, other archaics, and some recent human populations (see also Lahr, 1996, pg. 64-65).

The second atomized portion of character 1 addressed by Franciscus (1999) refers to the medial projection. In particular, he argued that the medial projections reported by Schwartz and Tattersall (which they reported in both young and adult Neanderthals) merely represent conchal crests. Although Franciscus comments that some modern human conchal crests project somewhat towards the midline, he failed to show that the modern human conchal crest is developmentally or functionally the same structure as the Neanderthal MP. Furthermore, Franciscus claimed

Figure 5-4. Three dimensional reconstruction of a CT scan of the author's cranium showing a true representation of the orientation of the anterior attachment of the inferior turbinate with a posterior rather than medial projection. Black arrow is pointing to piriform aperture rim and just posterior to it is the site of attachment of the inferior turbinate.



Figure 5-4.

that the accentuated size and shape of the Neanderthal medial projection and the degree to which some recent human conchal crests project to the midline reflect only a wide nasal fossa opening. Expanding on this idea, Franciscus stated that a Neanderthal medial projection ultimately resulted from secondary spatial consequences generated by other primary developmental factors in the mid-upper facial region. These reported primary developmental factors constitute the lateral eversion of the nasal bones and of the frontal processes of the maxillae. Franciscus suggested that a wider nasal opening offers the illusion of a medial projection (his conchal crest) that appears to be projected towards the midline of the internal nasal fossa, when in reality it does not. Franciscus further stated that the medial projection, because it grows as a secondary consequence to other primary midfacial developmental changes, is not a useful character for identifying phylogenetic affinities.

Based on personal examination of fossil and modern human crania, it is clear that modern human conchal crests are totally dissimilar in overall morphology to the Neanderthal MP, especially in the area comprising the superior portion of the MP base. I have yet to find a human conchal crest that projects as far to the midline or one that is similar in architecture to that of the Neanderthal MP. As noted above, no human conchal crest examined thus far has the large area of the MP base, rising vertically to become confluent with the lateral wall of the nasal aperture to end well above the level of the inferior orbital rim, as seen in Neanderthals. It has been established that Neanderthals have significantly wider nasal apertures than recent humans and many non-Neanderthal fossil hominins such as Kabwe (Márquez et al.,

1998). Although Franciscus (1999) correctly states that the lateral eversion of the nasal bones and frontal processes of the maxillae in Neanderthals affect the overall dimensions of the piriform aperture, even the widest apertures in recent humans fail to exhibit anything resembling the internal nasal morphology of the Neanderthals.

Franciscus (1999) also remarked that the medial projection is inappropriate for cladistic analyses because it is a product of secondary spatial consequences. It is interesting to note, however, that when Franciscus and Trinkaus (1988) discussed the shifts in nasal morphology in *Homo*, they stated that it would be overly simplistic to view the various changes in nasal morphology as merely secondary consequences of other mid-lower facial changes. Rather, they concluded that the evidence based on recent human and nonhuman primate clinical research suggests the “possibility of a semi-independent evolutionary trajectory for nasal morphology” (Franciscus and Trinkaus, 1988, pg. 525).

The general accepted definition of a character, or feature used in systematics is the following: a collection of mutually exclusive states which have a fixed order of evolution such that each state is derived directly from just one other state, and that there is a unique state from which every other state eventually derives (Farris et al., 1970; see also Cracraft and Eldredge, 1979). Essentially, if a character is dichotomous, it makes no difference if it results due to a cause or effect. Accordingly, the so-called secondary spatial consequences of other primary growth processes, which Franciscus (1999) argues to be untenable for cladistic analyses, may be indicative of important changes in overall growth and developmental

trajectories. This is precisely the kind of information needed to elucidate why two closely related species exhibit different bony morphologies.

In addition to my results based on comparative anatomy among adults, I argue that the real strength in support of the uniqueness of the Neanderthal nasal region lies in the developmental evidence. The examination of both modern human subadult material (upper third molar not erupted, $n=70$) and Neanderthal specimens (Table 1) suggests that Neanderthals appear to have developed medial swellings at very young ages, while modern humans never exhibit this peculiar nasal anatomy at any stage of development. From a developmental perspective, the nasal regions of modern humans clearly grow and develop in a different manner than those of Neanderthals. Taken together, the comparative anatomy and the developmental evidence strongly indicate that the Neanderthal internal nasal region is highly apomorphic.

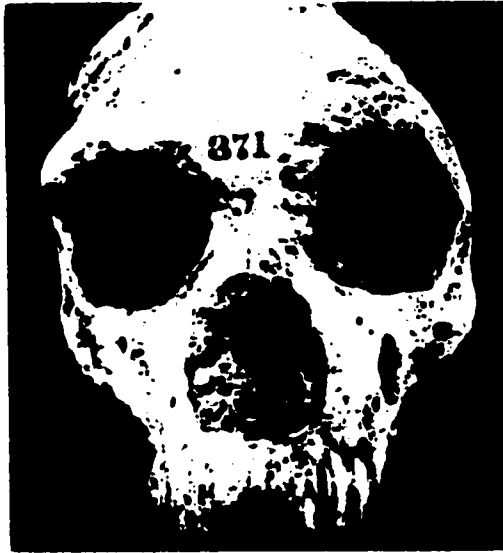
**Table 5-1 Neanderthal specimens which possess the MP trait
(From Schwartz and Tattersall, 1996)**

<u>Subadult</u>	<u>Adult</u>
Subalyuk	Gibraltar 1
Roc de Marsal	Krapina 3
Engis 2	Shanidar 1
Pech de l'Azé	La Ferrassie 1

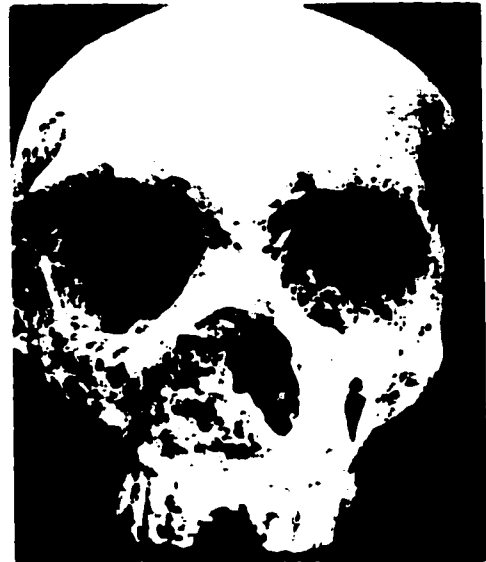
Franciscus (1999) also claimed that the MP in Gibraltar 1 might be an artifact created with a pneumatic device during the cleaning of the specimen. As Figure 5-5a shows, the nasal cavity of this fossil was initially filled with breccia (Sollas, 1907), which had to be removed before revealing the present internal nasal morphology of Gibraltar 1 (Figure 5-5d). After some cleaning had been completed, an updated photograph of the original fossil (Hrdlicka, 1914) revealed for the first time the left side MP (Figure 5-5b). It was not until two decades later, when enough breccia had been removed from the nasal cavity of Gibraltar 1, that both MPs and related structures were finally visible (McCown and Keith, 1937, pg. 262 and Figure 170). As Figure 5-5c shows, the MP and the internal secondary crest are easily recognized from the right side of the piriform aperture. In their discussion, McCown and Keith briefly mentioned the peculiarities of the Gibraltar 1 nasal region, especially the internal secondary crest of bone, yet they never entertained the idea that the nasal region of this Neanderthal could be the result of lapidary creativity, rather than genetic or epigenetic processes. It seems highly improbable that a preparator would have “sculpted” the nasal region in a manner so radically different from any modern human, or in such a way as to mimic the anatomy of Neanderthal fossils that had yet to be discovered (e.g., Shanidar 1).

Figure 5-5 - The four pictures above show the historical progression of matrix removal from the nasal cavity of Gibraltar I. It is interesting to note that by 1908 the left medial projection is clearly visible within the nasal cavity, yet it also appears that little preparation had taken place. Unfortunately, these photos do not show the three tiny apertures located superiorly on the right medial wall inside the nasal cavity, which lead into the maxillary sinus. These apertures attest to the competence and level of skill necessary for a preparator to distinguish matrix from fossilized bone.

a) Sollas, 1908



b) Hrdlicka, 1914



c) McCown & Keith, 1937



d) Present day

**Figure 5-5.**

5.4. CHARACTER 2: SWELLING OF THE LATERAL NASAL CAVITY WALL INTO THE POSTERIOR NASAL CAVITY.

Schwartz and Tattersall (1996) contended that the posterior portion of the nasal cavity exhibits a distinct swelling or bulging of the lateral nasal cavity wall that appears to house a medially expanded maxillary sinus. This character is reported from observations taken from Gibraltar I and Kulna.

The examination of Gibraltar I reveals distinct swellings not only in the posterolateral nasal cavity wall but also in the maxillary portion of the orbital floor and anterior midfacial region. It appears that this fossil's extensively inflated maxillary sinuses have greatly influenced the facial contours, orbital floors, and lateral nasal cavity wall morphologies, more so than in other hominins (e.g., Kimbel et al., 1997). While the maxillary sinuses of Gibraltar I and other Neanderthals obviously have profound effects on the contiguous bony elements of the splanchnocranium, it is important to note that the presence of the MP in Neanderthal subadults occurs long before maxillary sinus expansion begins. Kulna also reveals a swelling of the lateral maxillary wall as revealed by the remaining edge of broken bone that outlines the extent of the maxillary sinus.

Reviewing this character, Franciscus (1999) claimed that a bilateral bulging of the nasal cavity wall would encroach upon the available space in the nasal cavity and would therefore narrow the posterior nasal cavity breadth considerably. To test this hypothesis, he introduced measures of internal nasal and choanal breadths to compare among archaic and recent humans. His findings show that Neanderthals fall within the range of modern human variation; therefore, Franciscus "logically" rejected the autapomorphic status of character 2. His results, however, are based on the specious assumption that Schwartz and Tattersall meant that the swellings of the lateral nasal cavity walls result in a narrowing of the internal fossa. This is not the

case, as medial swellings may be accompanied by lateral expansion, thus not necessarily “narrowing” the nasal cavity. Thus, the two key measures employed by Franciscus are inappropriate here and fail to address the issue of whether Neanderthals possess a swelling of the lateral nasal wall.

5.5. CHARACTER 3: THE LACK OF AN OSSIFIED ROOF OVER THE LACRIMAL CANAL.

Schwartz and Tattersall (1996) described the Neanderthal lacrimal groove as open or lacking an “ossified roof.” The lacrimal groove sits behind the medial projection, which does not send a bony flange over the lacrimal canal, thus the canal remains patent (Schwartz, pers. comm.).

Of the three characters reported by Schwartz and Tattersall (1996), this character most requires elucidation. The roof, or “covering,” of the lacrimal groove is more accurately described as the medial ossified wall of the nasolacrimal canal. In the adult modern human condition, it is primarily formed by the lacrimal bone abutted anteriorly to the maxilla, posteriorly to the ethmoid, superiorly to the frontal, and inferiorly to the lacrimal process of the inferior nasal concha (Warwick and Williams, 1973; Schwartz, 1995). Examination of human fetal and infant material reveals that the lacrimal bone is already ossified at early stages of development, although it is generally diaphanous, which makes the bone extremely friable. During these early stages, however, the nasolacrimal canals lack ossified inferior borders due to the undeveloped lacrimal processes of the inferior conchae. The result is an unossified lacrimal groove (Figure 5-6a). During later development, the lacrimal process of the inferior concha remodels as the face grows, and by early adulthood the inferior concha fuses to the inferior portion of the lacrimal bone, completing the formation of the medial bony covering of the nasolacrimal canal (Figure 5-6b). It is

important to be aware that open spaces exist on the lateral wall of dry crania, but during life, these spaces are covered by dense connective membranous tissue that Zuckerkandl (1893) described as the anterior and posterior fontanelles of the lateral nasal wall. However, these fontanelles are situated distinctly posterior to the nasolacrimal pathway and thus do not affect the morphology of the canal.

Franciscus' (1999) evaluation of this feature is based only on the study by Murphy et al. (1998), in which they reported seeing both open and unopened lacrimal grooves in a sample of 206 modern humans. However, it is unclear from Murphy et al. (1998) what the age of their sample was and the criteria used to obtain their results. Unlike the findings by Murphy et al. (1998), the present study shows a remarkable coincidence between the appearance of an open medial covering of the nasolacrimal canal and missing inferior concha and/or a broken lacrimal-maxillary wall (Table 2). This was based on the examination of both nares of each individual in combined adult (n=367) and subadult (n=70) mixed sex sample. In adult specimens with undamaged nasal cavity walls and conchae, there was no evidence of an unossified medial covering of the nasolacrimal canal while two specimens in the subadult sample were found to have an unossified medial covering. These results strongly suggest that adult recent humans do not normally exhibit an unossified medial wall of the nasolacrimal canal.

2

Figure 5-6 Medial view of nasal cavity and related structures in **a)** neonatal modern human skull cut in a midsagittal plane and **b)** the same area in a young adult. In **a)** the lacrimal process of the inferior concha has yet to ossify superiorly to the lacrimal bone. This is the same anatomical area where I observed unossified nasolacrimal coverings in two subadults from the sample of 437 mixed adult and subadult individuals (Type 5 category in Table 2). **1** – Medial wall of the nasolacrimal canal; **2** – Unossified lacrimal process; **3** – Maxillary sinus; **4** – Inferior concha. In **b)** the lacrimal process of the inferior concha has ossified to the lacrimal bone.

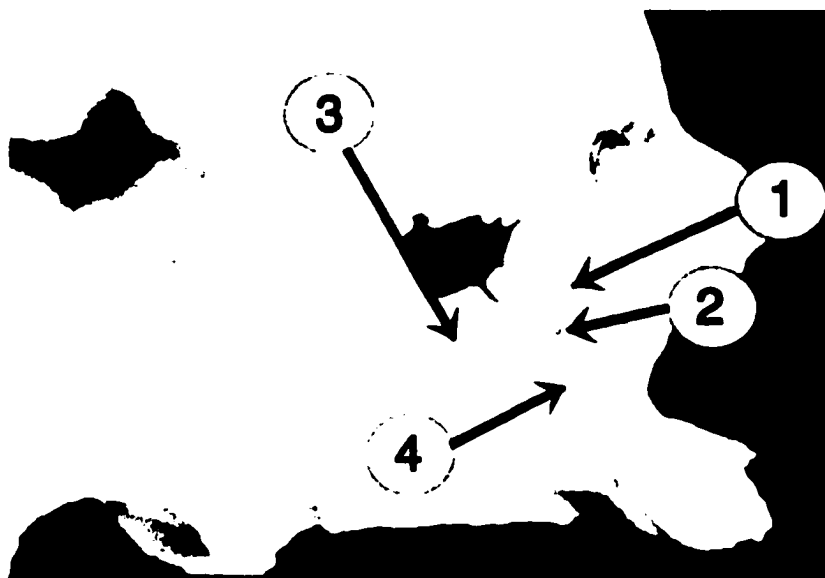


Figure 5-6a

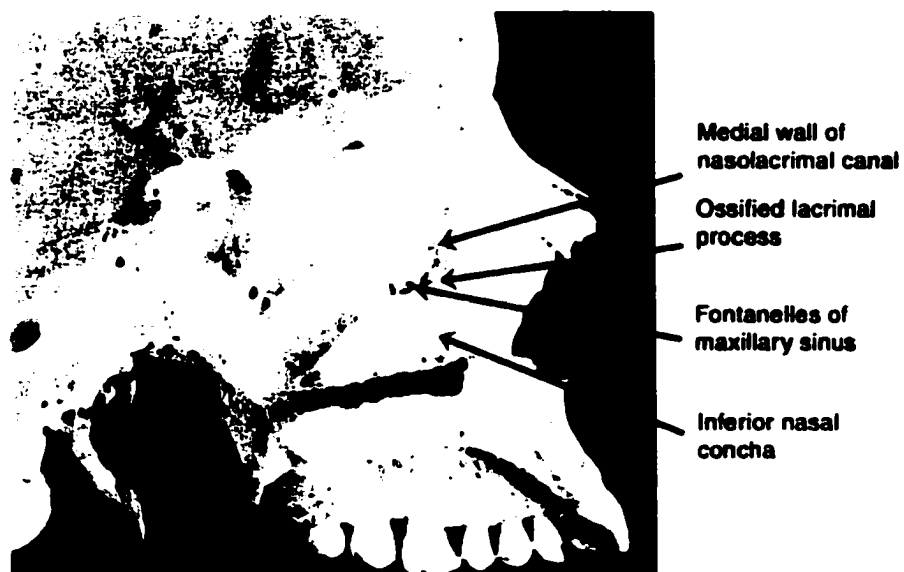


Figure 5-6b

Table 5-2 The occurrence of an open nasolacrimal covering in recent humans
All samples contain males and females.

Type 1: Intact inferior concha and intact ossified nasolacrimal covering

Mixed Adult Sample	Mixed Subadult Sample
85/367	7/70

Type 2: Intact inferior concha and damaged nasolacrimal covering

Mixed Adult Sample	Mixed Subadult Sample
110/367	29/70

Type 3: Damaged inferior concha and intact ossified nasolacrimal covering

Mixed Adult Sample	Mixed Subadult Sample
43/367	14/70

Type 4: Damaged inferior concha and damaged nasolacrimal covering

Mixed Adult Sample	Mixed Subadult Sample
129/367	18/70

Type 5: An unossified nasolacrimal covering

Mixed Adult Sample	Mixed Subadult Sample
0/367	2/70

5.6. THE NEANDERTHAL FACE AND PARANASAL SINUS SYSTEM

The craniofacial anatomy of Neanderthals features prominent faces with their zygomatic bones angling strongly backward, a dome shaped cranial vault, and a relatively flat cranial base. But it is clear from the literature that the one morphological aspect that dominates their craniofacial and dental anatomy is their enormous and projecting nose. While other specialists have focused on the browridge, which is well developed medially but reduced laterally, and on midfacial prognathism as one of the hallmarks that typifies this group, little has been done regarding the examination of their internal nasal complex components. Qualitative investigations regarding their paranasal sinuses have been reported with descriptions that range from expansive to extensive and finally to enormous. Examination of a typical classic Neanderthal such as Gibraltar leaves little doubt that the impact large maxillary sinuses have on their faces which give the midface a bulging appearance and a convex surface (see Figure 5-4). Another characteristic is in zygomatic region which lies in a flat, backwards angled plane. Combined with the great cranial breadth, the total effect of these features is a strongly projecting midfacial profile lateral to a large projecting nose, which could only have accentuated its appearance in life (Wolpoff, 1996). Support for this interpretation is found in the few remaining nasal bones, those not destroyed by what appears to have been a Neanderthal tradition of breaking open the midface to remove the brain. The position of these nasal bones indicate that north of the circum-Mediterranean area the nasal profile was highly angled so that the fleshy nose would have been extremely prominent. The combination of a large prominent nose and expansive maxillary sinus characterize the Würm Neanderthal adaptive complex expressed in the prognathism of the total face. The central question remains, however, as to whether this

adaptation is of a thermoregulatory nature, or a biomechanical one, or a combination of both.

The problem of previous investigations of not including the constituent components of the nasal complex in their examinations has not been confined to only fossil humans but also include extant human populations. Studies of the nasal complex in modern human populations have focused largely on external bony parameters with little attention to the internal components to assess ecophysiological adaptations to climate. In addition, while increased attention has been focused on extant groups, few studies have investigated the region at all in fossil hominids. Accordingly, a qualitative and quantitative examination of the nasal complex of two fossil hominins assessed against a large sample of modern crania was undertaken in order to factor in these nasal complex (external and internal) components in order to evaluate the relative weight that they may offer for optimal functioning of the region.

Crania of Broken Hill (Kabwe, Zambia) and Gibraltar I (Forbes' Quarry) were studied at the British Museum, London to assess their nasal complex. Assessment of internal anatomy was assisted via transillumination. A sample of European ($n=10$), Eskimo ($n=8$) and San ($n=10$) populations were studied from the collections of the division of Anthropology at the American Museum of Natural History and supplemented by data of 1,075 adult human crania representing both sexes and reflecting a range of extant regional populations from Howells's dataset (1973) (see table 3). Both external linear measures (e.g., nasal height, breadth) and internal volumes (e.g., maxillary sinus volumes) were assessed. Endocranial volumes were derived for the modern sample to standardized maxillary sinus size while endocranial volumes for the fossil specimens were obtained from the literature (see Márquez et al., 1995). Due to the condition of the fossil material only unilateral sinus cavity volumes were obtained for each individual.

Table 5-3. A multiregional modern human sample (n = 1,075). (From Howell, 1973).

Africa	Egypt (Gizeh 600-200 B.C.) (n=111)
Americas	Arikara (n = 69), Santa Cruz Island (n = 102)
	Peru (n = 110) Eskimo (n = 107)
Europe	Norse (n = 110), Hungary (n = 98)
	Austria (n = 107)
Asia	Japan (Hokkaido Island) (n = 87),
	Japan (Kyushu Island) (n = 91), China (n= 83)

Results indicate that while both specimens exhibited extensive sinusal pneumatization, Kabwe presented particularly large ethmoid sinuses, while Gibraltar 1 had an expansive maxillary sinus complex (Figure 5-7). Volumetric assessment of the maxillary sinuses shows Gibraltar 1 to fall at the limit of the extant human range, with Kabwe being identified within it (Figure 5-8). Assessment of nasal breadths of extant populations showed that narrow breadths were associated with cold weather populations while wide nasal breadths were more aligned with warm weather groups (Figure 5-9). When the dimension of nasal breadth was compared between the two fossil specimens and the multi-regional modern human sample, Gibraltar fell outside the modern human range while Kabwe fell conformably within it (Figure 5-10).

Figure 5-7. Frontal view of Gibraltar I cranium illustrating the effects of an expansive maxillary sinus on its contiguous structures such as the anterior face of the maxilla and orbital floors.

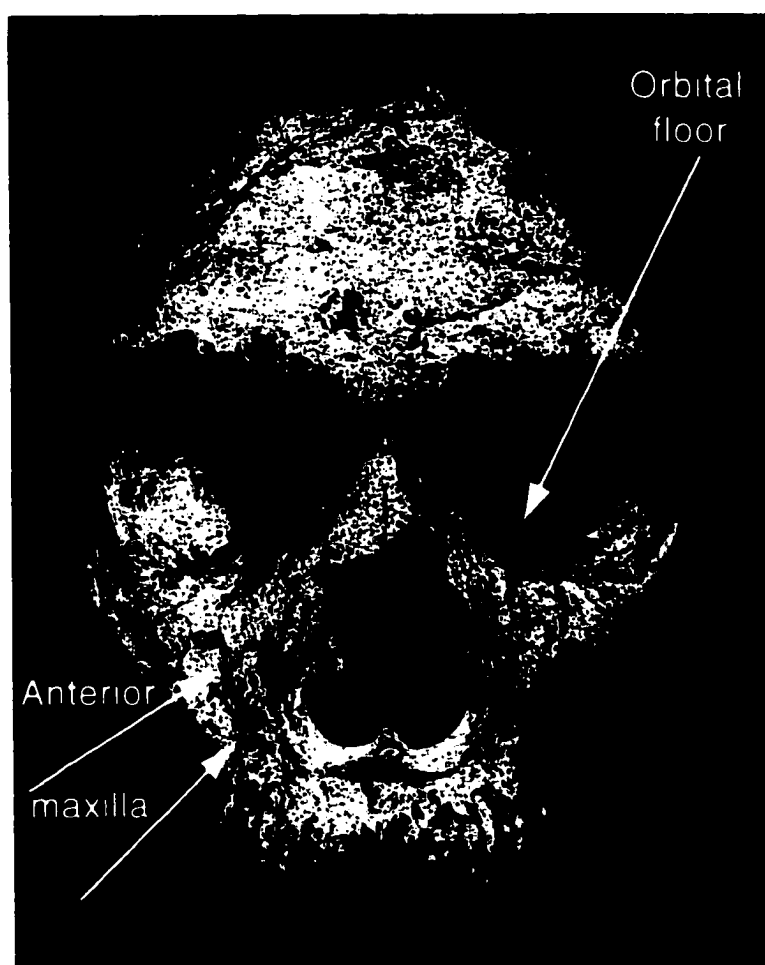


Figure S-7.

Figure 5-8. The maxillary sinus volume of Gibraltar I plotted against a sample of European and Eskimo sinus volumes (n=18).

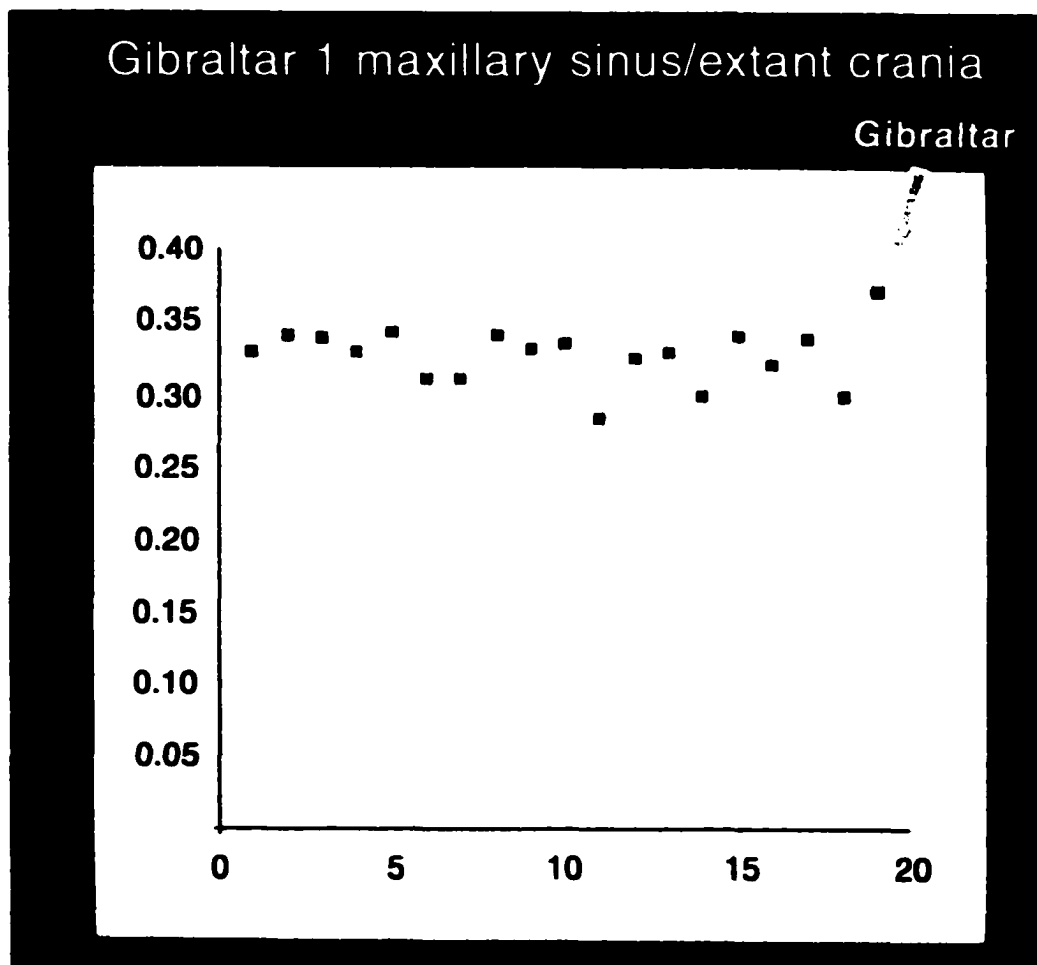


Figure 5-8.

Figure 5-9. Composite of nasal breadth profiles illustrating the narrow breadths clustering around cold weather populations (see a through c) whereas wide nasal breadths were associated with warm weather populations (see d through f).

a) European (Cat. No. 466), b) Eskimo (Cat. No. 99/6690), c) European (Cat. No. 193), d) San (Cat. No. 99/8449), e) San (Cat. No. 9976), f) San (Cat. No. 9978).

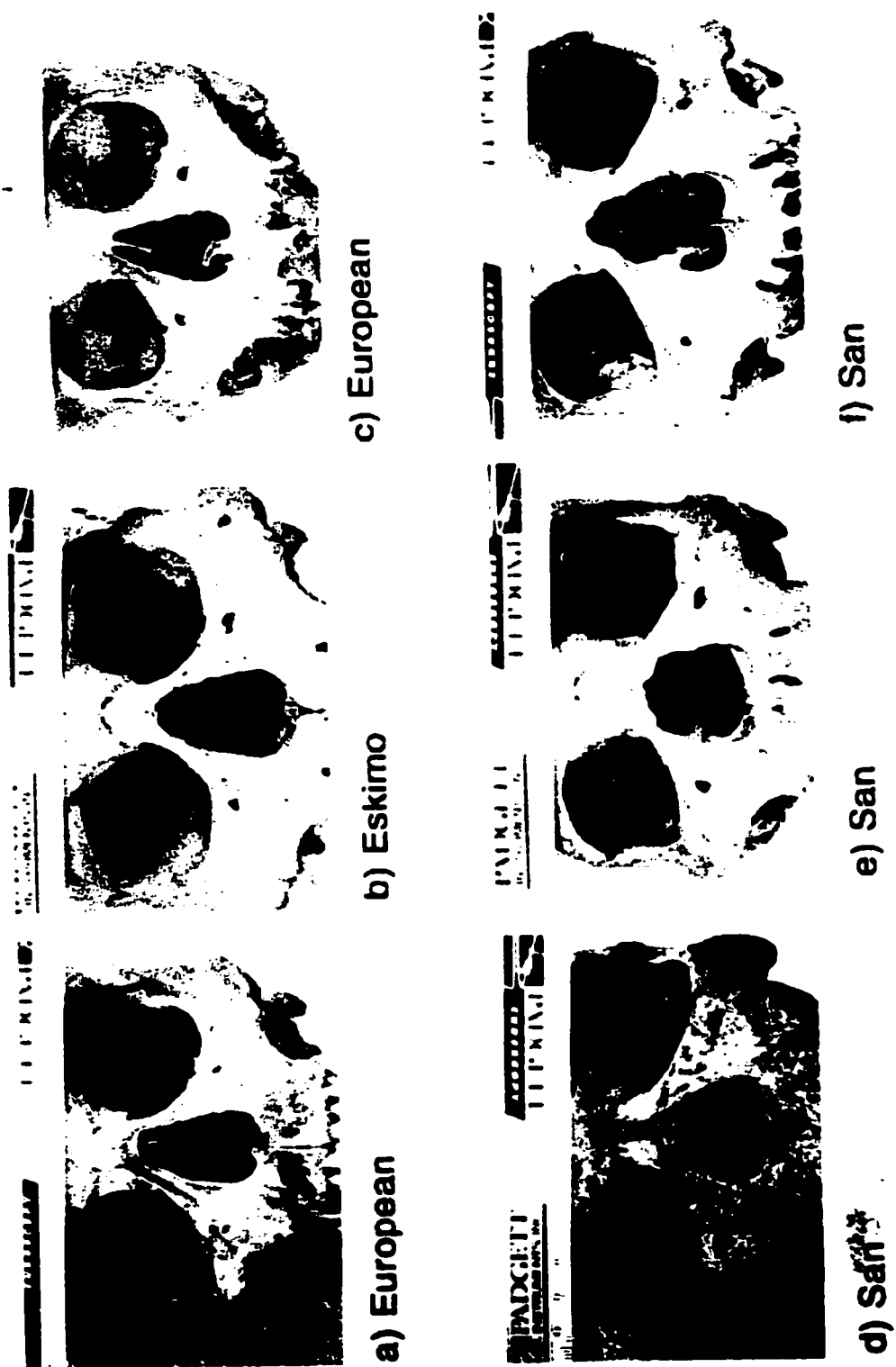


Figure 5-9.

Figure 5-10. Plot of log transformed data of nasal breadth dimension of Gibraltar I and Kabwe specimens compared to a multiregional population (n=1,075). Each data point represents a regional population. Note Gibraltar I falls outside the range of the modern sample while Kabwe is contained within it.

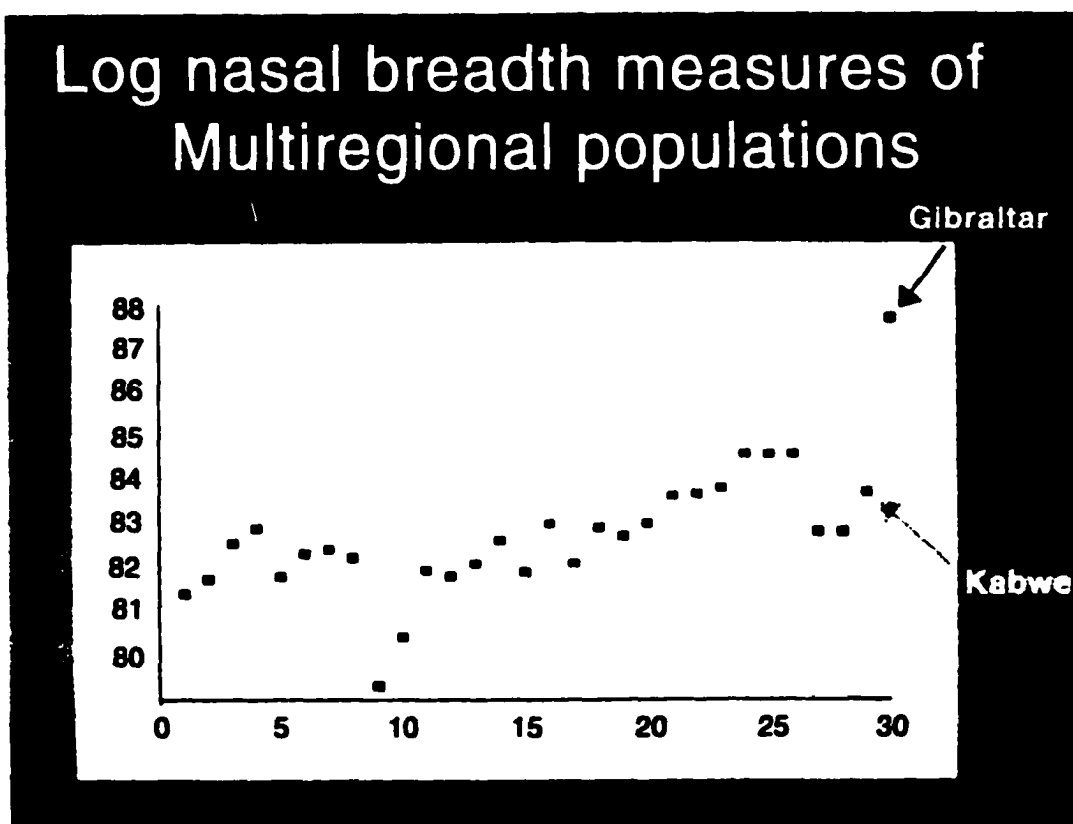


Figure 5-10.

5.7. DISCUSSION

After reviewing the evidence presented by Schwartz and Tattersall (1996) and Franciscus (1999), the ongoing research on the nasal complex in hominid specimens has generated the following conclusions. First, this review and study suggest that the presence of an unossified nasolacrimal roof in the Neanderthals studied by Schwartz and Tattersall (1996) may be due to broken lacrimal bones and damaged turbinate systems. The present findings showed that contrary to Franciscus (1999), the first two character states identified by Schwartz and Tattersall (1996) are unique to Neanderthals when compared to modern humans. Second, contrary to the suggestions of Franciscus (1999), the Neanderthal nasal configuration of the MP and the swollen lateral wall, when compared to the bony nasal morphology of any non-Neanderthals and modern humans, is apomorphic.

The physiologic functions of the MP may be to: serve to increase surface area for respiratory epithelium; be a strategic location for the initial site of impact of inspiratory airflow in order to minimize the traumatic effect of cold air on its mucous membranes; create airflow turbulence; serve as a protective measure; or be a cost/effective mechanism for heat reclamation. Recent physiologic and molecular studies have pointed to the paranasal sinuses as a prime site for the production of nitric oxide (NO), a gas with neurotransmitter-like functions. In the upper respiratory system, NO has a direct effect on ciliary activity, gland stimulation, and as an aerocrine messenger between the upper and lower airways that selectively reverses hypoxic pulmonary vasoconstriction without causing systemic vasodilation.

NO also functions in host defense (Fliegelman et al., 1998) insuring sterility of the paranasal sinuses, permitting mucus drainage through their ostia into the airflow pathway, and thus serving as a valuable adjunct in the air-conditioning process of humidification (Gannon et al., 1997).

The fact that modern populations exhibit specific morphology for their paranasal sinuses with respect to their ecogeographic localities whereas the Neanderthal sinus system differed from extant populations in the areas in which they are found, suggests that Neanderthal sinus volumes may reflect a different clade trajectory. This may be due to differing NO production rates and utilization relative to physiologic demands. Although we are just at the beginning of understanding this important gas in normal physiology, it is here hypothesized that the large size and idiosyncratic structure of Neanderthal paranasal sinuses may reflect a greater production of NO with selection maintaining their overall nasal complex configuration. As the amount of NO has been related to energy levels it is possible that a higher gas production in Neanderthals similarly reflects extensive respiratory activity, facilitating greater cardiopulmonary efficiency. The strategic location of the MP, the large maxillary sinus subserving hyperbehavioral activities while simultaneously serving as an adjunct to humidifying inspiratory air flow (see Gannon et al., 1997), and the relatively large entry portal of the upper respiratory tract as reflected by the nasal breadth dimension strongly indicates an adaptive thermoregulatory complex in Neanderthals rather than a biomechanical, or dietary design feature. These nasal complex features strongly suggest a distinctive morphological package that appeared to complement their behavioral patterns of

survival and was a highly successful system to combat the challenges offered by the climatic conditions of their time period.

5.8. CONCLUDING REMARKS

Both Schwartz and Tattersall (1996) and Franciscus (1999) have greatly contributed to the recent resurgence of interest in nasal morphology and upper respiratory physiology in hominins (see for example: Laitman et al., 1996; Márquez et al., 1997; Maurielle and Houet, 1998; Churchill et al., 1999; Murphy et al., 1999; Yokley, 1999). The ongoing examination of the nasal region in human and nonhuman primates has shown that intimate ties exist among the various components comprising the nasal complex. These relationships suggest that adaptive responses to environmentally challenging conditions may be expressed in one or more of the following: 1) anteriorly - piriform aperture dimensions, 2) internally - nasal cavity dimensions, 3) maxillary sinus dimensions, and 4) posteriorly - choanal dimensions. Restricting analysis to only one or two components may result in missing out on the totality of data offered by the overall nasal complex, which is a developmentally complex, functionally crucial, and phylogenetically important region.

CHAPTER 6

SUMMARY

This dissertation has focused on a comparative study of the human nose and paranasal sinuses to better elucidate its place in mammals and to understand specific features of the human condition. For this study, the research design included a three-phase approach. The first phase involved the preliminary investigation of the nasal region in a variety of terrestrial, non-human mammals and extant humans by traditional dissection, endoscopic examination and the use of CT imaging. The second phase involved a morphometric and CT examination of the effects of climate on the nasal complex of closely related macaques living at high and low altitudes, thus serving as a natural experiment. The third phase implemented a quantitative and qualitative study of modern and extinct humans in order to investigate similarities and differences in their nasal complex. This three-phase approach allowed for the integration of different methodologies that included invasive and non-invasive techniques, different imaging modalities, and a morphometric component in the examination of the nasal region. The advantage over previous nasal investigations was the ability to include and evaluate internal as well as classic external parameters.

The terrestrial nonhuman mammal examination revealed considerable inter-species variation with regard to the size of the bony elements surrounding the nasal cavity and paranasal sinuses and in the detailed composition of its boundaries. One particular finding showed a transverse lamina situated in the posterior upper portion of the nasal

cavity present only in the carnivores in the sample. This important structural element served to compartmentalize the nasal cavity into respiratory and olfactory regions. All members of the mammalian sample exhibited extensive branching of the ethmoturbinates (olfactory plates). Those specimens that presented a transverse lamina had ethmoturbinates located and concentrated solely in an olfactory recess. Due to this semi-enclosure of the olfactory recess the olfactory area is now removed from direct respiratory currents. An animal must engage in forced inhalation, or must be dependent upon diffusion of the inspired air into the olfactory region, in order for olfactory analysis to take place. A potential value of compartmentalizing the olfactory recess may be that the inspired air within it will not be readily washed out during exhalation, thus permitting a longer time for olfactory resolution. This would be of potential value in the localization and discrimination of a food source.

Assessment of the region in humans highlighted the “evolution” of our knowledge of nasal complex anatomy due to the opportunities provided by recent technological imaging advances in biomedicine. For example, as described, the advent of endoscopic or CT visualizations have literally re-written our concept and definitions of anatomical compartments of the region. The ability to view aspects of components such as the ostia or ethmoturbinates under a new “microscope” has enabled a precise detail of anatomy and refinement of functional attributions. Such specificity has already begun to redirect and focus clinical and surgical procedures.

The investigation of environmental differences in two closely related macaques, *Macaca fascicularis* and *Macaca mulatta*, allowed for a natural experiment to compare the affects of climate on the nasal complex. Results showed smaller sinuses in the high

altitude macaque group (i.e., *M. mulatta*) while nasal breadths were relatively larger in the low altitude macaques (i.e., *M. fascicularis*). These findings suggest that the region of the nasal complex and paranasal sinuses are very different between these groups. Whether this difference is, however, solely related to climatic influence rather than a biomechanical one is difficult to determine definitively. Morphometric analysis appear to indicate intimate ties between sinus anatomy and respiratory function lending support to a respiratory rather than a biomechanical role for the sinuses. The great dissimilarity between the two macaque groups, however, may reflect the genetic underpinnings of two different species that are further separated than previously thought.

The two fossil specimens examined - one generally considered to be a Neanderthal (Gibraltar), the other agreed by most to be an archaic *Homo sapiens* (Kabwe) - appear to be significantly different from each other in a number of parameters. In addition, Kabwe frequently fell within the extant human range for a number of key variables (e.g., nasal breadth, maxillary sinus volume) while Gibraltar clearly fell outside these ranges. These data strongly suggest that, regarding the nasal complex, Kabwe is within the range for extant *Homo sapiens* while Gibraltar is not. This further suggests that Neanderthals are substantively different from both contemporaries such as archaic *Homo sapiens* or extant populations. Interestingly, while most living cold weather modern populations exhibit narrow nasal breadths and smaller paranasal sinuses than warm weather groups, Neanderthals represented here by Gibraltar seem to show enlargement of nasal breadth, nasal cavity, and paranasal sinuses. Thus, they do not fall within other populations of similar time and do not fall within extant human populations that inhabit cold weather. This suggests that Neanderthals may have long and species-

specific trajectories in the evolution of the nose and paranasal sinuses and may have answered questions differently from those of either other early hominins or extant cold weather populations.

The data presented here, speak not only to the highly specialized nature of the nasal complex, but to the entirety of the upper respiratory tract in Neanderthals. Differences between Neanderthals and extant humans in laryngeal position, vocal tract configuration, and middle and inner ear structure have frequently been advanced. Assessment of the Neanderthal nasal complex, the “upper” portion of the upper respiratory tract, gives considerable support to these studies and the suggestion that the Neanderthal upper respiratory tract was apomorphic and had a distinct trajectory in its evolution. Due to the centrality of the respiratory system in mammals, differences between the upper respiratory system (including the nasal complex) in humans and Neanderthals, supports a species level distinction for Neanderthals, *Homo neanderthalensis*.

APPENDIX

Appendix A:

Raw data of *Macaca mulatta* and *Macaca fascicularis*

**Abbreviations for Institutions and Catalogue Numbers from which
Research Materials Were Acquired. All linear measurements are in
millimeters and volumes are in milliliters**

NMNH	National Museum of Natural History, Smithsonian Institution, Washington, D.C.
MCZ	Museum of Comparative Zoology, Harvard University Cambridge, Massachusetts
AMNH	American Museum of Natural History New York City, New York
BMNH	British Museum (Natural History) London, England

Appendix A

Museum	Cat. No.	Species	Bizygomatic_Breadth	Superior_bimaxillare_breadth	Inferior_bimaxillare_breadth
NMNH	114163	F	77.5	21.6	47.8
NMNH	111111	F	86.2	26.7	55.9
NMNH	123991	F	76.3	20.6	46.9
NMNH	114506	F	75.1	31.3	49.4
NMNH	121512	F	82.6	25.0	54.7
NMNH	114505	F	74.2	24.3	46.3
MCZ	35571	F	73.8	24.6	47.3
MCZ	35611	F	74.7	23.0	48.1
MCZ	35612	F	77.5	20.6	53.6
MCZ	35613	F	80.8	18.1	44.9
MCZ	35608	F	79.0	26.1	46.2
MCZ	35629	F	74.1	20.7	51.2
MCZ	35681	F	80.8	20.6	52.5
AMNH	3056	F	85.6	28.3	52.7
AMNH	99.1/3030	F	87.3	27.0	52.8
AMNH	99/3062	F	87.8	30.6	50.9
AMNH	102765	F	79.5	29.1	51.4
AMNH	103648	F	74.7	27.7	46.0
AMNH	106283	F	83.4	27.8	53.5
AMNH	106566	F	77.9	30.5	51.3
AMNH	106568	F	79.0	19.1	46.6
AMNH	106569	F	78.3	23.5	47.4
AMNH	107099	F	77.5	29.0	51.6
AMNH	187215	F	82.9	33.7	55.5
AMNH	175460	F	78.0	33.6	50.2
MCZ	37406	F	77.98	24.14	46.07
MCZ	35736	F	77.02	23.4	51.04
MCZ	35729	F	76.78	23.33	49.9
MCZ	37415	F	72.26	27.24	46.65
MCZ	37414	F	79.16	23.53	49.16
MCZ	35673	F	72.81	25.11	45.94

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MCZ	35677	F	78.96	23.07	44.41
MCZ	35656	F	80.35	30.59	53.52
MCZ	35619	F	74.91	21.84	45.64
MCZ	30384	f	78.58	29.99	54.15
BMNH	239-1-118rh	M	90.4	36.5	58.7
BMNH	14-7-10-4	M	87.8	31.9	57.7
BMNH	23-11-4-1	M	91.5	29.1	59.7
BMNH	31.1.11.8	M	79.3	31.4	47.4
BMNH	31.1.11.31	M		32.2	
BMNH	31.1.11.32	M	75.9	27.1	51.4
BMNH	48.2.1.26	M	88.0	37.6	58.1
BMNH	31.1.11.35	M	84.4	28.1	55.2
BMNH	14.7.10.2	M	81.0	34.6	55.9
BMNH	14-7-10-1	M	87.7	31.2	56.8
BMNH	451.8.223	M		32.3	
BMNH	1843.5.27.2rh	M	89.0	35.4	61.8
NMNH	35488rh	M	95.2	34.7	64.9
NMNH	173813rh	M	95.7	36.6	69.6
NMNH	267851rh	M	91.4	36.1	62.1
NMNH	353186rh	M	86.9	32.5	57.4
NMNH	63471rh	M	92.2	33.2	62.3
NMNH	35489rh	M	87.7	30.3	61.4
MCZ	30384rh	M	78.6	30.0	54.2
MCZ	57939rh	M	68.5	26.1	48.3
MCZ	60629rh	M	73.6	25.9	54.1
MCZ	26478rh	M	71.0	27.9	50.2
MCZ	26475rh	M	72.4	27.5	51.5
AMNH	7947	M	94.0		63.9
AMNH	112741	M		24.3	49.8
AMNH	26646	M	80.6	30.4	52.7
AMNH	54681	M	75.4	17.0	48.3
AMNH	54816	M	74.4	25.7	50.9

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AMNH	57039	M	78.8	36.4	53.3
AMNH	84474	M	91.6	33.6	62.8
AMNH	87264	M	75.0	28.0	52.9
AMNH	112741	M	78.4	27.6	55.6
AMNH	114547	M	75.8	23.9	48.0
AMNH	163613	M	79.3	26.6	55.7

Appendix A

Museum	Cat. No.	Species	inf_max_midpt_glenoid_tub_LEFT	inf_max_midpt_glenoid_tub_RIGHT
NMNH	114163	F	41.9	41.0
NMNH	111111	F	44.1	44.1
NMNH	123991	F	41.3	39.9
NMNH	114506	F	37.3	37.0
NMNH	121512	F	41.7	42.2
NMNH	114505	F	40.8	40.8
MCZ	35571	F	37.4	37.7
MCZ	35611	F	40.9	41.2
MCZ	35612	F	38.5	
MCZ	35613	F	47.0	47.7
MCZ	35608	F	40.5	41.9
MCZ	35629	F	36.8	36.5
MCZ	35681	F	43.8	43.6
AMNH	3056	F	43.1	43.1
AMNH	99.1/3030	F	42.9	43.9
AMNH	99/3062	F	46.7	46.0
AMNH	102765	F	41.5	40.6
AMNH	103648	F	37.6	37.6
AMNH	106283	F	42.8	42.8
AMNH	106566	F	40.0	40.4
AMNH	106568	F	41.3	41.3
AMNH	106569	F	42.5	42.5
AMNH	107099	F	37.5	36.7
AMNH	187215	F	43.4	43.9
AMNH	175460	F	43.2	43.2
MCZ	37406	F	40.41	40.49
MCZ	35736	F	40.2	40.69
MCZ	35729	F	40.05	39.9
MCZ	37415	F	39.1	38.57

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MCZ	37414	F	41.72	41.16
MCZ	35673	F	36.74	37.67
MCZ	35677	F	43.34	41.69
MCZ	35656	F	41.7	40.75
MCZ	35619	F	41.2	
MCZ	30384	f	41.47	40.62
BMNH	239-1-118rh	M	44.5	42.8
BMNH	14-7-10-4	M	46.4	45.6
BMNH	23-11-4-1	M	45.5	44.9
BMNH	31.1.11.8	M	41.4	40.1
BMNH	31.1.11.31	M		42.8
BMNH	31.1.11.32	M	41.9	42.7
BMNH	48.2.1.26	M	45.9	44.6
BMNH	31.1.11.35	M	40.1	42.7
BMNH	14.7.10.2	M	43.7	44.3
BMNH	14-7-10-1	M	46.5	43.9
BMNH	451.8.223	M	43.5	
BMNH	1843.5.27.2rh	M	42.9	42.9
NMNH	35488rh	M	47.0	46.7
NMNH	173813rh	M	47.5	48.6
NMNH	267851rh	M	49.3	49.2
NMNH	353186rh	M	43.9	45.6
NMNH	63471rh	M	45.6	44.1
NMNH	35489rh	M	44.1	44.1
MCZ	30384rh	M	41.5	40.6
MCZ	57939rh	M	35.3	34.9
MCZ	60629rh	M	38.0	
MCZ	26478rh	M	34.6	34.8
MCZ	26475rh	M	36.3	36.9
AMNH	7947	M	44.0	45.7

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AMNH	112741	M	41.7	41.7
AMNH	26646	M	40.7	40.4
AMNH	54681	M	36.4	36.5
AMNH	54816	M	39.2	39.2
AMNH	57039	M	41.0	41.3
AMNH	84474	M	46.0	45.8
AMNH	87264	M	37.0	36.6
AMNH	112741	M	38.1	37.3
AMNH	114547	M	38.9	38.9
AMNH	163613	M	37.5	37.9

Appendix A

Museum	Cat. No.	Species	inf_maxillare_pt_to_inion_LEFT	inf_maxillare_pt_to_inion_RIGHT
NMNH	114163	F	82.9	82.4
NMNH	111111	F	85.0	85.1
NMNH	123991	F	78.5	77.9
NMNH	114506	F	77.5	77.0
NMNH	121512	F	84.8	84.6
NMNH	114505	F	80.2	80.1
MCZ	35571	F	72.9	73.2
MCZ	35611	F	74.0	73.5
MCZ	35612	F	70.8	
MCZ	35613	F	76.4	77.2
MCZ	35608	F	70.0	70.6
MCZ	35629	F	67.8	68.3
MCZ	35681	F	74.8	74.1
AMNH	3056	F	83.7	84.5
AMNH	99.1/3030	F	83.2	84.5
AMNH	99/3062	F	84.1	83.2
AMNH	102765	F	80.3	80.4
AMNH	103648	F	72.8	73.8
AMNH	106283	F	81.1	81.7
AMNH	106566	F	81.3	81.8
AMNH	106568	F	77.5	77.7
AMNH	106569	F	82.7	82.5
AMNH	107099	F	76.6	76.1
AMNH	187215	F	89.4	89.5
AMNH	175460	F	83.4	83.0
MCZ	37406	F	70.17	71.3
MCZ	35736	F	70.8	70.12
MCZ	35729	F	69.22	69.02
MCZ	37415	F	72.72	72.75

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MCZ	37414	F	72.97	72.68
MCZ	35673	F	67.02	66.86
MCZ	35677	F	73.43	71.43
MCZ	35656	F	72.43	72.99
MCZ	35619	F	71.72	
MCZ	30384	F	80.47	86.88
BMNH	239-1-118rh	M	82.2	79.9
BMNH	14-7-10-4	M	80.8	80.0
BMNH	23-11-4-1	M	84.2	84.3
BMNH	31.1.11.8	M	75.0	74.3
BMNH	31.1.11.31	M		77.6
BMNH	31.1.11.32	M	75.9	76.0
BMNH	48.2.1.26	M	81.8	81.8
BMNH	31.1.11.35	M	81.0	79.6
BMNH	14.7.10.2	M	80.0	80.0
BMNH	14-7-10-1	M	80.8	79.3
BMNH	451.8.223	M	79.1	
BMNH	1843.5.27.2rh	M	82.7	83.0
NMNH	35488rh	M	96.5	96.3
NMNH	173813rh	M	93.7	95.8
NMNH	267851rh	M	96.2	96.1
NMNH	353186rh	M	89.4	89.4
NMNH	63471rh	M	94.4	93.7
NMNH	35489rh	M	89.6	91.2
MCZ	30384rh	M	87.5	86.9
MCZ	57939rh	M	72.8	72.3
MCZ	60629rh	M	80.3	
MCZ	26478rh	M	78.7	78.0
MCZ	26475rh	M	77.3	76.8
AMNH	7947	M	89.9	90.0

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AMNH	112741	M	84.7	84.3
AMNH	26646	M	85.2	84.1
AMNH	54681	M	73.6	74.3
AMNH	54816	M	80.2	79.0
AMNH	57039	M	86.3	85.3
AMNH	84474	M	92.6	93.9
AMNH	87264	M	80.1	80.1
AMNH	112741	M	79.1	79.1
AMNH	114547	M	82.4	81.7
AMNH	163613	M	79.5	79.9

Appendix A

Museum	Cat. No.	Species	prosthion_to_inf_maxillare_pt_LE	prosthion_to_inf_maxillare_pt_RI	prosthion_to_hormion
NMNH	114163	F	48.7	50.7	65.0
NMNH	111111	F	51.5	49.7	63.3
NMNH	123991	F	44.6	43.8	62.6
NMNH	114506	F	45.4	45.9	59.0
NMNH	121512	F	49.1	49.5	64.7
NMNH	114505	F	45.3	45.3	61.8
MCZ	35571	F	47.5	47.9	60.6
MCZ	35611	F	44.4	44.0	61.0
MCZ	35612	F	54.3		64.6
MCZ	35613	F	48.7	48.7	68.1
MCZ	35608	F	46.6	45.9	58.7
MCZ	35629	F	48.7	47.8	58.5
MCZ	35681	F	50.9	50.1	66.4
AMNH	3056	F	50.9	49.9	65.6
AMNH	99.1/3030	F	51.6	51.6	64.5
AMNH	99/3062	F	49.8	50.9	67.2
AMNH	102765	F	47.8	48.0	60.9
AMNH	103648	F	45.2	44.4	56.1
AMNH	106283	F	50.3	50.9	64.9
AMNH	106566	F	50.6	50.7	66.5
AMNH	106568	F	48.7	48.9	66.3
AMNH	106569	F	50.3	49.9	64.9
AMNH	107099	F	53.6	54.5	65.4
AMNH	187215	F	54.9	54.9	80.7
AMNH	175460	F	58.8	58.8	70.8
MCZ	37406	F	44.71	44.2	57.77
MCZ	35736	F	46.99	47.94	62.75
MCZ	35729	F	51.71	51.04	67.24
MCZ	37415	F	42.99	42.44	52.82

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MCZ	37414	F	43.09	42.91	57.47
MCZ	35673	F	41.31	41.97	54.28
MCZ	35677	F	48.97	47.98	64.13
MCZ	35656	F	51.59	51.84	64.67
MCZ	35619	F	48.76		64.56
MCZ	30384	F	45.11	44.31	61.09
BMNH	239-1-118rh	M	53.7	54.5	64.5
BMNH	14-7-10-4	M	48.7	49.7	64.5
BMNH	23-11-4-1	M	53.9	53.9	66.2
BMNH	31.1.11.8	M	47.3	46.4	63.3
BMNH	31.1.11.31	M		46.5	60.6
BMNH	31.1.11.32	M	45.3	45.7	61.0
BMNH	48.2.1.26	M	52.6	53.7	66.8
BMNH	31.1.11.35	M	49.1	50.9	64.3
BMNH	14.7.10.2	M	51.8	51.9	68.9
BMNH	14-7-10-1	M	48.4	48.8	64.3
BMNH	451.8.223	M	45.1	50.8	60.0
BMNH	1843.5.27.2rh	M	52.3		62.1
NMNH	35488rh	M			68.2
NMNH	173813rh	M			73.5
NMNH	267851rh	M	53.4	54.0	70.4
NMNH	353186rh	M	51.6	50.2	66.8
NMNH	63471rh	M	52.9	54.1	66.8
NMNH	35489rh	M	54.0	53.3	63.6
MCZ	30384rh	M	45.1	44.3	61.1
MCZ	57939rh	M	38.1	38.1	49.5
MCZ	60629rh	M	47.7		60.8
MCZ	26478rh	M	42.9	43.6	55.5
MCZ	26475rh	M	41.5	41.1	55.6
AMNH	7947	M	57.6	56.3	70.6

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AMNH	112741	M	45.7	46.0	63.4
AMNH	26646	M	47.5	47.0	61.4
AMNH	54681	M	38.9	40.7	51.0
AMNH	54816	M	44.2	42.8	53.7
AMNH	57039	M	47.8	49.4	65.3
AMNH	84474	M	49.9	51.0	65.9
AMNH	87264	M	44.7	46.2	59.3
AMNH	112741	M	49.4	48.5	60.3
AMNH	114547	M	39.8	40.3	53.4
AMNH	163613	M	46.4	46.3	58.4

Appendix A

Museum	Cat. No.	Species	prosthion_to_staphylon	prosthion_to_alveolar_spine	prosthion_to_sphenobasion
NMNH	114163	F	50.6	53.1	71.2
NMNH	111111	F	50.3	53.6	71.9
NMNH	123991	F	45.9	48.6	68.6
NMNH	114506	F	43.9	47.9	67.8
NMNH	121512	F	49.7	52.3	73.4
NMNH	114505	F	47.8	50.6	70.4
MCZ	35571	F	46.5	49.7	67.7
MCZ	35611	F	45.1	47.5	66.6
MCZ	35612	F	48.5	50.4	72.3
MCZ	35613	F	50.4	53.8	75.9
MCZ	35608	F	45.6	47.7	68.6
MCZ	35629	F	45.1	47.4	66.6
MCZ	35681	F	49.0	52.1	73.8
AMNH	3056	F	52.7	55.9	75.3
AMNH	99.1/3030	F	49.8	52.6	72.5
AMNH	99/3062	F	52.3	55.5	78.0
AMNH	102765	F	47.7	51.2	70.7
AMNH	103648	F	43.2	46.2	65.4
AMNH	106283	F	48.3	52.0	72.0
AMNH	106566	F	52.1	54.2	73.7
AMNH	106568	F	49.5	52.7	74.8
AMNH	106569	F	49.2	52.3	72.6
AMNH	107099	F	52.9	54.8	72.9
AMNH	187215	F	58.4	61.3	86.7
AMNH	175460	F	54.9	56.9	85.8
MCZ	37406	F	45.25	49.2	67.65
MCZ	35736	F	47.2	50.22	70.28
MCZ	35729	F	50.94	53.02	73.7
MCZ	37415	F	42.92	44.93	64.67

Museum	Cat. No.	Species	prosthion_to_staphylion	prosthion_to_alveolar_spine	prosthion_to_sphenobasion
NMNH	114163	F	50.6	53.1	71.2
NMNH	111111	F	50.3	53.6	71.9
NMNH	123991	F	45.9	48.6	68.6
NMNH	114506	F	43.9	47.9	67.8
NMNH	121512	F	49.7	52.3	73.4
NMNH	114505	F	47.8	50.6	70.4
MCZ	35571	F	46.5	49.7	67.7
MCZ	35611	F	45.1	47.5	66.6
MCZ	35612	F	48.5	50.4	72.3
MCZ	35613	F	50.4	53.8	75.9
MCZ	35608	F	45.6	47.7	68.6
MCZ	35629	F	45.1	47.4	66.6
MCZ	35681	F	49.0	52.1	73.8
AMNH	3056	F	52.7	55.9	75.3
AMNH	99.1/3030	F	49.8	52.6	72.5
AMNH	99/3062	F	52.3	55.5	78.0
AMNH	102765	F	47.7	51.2	70.7
AMNH	103648	F	43.2	46.2	65.4
AMNH	106283	F	48.3	52.0	72.0
AMNH	106566	F	52.1	54.2	73.7
AMNH	106568	F	49.5	52.7	74.8
AMNH	106569	F	49.2	52.3	72.6
AMNH	107099	F	52.9	54.8	72.9
AMNH	187215	F	58.4	61.3	86.7
AMNH	175460	F	54.9	56.9	85.8
MCZ	37406	F	45.25	49.2	67.65
MCZ	35736	F	47.2	50.22	70.28
MCZ	35729	F	50.94	53.02	73.7
MCZ	37415	F	42.92	44.93	64.67

NOTE TO USERS

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AMNH	112741	M	48.3	50.6	71.1
AMNH	26646	M	44.9	47.9	66.8
AMNH	54681	M	37.6	41.7	59.4
AMNH	54816	M	44.0	46.2	68.2
AMNH	57039	M	47.4	51.3	74.1
AMNH	84474	M	50.4	54.9	88.1
AMNH	87264	M	45.1	49.4	66.4
AMNH	112741	M	46.0	50.0	66.1
AMNH	114547	M	41.3	44.4	63.6
AMNH	163613	M	45.4	48.0	66.4

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Museum	Cat. No.	Species	prosthion_to_basion	prosthion_to_nasion	staphylion_to_hormion	staphylion_to_sphenobasion
NMNH	114163	F	84.7	54.3	15.0	20.6
NMNH	111111	F	87.7	53.6	15.0	21.8
NMNH	123991	F	79.6	52.7	16.6	22.1
NMNH	114506	F	80.0	49.3	15.7	23.9
NMNH	121512	F	84.3	59.5	15.9	23.0
NMNH	114505	F	82.9	53.4	14.2	22.9
MCZ	35571	F	81.9	53.5	14.9	21.2
MCZ	35611	F	80.0	53.6	15.6	21.4
MCZ	35612	F	85.3	54.5	15.1	23.0
MCZ	35613	F	89.1	62.1	18.1	25.4
MCZ	35608	F	82.1	46.4	15.1	22.6
MCZ	35629	F	78.4	54.4	13.3	20.8
MCZ	35681	F	87.5	58.5	17.7	24.7
AMNH	3056	F	91.3	50.2	15.2	21.8
AMNH	99.1/3030	F	86.7	59.9	14.9	22.4
AMNH	99/3062	F	90.9	58.7	15.2	25.1
AMNH	102765	F	82.1	49.2	13.3	22.7
AMNH	103648	F	77.6	51.1	13.8	21.2
AMNH	106283	F	85.9	55.5	16.6	22.8
AMNH	106566	F	87.2	50.8	14.1	21.1
AMNH	106568	F	86.9	44.3	16.5	24.2
AMNH	106569	F	87.0	52.0	16.7	24.3
AMNH	107099	F	86.0	55.7	13.4	19.9
AMNH	187215	F	100.3	69.9	16.3	28.1
AMNH	175460	F	98.2	59.4	16.1	30.9
MCZ	37406	F	79.7	51.11	14.47	22.71
MCZ	35736	F	84.59	54.06	15.72	22.74
MCZ	35729	F	85.45	59.29	16.38	23.12
MCZ	37415	F	78.16	44.25	12.14	21.84

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MCZ	37414	F	79.68	48.26	13.99	24.73
MCZ	35673	F	74.34	45.84	13	20.96
MCZ	35677	F	86.48	54.39	16.05	24.37
MCZ	35656	F	86.91	58.3	15.07	22.33
MCZ	35619	F	85.95	56.59	14.88	23.51
MCZ	30384	F	81.09	48.55	14.84	21.35
BMNH	239-1-118rh	M	90.2	55.0	27.9	36.6
BMNH	14-7-10-4	M	86.7	57.3	15.1	22.7
BMNH	23-11-4-1	M	93.0	63.5	15.2	24.4
BMNH	31.1.11.8	M	84.3	53.2	14.0	20.3
BMNH	31.1.11.31	M	83.2	52.7	15.9	23.6
BMNH	31.1.11.32	M	80.3	49.8	12.4	20.3
BMNH	48.2.1.26	M	89.5	55.1	15.3	22.8
BMNH	31.1.11.35	M	86.8	51.9	15.3	22.9
BMNH	14.7.10.2	M	92.2	57.7	16.3	22.8
BMNH	14-7-10-1	M	86.7	57.2	15.0	22.2
BMNH	451.8.223	M	82.6	48.6	13.1	21.5
BMNH	1843.5.27.2rh	M	89.0	48.6	16.0	23.9
NMNH	35488rh	M	96.1	59.2	13.3	40.3
NMNH	173813rh	M	98.4	58.8	14.6	24.0
NMNH	267851rh	M	97.0	58.0	16.7	26.6
NMNH	353186rh	M	91.0	53.4	15.9	25.4
NMNH	63471rh	M	91.4	57.0	13.0	23.6
NMNH	35489rh	M	89.1	47.9	12.4	22.7
MCZ	30384rh	M	81.1	48.6	14.8	21.4
MCZ	57939rh	M	70.9	35.2	10.9	19.4
MCZ	60629rh	M	80.5	38.0	15.1	21.8
MCZ	26478rh	M	76.7	51.6	13.4	21.1
MCZ	26475rh	M	73.7	44.8	13.7	20.6
AMNH	7947	M	93.1		17.0	23.2

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AMNH	112741	M	81.5	54.6	16.0	23.4
AMNH	26646	M	80.4	50.5	17.1	21.6
AMNH	54681	M	69.4	52.7	14.8	21.8
AMNH	54816	M	77.4	48.3	12.5	22.4
AMNH	57039	M	87.5	56.9	17.1	26.5
AMNH	84474	M	88.3	54.1	17.2	24.5
AMNH	87264	M	75.0	52.4	13.6	20.2
AMNH	112741	M	61.9	54.8	12.7	20.0
AMNH	114547	M	76.1	51.3	11.4	22.1
AMNH	163613	M	79.4	46.6	13.5	21.4

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Museum	Cat. No.	Species	staphylion_to_basion	inter_canine_breadth	ectomolar_breadth	endomolar_breadth
NMNH	114163	F	34.9	19.1	35.3	19.1
NMNH	111111	F	37.2	23.5	40.0	22.7
NMNH	123991	F	34.1	21.2	36.5	20.4
NMNH	114506	F	36.6	18.6	33.2	19.2
NMNH	121512	F	35.8	21.0	36.7	20.8
NMNH	114505	F	35.2	20.6	35.2	20.1
MCZ	35571	F	35.4	19.2	34.2	20.4
MCZ	35611	F	34.4	18.0	33.7	20.4
MCZ	35612	F	37.3	21.9	35.4	20.9
MCZ	35613	F	39.3	21.5	34.9	21.2
MCZ	35608	F	36.4	22.2	34.0	19.6
MCZ	35629	F	33.2	21.1	35.4	21.3
MCZ	35681	F	38.9	20.6	36.9	20.6
AMNH	3056	F	38.4	17.7	34.7	19.6
AMNH	99.1/3030	F	36.3	19.4	35.2	18.1
AMNH	99/3062	F	38.7	17.3	35.9	20.8
AMNH	102765	F	34.3	22.1	33.6	20.1
AMNH	103648	F	35.1	18.3	33.2	19.5
AMNH	106283	F	37.8	22.3	37.2	24.0
AMNH	106566	F	35.3	24.7	36.7	23.1
AMNH	106568	F	37.3	16.0	34.9	20.8
AMNH	106569	F	37.4	21.6	34.8	21.0
AMNH	107099	F	33.7	23.8	35.3	21.6
AMNH	187215	F	41.7	24.6	38.9	23.7
AMNH	175460	F	43.5	19.5	35.7	20.5
MCZ	37406	F	36.6	17.03	34.82	20.25
MCZ	35736	F	36.35	21.36	35.66	19.8
MCZ	35729	F	35.63	21.01	35.25	18.99
MCZ	37415	F	34.93	17.26	33.67	17.79

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MCZ	37414	F	35.49	20.25	34.14	18.76
MCZ	35673	F	33.05	18.68	32.48	17.09
MCZ	35677	F	39.41	18.95	32.7	18.25
MCZ	35656	F	37.33	19.81	36.69	18.1
MCZ	35619	F	37.18	16.21	33.14	19.62
MCZ	30384	F	33.73	16.7	36.67	20.95
BMNH	239-1-118rh	M	53.5	21.9	39.7	21.6
BMNH	14-7-10-4	M	37.9	21.4	38.2	22.2
BMNH	23-11-4-1	M	41.7	19.7	40.4	22.7
BMNH	31.1.11.8	M	35.8	18.4	37.1	20.4
BMNH	31.1.11.31	M	37.6	15.9	36.9	20.9
BMNH	31.1.11.32	M	34.9	16.2	36.1	20.2
BMNH	48.2.1.26	M	38.7	23.2	38.6	23.4
BMNH	31.1.11.35	M	38.2	16.5	38.2	22.3
BMNH	14.7.10.2	M	39.6	20.6	41.0	22.9
BMNH	14-7-10-1	M	37.2	21.3	38.4	21.8
BMNH	451.8.223	M	36.5	15.8	37.1	21.1
BMNH	1843.5.27.2rh	M	41.7	22.6	39.1	24.4
NMNH	35488rh	M	57.3	20.3	42.2	23.2
NMNH	173813rh	M	39.9	23.4	45.3	26.0
NMNH	267851rh	M	42.5	23.9	43.0	25.2
NMNH	353186rh	M	40.2	21.4	42.2	23.2
NMNH	63471rh	M	40.2	22.5	41.8	23.3
NMNH	35489rh	M	39.4	18.4	41.4	20.5
MCZ	30384rh	M	33.7	17.7	36.7	21.0
MCZ	57939rh	M	33.4	14.2	35.5	16.7
MCZ	60629rh	M	34.1	17.1	39.0	22.1
MCZ	26478rh	M	34.8	14.9	37.8	19.7
MCZ	26475rh	M	32.3	14.1	34.0	18.8
AMNH	7947	M		23.2	40.9	22.5

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AMNH	112741	M	33.9	17.8	38.4	21.2
AMNH	26646	M	36.6	21.0	36.4	22.3
AMNH	54681	M	32.7	14.1	30.0	16.8
AMNH	54816	M	33.9	17.0	36.1	20.0
AMNH	57039	M	41.1	22.2	35.9	22.2
AMNH	84474	M	38.4	20.7	39.7	23.4
AMNH	87264	M	32.2	15.2	36.0	20.1
AMNH	112741	M	32.5	17.1	35.5	19.2
AMNH	114547	M	34.6	14.6	32.8	19.7
AMNH	163613	M	33.3	16.0	35.1	20.1

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Museum	Cat. No.	Species	choanal_height_left	choanal_height_right	choanal_width_left	choanal_width_right	choanal_width_left	choanal_width_right
NMNH	114163	F	9.2	9.7	3.9	4.0	3.9	4.0
NMNH	111111	F	12.5	12.3	5.2	5.2	5.2	5.2
NMNH	123991	F	9.8	10.1	4.9	4.4	4.9	4.4
NMNH	114506	F	12.7	12.7	4.0	4.1	4.0	4.1
NMNH	121512	F	11.0	10.8	3.5	4.0	3.5	4.0
NMNH	114505	F	10.4	10.0	4.1	4.4	4.1	4.4
MCZ	35571	F	11.8	10.9	3.7	3.8	3.7	3.8
MCZ	35611	F	12.3	12.5	3.6	4.0	3.6	4.0
MCZ	35612	F	11.6	10.4	5.1	5.3	5.1	5.3
MCZ	35613	F	15.3	15.3	3.9	3.4	3.9	3.4
MCZ	35608	F	12.2	11.1	4.9	4.7	4.9	4.7
MCZ	35629	F	10.3	10.9	4.5	4.6	4.5	4.6
MCZ	35681	F	15.9	13.9	4.1	4.3	4.1	4.3
AMNH	3056	F	12.1	12.6	3.2	3.3	3.2	3.3
AMNH	99.1/3030	F	14.0	14.6	4.0	4.2	4.0	4.2
AMNH	99/3062	F	15.5	15.4	4.0	4.2	4.0	4.2
AMNH	102765	F	13.6	13.0	4.9	4.9	4.9	4.9
AMNH	103648	F	12.4	12.1	4.6	4.6	4.6	4.6
AMNH	106283	F	16.4	16.4	5.5	5.6	5.5	5.6
AMNH	106566	F	15.0	14.7	4.8	5.1	4.8	5.1
AMNH	106568	F	12.7	13.7	6.3	5.9	6.3	5.9
AMNH	106569	F	17.4	17.4	5.7	5.8	5.7	5.8
AMNH	107099	F	13.2	13.6	4.3	4.4	4.3	4.4
AMNH	187215	F	15.9	16.1	4.8	4.9	4.8	4.9
AMNH	175460	F	19.8	19.8	4.1	4.7	4.1	4.7
MCZ	37406	F	11.89	12.61	3.37	3.86	3.37	3.86
MCZ	35736	F	11.88	11.01	5.12	5.02	5.12	5.02
MCZ	35729	F	13.6	13.12	4.25	4.04	4.25	4.04
MCZ	37415	F	9.7	10.19	4.74	4.27	4.74	4.27

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MCZ	37414	F	10.55	11.85	3.38	5.13
MCZ	35673	F	10.73	10.08	4.55	4.74
MCZ	35677	F	12.49	12.21	4.3	4.11
MCZ	35656	F	12.75	13.1	3.45	4.87
MCZ	35619	F	11.24	8.37	4.09	3.89
MCZ	30384	F	10.85	11.18	5.14	5.71
BMNH	239-1-118rh	M	16.2	15.2	7.7	7.5
BMNH	14-7-10-4	M	13.6	14.0	5.9	5.6
BMNH	23-11-4-1	M	14.6	14.1	5.8	6.2
BMNH	31.1.11.8	M	11.2	11.2	5.5	5.8
BMNH	31.1.11.31	M		12.5		4.6
BMNH	31.1.11.32	M		11.4	4.5	4.5
BMNH	48.2.1.26	M	11.5	14.1	5.7	6.1
BMNH	31.1.11.35	M	12.2	12.1	6.0	6.5
BMNH	14.7.10.2	M	12.1	13.5	6.4	6.5
BMNH	14-7-10-1	M	13.6	14.0	6.1	
BMNH	451.8.223	M	11.9	11.6	5.9	5.8
BMNH	1843.5.27.2rh	M	13.8	14.0	6.9	6.7
NMNH	35488rh	M	14.2	14.0	5.0	5.2
NMNH	173813rh	M	13.0	12.5	6.4	6.4
NMNH	267851rh	M	12.5	12.6	6.1	6.5
NMNH	353186rh	M	13.9	14.1	5.5	6.0
NMNH	63471rh	M	13.4	12.2	6.1	6.0
NMNH	35489rh	M	12.5	12.4	4.7	4.9
MCZ	30384rh	M	10.9	11.2	5.1	5.7
MCZ	57939rh	M	9.8		3.5	
MCZ	60629rh	M	12.2		5.1	
MCZ	26478rh	M	11.3	10.9	4.7	4.1
MCZ	26475rh	M	11.4		5.7	
AMNH	7947	M	15.9	15.9	6.4	6.8

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AMNH	112741	M	14.7	14.5	4.3	5.2
AMNH	26646	M	13.6	13.9	5.8	6.2
AMNH	54681	M	10.5	9.8	4.4	5.0
AMNH	54816	M	10.9	10.9	4.6	5.1
AMNH	57039	M	11.0	11.8	6.7	6.3
AMNH	84474	M	15.1	15.7	6.8	6.0
AMNH	87264	M	11.4	12.2	5.2	6.5
AMNH	112741	M	12.2	10.5	5.2	5.5
AMNH	114547	M	12.3	12.6	5.2	5.2
AMNH	163613	M	13.1	13.0	5.0	5.0

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Museum	Cat. No.	Species	orbital_height_left	orbital_height_right	orbital_width_left	orbital_width_right
NMNH	114163	F	22.3	21.8	22.5	22.3
NMNH	111111	F	18.4	18.3	22.5	23.0
NMNH	123991	F	21.9	21.7	21.3	21.3
NMNH	114506	F	22.3	22.9	22.1	22.3
NMNH	121512	F	21.0	20.9	21.6	20.4
NMNH	114505	F	23.1	22.9	22.4	21.5
MCZ	35571	F	20.5	20.5	19.8	19.9
MCZ	35611	F	22.0	22.4	19.0	19.9
MCZ	35612	F	22.4	21.7	20.5	20.2
MCZ	35613	F	21.7	22.3	21.5	20.7
MCZ	35608	F	19.4	19.7	23.0	23.5
MCZ	35629	F	22.3	21.5	21.3	22.2
MCZ	35681	F	20.8	21.3	21.2	20.9
AMNH	3056	F	25.0	25.1	22.3	22.5
AMNH	99.1/3030	F	24.0	28.0	24.0	24.0
AMNH	99/3062	F	27.9	27.9	23.9	25.3
AMNH	102765	F	24.3	23.3	22.9	22.9
AMNH	103648	F	23.6	23.8	23.1	22.3
AMNH	106283	F	23.5	24.0	22.9	21.9
AMNH	106566	F	22.3	22.6	23.5	23.0
AMNH	106568	F	22.3	22.4	22.4	22.1
AMNH	106569	F	21.9	21.0	23.8	24.0
AMNH	107099	F	21.8	21.7	23.5	22.8
AMNH	187215	F	25.1	25.0	23.6	23.9
AMNH	175460	F	26.1	26.2	24.3	24.0
MCZ	37406	F	19.81	19.92	22.73	21.09
MCZ	35736	F	19.49	19.18	20.54	21.02
MCZ	35729	F	22.93	23.1	20.79	20.16
MCZ	37415	F	20.33	20.54	23.03	22.28

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MCZ	37414	F	21.38	22.07	21.35	21.87
MCZ	35673	F	19.61	20.17	21.66	20.98
MCZ	35677	F	22	21.25	19.86	20.2
MCZ	35656	F	23.12	21.71	22.28	20.94
MCZ	35619	F	22.59	21.69	20.44	20.42
MCZ	30384	F	24.67	25.22	26.16	25.48
BMNH	239-1-118rh	M	22.9	22.1	24.1	23.8
BMNH	14-7-10-4	M	25.3	25.4	26.4	26.0
BMNH	23-11-4-1	M	28.2	28.2	27.6	26.2
BMNH	31.1.11.8	M	23.6	23.9	24.1	24.8
BMNH	31.1.11.31	M	25.3	24.8	25.1	24.4
BMNH	31.1.11.32	M	25.5	25.5	25.1	25.5
BMNH	48.2.1.26	M	24.1	24.1	26.5	26.7
BMNH	31.1.11.35	M	22.5	22.9	24.0	24.4
BMNH	14.7.10.2	M	27.3	28.3	27.1	27.3
BMNH	14-7-10-1	M	24.7	25.3	26.2	26.1
BMNH	451.8.223	M	24.3	24.5	26.2	26.5
BMNH	1843.5.27.2rh	M	22.0	23.2	22.6	23.7
NMNH	35488rh	M	23.4	23.1	30.5	29.5
NMNH	173813rh	M	24.1	24.5	28.6	28.8
NMNH	267851rh	M	23.2	22.1	28.1	27.7
NMNH	353186rh	M	23.9	24.1	27.3	27.9
NMNH	63471rh	M	24.7	25.0	26.8	26.2
NMNH	35489rh	M	24.8	25.3	27.8	27.2
MCZ	30384rh	M	24.7	25.2	26.2	25.5
MCZ	57939rh	M	20.6		22.4	
MCZ	60629rh	M	22.6		25.0	
MCZ	26478rh	M	22.1	22.4	22.2	21.4
MCZ	26475rh	M	25.0		23.5	
AMNH	7947	M	27.1	26.8	23.8	24.2

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AMNH	112741	M	27.8	28.3		24.9
AMNH	26646	M				
AMNH	54681	M	23.9	23.9	23.1	23.6
AMNH	54816	M	22.6	22.2	25.5	25.5
AMNH	57039	M	21.0	21.8	24.8	23.5
AMNH	84474	M	22.9	23.5	23.7	26.0
AMNH	87264	M	23.4	24.1	24.7	23.7
AMNH	112741	M	22.3	22.0	24.9	23.7
AMNH	114547	M	24.5	24.6	24.4	23.8
AMNH	163613	M	23.8	23.4	22.1	22.2

Appendix A

Museum	Cat. No.	Species	nasal_height	nasal_breadth	aperture_height	nasion_alveolar__IDS_
NMNH	114163	F	46.4	10.2	16.6	57.2
NMNH	111111	F	43.1	11.8	15.1	53.7
NMNH	123991	F	46.3	11.5	17.2	54.0
NMNH	114506	F	42.6	10.0	15.1	49.9
NMNH	121512	F	50.6	10.4	15.6	62.8
NMNH	114505	F	45.2	13.4	17.3	53.8
MCZ	35571	F	46.5	9.9	16.6	53.5
MCZ	35611	F	46.1	9.2	15.9	53.4
MCZ	35612	F	45.3	11.3	16.9	57.2
MCZ	35613	F	54.7	11.2	18.5	62.3
MCZ	35608	F	42.2	10.2	17.7	46.2
MCZ	35629	F	47.8	8.5	16.7	54.5
MCZ	35681	F	46.3	11.3	17.0	58.3
AMNH	3056	F	38.4	10.8	17.4	50.6
AMNH	99.1/3030	F	48.5	12.6	16.6	61.1
AMNH	99/3062	F	48.6	11.4	18.3	58.4
AMNH	102765	F	38.8	11.2	16.5	48.4
AMNH	103648	F	43.5	11.7	17.6	50.8
AMNH	106283	F	44.7	12.3	17.2	57.0
AMNH	106566	F	39.5	10.2	16.0	53.6
AMNH	106568	F	34.0	10.0	15.7	44.1
AMNH	106569	F	40.4	10.9	17.1	51.6
AMNH	107099	F	43.5	11.9	18.4	55.0
AMNH	187215	F	59.0	14.0	24.1	71.6
AMNH	175460	F	49.1	13.8	22.1	58.2
MCZ	37406	F	38.47	11.07	14.57	50.88
MCZ	35736	F	46.25	10.25	16.44	53.99
MCZ	35729	F	47.04	10.67	17.18	59.55
MCZ	37415	F	44.24	8.84	15.14	44.14

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MCZ	37414	F	41.76	12.03	18.23	47.51
MCZ	35673	F	39.84	9.79	14.64	45.63
MCZ	35677	F	44.85	8.82	16.46	54.44
MCZ	35656	F	48.13	12.17	16.88	58.66
MCZ	35619	F	47.17	10.45	17.28	55.81
MCZ	30384	F	43.74	12.97	19.75	51.19
BMNH	239-1-118rh	M	47.87	15.0	21.5	55.2
BMNH	14-7-10-4	M	47.41	15.6	20.7	57.4
BMNH	23-11-4-1	M	53.86	14.3	20.9	62.5
BMNH	31.1.11.8	M	42.65	10.9	17.7	53.4
BMNH	31.1.11.31	M	43.60	12.0	20.0	53.1
BMNH	31.1.11.32	M	42.55	12.3	19.4	50.0
BMNH	48.2.1.26	M	46.12	13.6	20.3	55.1
BMNH	31.1.11.35	M	46.51	12.7	19.0	52.1
BMNH	14.7.10.2	M	40.23	18.2	21.2	57.9
BMNH	14-7-10-1	M	47.51	15.3	20.7	56.9
BMNH	451.8.223	M	40.27	12.8	18.7	48.4
BMNH	1843.5.27.2rh	M	40.27	10.7	19.2	48.6
NMNH	35488rh	M	50.30	13.9	23.2	60.3
NMNH	173813rh	M	47.76	13.2	21.2	60.5
NMNH	267851rh	M	47.67	14.1	20.1	58.2
NMNH	353186rh	M	45.11	14.9	18.8	56.0
NMNH	63471rh	M	47.95	16.1	20.3	58.8
NMNH	35489rh	M	43.29	11.4	21.7	50.1
MCZ	30384rh	M	43.74	13.0	19.8	51.2
MCZ	57939rh	M	31.55	11.0	16.7	35.6
MCZ	60629rh	M	37.86	11.3	16.1	46.5
MCZ	26478rh	M	42.11	12.2	16.0	51.3
MCZ	26475rh	M	42.47	9.7	19.3	48.2
AMNH	7947	M	55.52	16.8	21.6	66.9

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AMNH	112741	M	47.54	13.9	21.1	54.9
AMNH	26646	M	42.26	12.9	21.9	50.3
AMNH	54681	M	43.51	10.5	18.6	52.2
AMNH	54816	M	41.79	12.0	17.2	48.3
AMNH	57039	M	49.61	13.6	20.6	56.7
AMNH	84474	M	46.46	13.3	20.4	56.3
AMNH	87264	M	45.35	12.2	22.8	52.3
AMNH	112741	M	47.00	12.9	18.9	55.4
AMNH	114547	M	43.87	11.5	16.3	51.2
AMNH	163613	M	39.31	11.5	17.3	46.4

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Museum	Cat. No.	Species	glabella_opisthocranion	basion_nasion	alveolar_opisthocranion
NMNH	114163	F	82.7	60.7	122.8
NMNH	111111	F	87.9	67.1	122.9
NMNH	123991	F	74.8	57.0	111.5
NMNH	114506	F	78.2	60.8	112.2
NMNH	121512	F	80.5	63.7	121.6
NMNH	114505	F	80.5	59.2	116.1
MCZ	35571	F	72.7	57.1	112.8
MCZ	35611	F	75.5	57.3	111.6
MCZ	35612	F	78.9	59.8	117.3
MCZ	35613	F	78.8	63.4	120.5
MCZ	35608	F	77.3	61.0	109.6
MCZ	35629	F	73.7	56.5	110.0
MCZ	35681	F	75.8	60.3	118.7
AMNH	3056	F	79.6	61.9	122.0
AMNH	99.1/3030	F	82.1		122.5
AMNH	99/3062	F	80.3	65.6	126.0
AMNH	102765	F	79.2	58.2	116.0
AMNH	103648	F	74.0	58.8	108.2
AMNH	106283	F	79.5	60.9	119.5
AMNH	106566	F	79.5	59.6	120.7
AMNH	106568	F	76.3	60.6	117.2
AMNH	106569	F	81.7	59.4	122.7
AMNH	107099	F	77.7	59.2	118.9
AMNH	187215	F	87.8	64.4	136.1
AMNH	175460	F	80.6	60.7	131.1
MCZ	37406	F	75.05	60.73	110.62
MCZ	35736	F	74.02	58.88	112.78
MCZ	35729	F	75.84	58.55	117.14
MCZ	37415	F	79.68	60.4	109.33

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MCZ	37414	F	79.28	61.11	111.68
MCZ	35673	F	73.27	55.45	104.3
MCZ	35677	F	73.39	59.16	116.48
MCZ	35656	F	77.62	63.84	117.07
MCZ	35619	F	76.11	60.6	119
MCZ	30384	F	90.6	65.29	121.29
BMNH	239-1-118rh	M	91.2	69.4	129.1
BMNH	14-7-10-4	M	88.5	68.0	125.0
BMNH	23-11-4-1	M	89.3	72.4	130.6
BMNH	31.1.11.8	M	81.9	61.0	119.8
BMNH	31.1.11.31	M	84.0	65.2	117.3
BMNH	31.1.11.32	M	83.2	63.5	117.1
BMNH	48.2.1.26	M	88.8	68.9	127.1
BMNH	31.1.11.35	M	90.1	17.4	123.7
BMNH	14.7.10.2	M	90.2	71.1	127.9
BMNH	14-7-10-1	M	88.5	68.2	125.0
BMNH	451.8.223	M	86.7	64.7	119.0
BMNH	1843.5.27.2rh	M	86.0	69.9	121.2
NMNH	35488rh	M	95.5	74.1	134.2
NMNH	173813rh	M	93.7	72.8	137.5
NMNH	267851rh	M	93.1	73.4	134.1
NMNH	353186rh	M	90.4	71.5	127.0
NMNH	63471rh	M	93.8	71.7	129.9
NMNH	35489rh	M	91.3	70.2	128.1
MCZ	30384rh	M	90.6	65.3	121.3
MCZ	57939rh	M	78.4	59.5	99.3
MCZ	60629rh	M	84.9	62.5	115.4
MCZ	26478rh	M	82.4	61.7	110.7
MCZ	26475rh	M	78.6	60.8	105.2
AMNH	7947	M	89.0	68.0	131.4

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AMNH	112741	M	86.6	62.8	120.5
AMNH	26646	M	82.6	61.1	116.6
AMNH	54681	M	75.0	56.1	102.9
AMNH	54816	M	82.9	61.6	112.3
AMNH	57039	M	89.0	67.0	123.7
AMNH	84474	M	92.9	69.1	127.4
AMNH	87264	M	84.1	61.8	113.8
AMNH	112741	M	79.7	61.9	116.3
AMNH	114547	M	83.3	62.3	111.1
AMNH	163613	M	79.0	60.2	110.5

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Museum	Cat. No.	Species	Prosthion_Opisthiocranium	Prosthion_maxillopalatal_suture	Basion_Hormion
NMNH	114163	F	102.2	37.2	22.2
NMNH	111111	F	103.4	37.5	25.1
NMNH	123991	F	93.1	35.4	24.1
NMNH	114506	F	93.2	33.8	24.6
NMNH	121512	F	100.2	35.0	23.7
NMNH	114505	F	97.5	35.5	25.3
MCZ	35571	F	96.6	29.1	23.0
MCZ	35611	F	94.6	34.9	23.2
MCZ	35612	F	102.3	38.1	26.9
MCZ	35613	F	104.2	37.2	23.4
MCZ	35608	F	98.2	35.0	25.5
MCZ	35629	F	92.6	34.5	23.0
MCZ	35681	F	101.0	39.1	
AMNH	3056	F	105.7	36.6	26.0
AMNH	99.1/3030	F	100.4	37.9	24.2
AMNH	99/3062	F	106.9	38.3	25.6
AMNH	102765	F	95.4	35.9	23.7
AMNH	103648	F	91.6	33.7	22.8
AMNH	106283	F	100.7	36.4	25.0
AMNH	106566	F	101.5	38.9	24.4
AMNH	106568	F	101.6	36.5	24.3
AMNH	106569	F	103.7	37.1	24.3
AMNH	107099	F	101.3	38.8	25.4
AMNH	187215	F	113.8	47.6	28.4
AMNH	175460	F	112.5	44.7	26.8
MCZ	37406	F	95.17	32.49	23.54
MCZ	35736	F	96.81	36.91	23.16
MCZ	35729	F	98.59	36.53	23.69
MCZ	37415	F	94.5	33.15	27.08

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MCZ	37414	F	93.59	33.94	25.18
MCZ	35673	F	88.91	33.66	22.67
MCZ	35677	F	100.82	34.24	26.06
MCZ	35656	F	101.65	37.49	25.83
MCZ	35619	F	99.89	37.46	26.04
MCZ	30384	F	98.66	34.46	24.86
BMNH	239-1-118rh	M	127.0	37.2	30.0
BMNH	14-7-10-4	M	126.8	37.2	27.0
BMNH	23-11-4-1	M	133.8	39.2	32.7
BMNH	31.1.11.8	M		36.0	25.7
BMNH	31.1.11.31	M		34.0	26.3
BMNH	31.1.11.32	M		34.5	26.7
BMNH	48.2.1.26	M		37.1	27.8
BMNH	31.1.11.35	M		37.9	28.3
BMNH	14.7.10.2	M		38.2	28.9
BMNH	14-7-10-1	M		36.6	26.9
BMNH	451.8.223	M		31.4	28.1
BMNH	1843.5.27.2rh	M		37.6	29.7
NMNH	35488rh	M	113.7	38.8	33.1
NMNH	173813rh	M	116.5	43.7	31.0
NMNH	267851rh	M	112.4	39.5	29.7
NMNH	353186rh	M	107.0	38.3	29.3
NMNH	63471rh	M	108.3	38.0	31.3
NMNH	35489rh	M	107.0	37.7	31.2
MCZ	30384rh	M	98.7	34.5	24.9
MCZ	57939rh	M	84.8	27.0	24.3
MCZ	60629rh	M	97.1	36.0	24.8
MCZ	26478rh	M	91.1	33.6	27.3
MCZ	26475rh	M	89.3	31.7	24.6
AMNH	7947	M	109.3	37.9	27.8

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AMNH	112741	M	102.2	38.4	23.8
AMNH	26646	M	96.6	34.9	24.2
AMNH	54681	M	85.0	31.4	22.8
AMNH	54816	M	95.6	33.7	24.7
AMNH	57039	M	105.0	36.8	26.3
AMNH	84474	M	106.2	38.0	28.3
AMNH	87264	M	93.1	33.6	25.7
AMNH	112741	M	97.8	37.7	24.5
AMNH	114547	M	92.1	29.2	26.6
AMNH	163613	M	92.4	32.2	23.2

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Museum	Cat. No.	Species	EndoCrvol(mL)	LtMaxSinus(mL)	RtMaxSinus(mL)	Internal_palatal_length
NMNH	114163	F	70.11	3.23	2.96	45.3
NMNH	111111	F	57.42	3.23	3.50	46.5
NMNH	123991	F	61.78	3.64	3.36	43.2
NMNH	114506	F	62.33	2.82	2.82	40.3
NMNH	121512	F	62.33	4.18	3.23	45.5
NMNH	114505	F	61.24	2.14	2.00	43.1
MCZ	35571	F	71.07	2.82	2.82	42.5
MCZ	35611	F	69.15	3.36	3.64	42.3
MCZ	35612	F	65.20	2.41	2.55	44.7
MCZ	35613	F	71.20	5.41	4.87	45.8
MCZ	35608	F	62.88	2.55	2.82	41.9
MCZ	35629	F	58.24	3.50	3.91	41.3
MCZ	35681	F	64.10	4.18	4.32	44.0
AMNH	3056	F	48.18	2.83	3.04	
AMNH	99.1/3030	F	47.26	2.94	3.14	
AMNH	99/3062	F	57.81	3.14	3.24	
AMNH	102765	F	46.24	1.91	2.32	
AMNH	103648	F	46.03	2.32	2.22	
AMNH	106283	F	50.64	3.24	3.24	
AMNH	106566	F	54.02	2.53	2.32	
AMNH	106568	F	48.59	2.94	2.94	
AMNH	106569	F	53.20	2.83	2.94	
AMNH	107099	F	52.38	3.04	2.53	
AMNH	187215	F	55.25	3.04	3.14	
AMNH	175460	F	45.83	2.94	2.22	
MCZ	37406	F	74.61	2.82	2.41	38.93
MCZ	35736	F	64.10	2.82	2.82	44.12
MCZ	35729	F	59.05	4.87	4.73	43.69
MCZ	37415	F	72.57	2.82	2.82	38.7

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MCZ	37414	F	68.34	2.41	2.55	40.64
MCZ	35673	F	58.78	2.82	2.96	36
MCZ	35677	F	60.01	3.23	3.23	43.65
MCZ	35656	F	70.38	4.59	4.32	47.35
MCZ	35619	F	63.69	4.05	4.18	44.73
MCZ	30384	F	100.68	2.14	2.00	41.92
BMNH	239-1-118rh	M	71.47	2.14	2.00	45.7
BMNH	14-7-10-4	M	62.47	2.96	3.09	46.1
BMNH	23-11-4-1	M	63.97	2.27	2.41	47.0
BMNH	31.1.11.8	M	57.14	2.41	2.41	44.8
BMNH	31.1.11.31	M	63.15	1.45	2.27	41.7
BMNH	31.1.11.32	M	56.73	2.27	2.41	40.4
BMNH	48.2.1.26	M	61.92	2.00	2.00	47.6
BMNH	31.1.11.35	M	64.51	2.14	2.14	43.9
BMNH	14.7.10.2	M	64.79	2.68	2.68	49.9
BMNH	14-7-10-1	M	70.52	2.41	2.27	45.9
BMNH	451.8.223	M	55.37	2.14	2.00	41.0
BMNH	1843.5.27.2rh	M	53.18	2.14	2.14	44.6
NMNH	35488rh	M	109.01	2.55	2.68	48.0
NMNH	173813rh	M	111.74	2.68	2.55	54.2
NMNH	267851rh	M	92.36	2.27	2.41	49.8
NMNH	353186rh	M	103.55	2.27	2.41	47.0
NMNH	63471rh	M	108.87	2.00	2.41	48.9
NMNH	35489rh	M	103.14	2.82	2.96	44.9
MCZ	30384rh	M	68.88	2.14	2.00	41.9
MCZ	57939rh	M	68.88	2.14	2.00	33.6
MCZ	60629rh	M	70.52	2.00	2.14	41.2
MCZ	26478rh	M	85.12	2.41	2.14	37.6
MCZ	26475rh	M	76.80	2.14	2.14	37.8
AMNH	7947	M	79.80	3.50	3.23	

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AMNH	112741	M	105.05	4.05	4.18
AMNH	26646	M	87.04	3.36	3.23
AMNH	54681	M	72.02	2.55	1.85
AMNH	54816	M	80.48	2.96	3.23
AMNH	57039	M	91.27	3.36	3.23
AMNH	84474	M	123.75	3.50	3.09
AMNH	87264	M	89.63	3.64	3.50
AMNH	112741	M	79.80	2.68	2.82
AMNH	114547	M	83.08	2.96	2.82
AMNH	163613	M	82.26	2.41	2.14

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Museum	Cat. No.	Species	Nasal_Index	MaxilloAlveolar_Index	Palatal_Index
NMNH	114163	F	22.04	70.06	37.80
NMNH	111111	F	27.42	62.16	45.18
NMNH	123991	F	24.80	69.04	44.50
NMNH	114506	F	23.40	65.58	43.84
NMNH	121512	F	20.47	72.03	41.85
NMNH	114505	F	29.66	72.04	42.04
MCZ	35571	F	21.28	72.52	43.85
MCZ	35611	F	20.06	71.86	45.24
MCZ	35612	F	24.91	70.28	43.19
MCZ	35613	F	20.48	76.93	41.98
MCZ	35608	F	24.13	58.69	43.08
MCZ	35629	F	17.71	73.44	47.24
MCZ	35681	F	24.37	72.35	41.98
AMNH	3056	F	28.02	58.68	37.11
AMNH	99.1/3030	F	25.95	68.63	36.24
AMNH	99/3062	F	23.51	66.89	39.82
AMNH	102765	F	28.93	61.86	42.04
AMNH	103648	F	26.88	68.41	45.23
AMNH	106283	F	27.60	66.53	49.63
AMNH	106566	F	25.70	65.19	44.39
AMNH	106568	F	29.50	56.01	42.01
AMNH	106569	F	26.94	66.39	42.73
AMNH	107099	F	27.30	71.81	40.89
AMNH	187215	F	23.78	84.33	40.55
AMNH	175460	F	28.01	76.16	37.39
MCZ	37406	F	28.78	65.54	35.05
MCZ	35736	F	22.16	70.19	31.55
MCZ	35729	F	22.68	77.22	28.24
MCZ	37415	F	19.98	61.24	33.68

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MCZ	37414	F	28.81	60.97	32.64
MCZ	35673	F	24.57	62.96	31.48
MCZ	35677	F	19.67	68.88	28.46
MCZ	35656	F	25.29	72.56	27.99
MCZ	35619	F	22.15	75.54	30.39
MCZ	30384	F	29.65	61.78	34.29
BMNH	239-1-118rh	M	31.23	60.85	44.60
BMNH	14-7-10-4	M	32.88	65.22	44.16
BMNH	23-11-4-1	M	26.53	69.44	43.30
BMNH	31.1.11.8	M	25.63	67.07	41.03
BMNH	31.1.11.31	M	27.59		45.52
BMNH	31.1.11.32	M	28.79	65.61	43.00
BMNH	48.2.1.26	M	29.38	62.63	45.04
BMNH	31.1.11.35	M	27.35	61.53	45.17
BMNH	14.7.10.2	M	45.22	71.21	42.64
BMNH	14-7-10-1	M	32.20	65.17	43.60
BMNH	451.8.223	M	31.69		46.35
BMNH	1843.5.27.2rh	M	26.50	54.59	51.45
NMNH	35488rh	M	27.57	62.14	42.48
NMNH	173813rh	M	27.68	61.40	43.64
NMNH	267851rh	M	29.49	63.43	46.06
NMNH	353186rh	M	33.01	61.38	44.81
NMNH	63471rh	M	33.60	61.83	44.26
NMNH	35489rh	M	26.43	54.61	40.97
MCZ	30384rh	M	29.65	61.78	43.56
MCZ	57939rh	M	34.71	51.39	44.05
MCZ	60629rh	M	29.79	51.70	47.34
MCZ	26478rh	M	29.02	72.70	46.75
MCZ	26475rh	M	22.86	61.88	44.58
AMNH	7947	M	30.31		41.66

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AMNH	112741	M	29.15		43.88
AMNH	26646	M	30.50	62.68	49.61
AMNH	54681	M	24.04	69.86	44.70
AMNH	54816	M	28.76	64.95	45.45
AMNH	57039	M	27.47	72.25	46.74
AMNH	84474	M	28.54	59.05	46.46
AMNH	87264	M	26.86	69.94	44.63
AMNH	112741	M	27.47	69.80	41.62
AMNH	114547	M	26.15	67.59	47.75
AMNH	163613	M	29.20	58.74	44.22

Appendix A

Museum	Cat. No.	Species	mesial_distal_length_M3_left	buccal_lingual_length_M3_left	Inferior_Superior_length_M3_left
NMNH	114163	F			
NMNH	111111	F			
NMNH	123991	F			
NMNH	114506	F			
NMNH	121512	F			
NMNH	114505	F			
MCZ	35571	F	6.6	6.1	4.8
MCZ	35611	F	6.9	5.6	5.2
MCZ	35612	F	6.6	5.9	4.4
MCZ	35613	F	6.4	6.1	5.4
MCZ	35608	F	6.4	6.1	4.5
MCZ	35629	F	7.1	5.9	4.4
MCZ	35681	F	7.0	6.2	4.4
AMNH	3056	F			
AMNH	99.1/3030	F			
AMNH	99/3062	F			
AMNH	102765	F			
AMNH	103648	F			
AMNH	106283	F			
AMNH	106566	F			
AMNH	106568	F			
AMNH	106569	F			
AMNH	107099	F			
AMNH	187215	F			
AMNH	175460	F			
MCZ	37406	F	7.06	6.55	4.81
MCZ	35736	F	7.32	6.06	4.63
MCZ	35729	F	7.13	6.61	4.51
MCZ	37415	F	6.79	6.28	5.47
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MCZ	37414	F	6.2	5.83	5.11
MCZ	35673	F	6.71	5.98	3.72
MCZ	35677	F	6.49	6.13	3.85
MCZ	35656	F	6.74	6.46	4.92
MCZ	35619	F	6.66	6.35	4.47
MCZ	30384	F	8.86	7.8	5.3
BMNH	239-1-118rh	M	7.8	8.6	6.3
BMNH	14-7-10-4	M	8.1	8.0	5.4
BMNH	23-11-4-1	M	8.8	8.5	5.9
BMNH	31.1.11.8	M	8.6	8.3	6.4
BMNH	31.1.11.31	M			
BMNH	31.1.11.32	M	8.4	7.6	5.3
BMNH	48.2.1.26	M	7.5	8.1	5.6
BMNH	31.1.11.35	M	8.3	7.8	5.6
BMNH	14.7.10.2	M	8.1	7.9	7.4
BMNH	14-7-10-1	M	8.0	7.9	5.4
BMNH	451.8.223	M	8.7	8.0	5.7
BMNH	1843.5.27.2rh	M	8.3	8.5	5.8
NMNH	35488rh	M			
NMNH	173813rh	M			
NMNH	267851rh	M			
NMNH	353186rh	M			
NMNH	63471rh	M			
NMNH	35489rh	M			
MCZ	30384rh	M	8.9	7.8	5.3
MCZ	57939rh	M	8.2	7.9	6.6
MCZ	60629rh	M			
MCZ	26478rh	M			
MCZ	26475rh	M	7.1	7.3	4.5
AMNH	7947	M			516

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Museum	Cat. No.	Species	mesial_distal_lgth_M3_right	buccal_lingual_lgth_M3_right	Inf_Sup_lgth_M3_right
NMNH	114163	F			
NMNH	111111	F			
NMNH	123991	F			
NMNH	114506	F			
NMNH	121512	F			
NMNH	114505	F			
MCZ	35571	F	6.8	6.2	5.3
MCZ	35611	F	6.8	5.5	4.9
MCZ	35612	F	6.6	5.9	4.2
MCZ	35613	F	6.4	6.1	5.0
MCZ	35608	F	6.5	6.1	4.1
MCZ	35629	F	6.8	6.0	4.9
MCZ	35681	F	6.9	6.1	4.4
AMNH	3056	F			
AMNH	99.1/3030	F			
AMNH	99/3062	F			
AMNH	102765	F			
AMNH	103648	F			
AMNH	106283	F			
AMNH	106566	F			
AMNH	106568	F			
AMNH	106569	F			
AMNH	107099	F			
AMNH	187215	F			
AMNH	175460	F			
MCZ	37406	F	7.15	5.94	4.44
MCZ	35736	F	7.24	5.49	4.44
MCZ	35729	F	7.15	6.14	4.55
MCZ	37415	F	6.94	6.12	4.92

MCZ	37414	F	6.1	5.91	4.79
MCZ	35673	F	6.78	5.51	3.8
MCZ	35677	F	6.56	6.09	3.62
MCZ	35656	F	6.71	6.62	4.89
MCZ	35619	F	6.56	6.12	4.32
MCZ	30384	F	8.93	7.71	5.82
BMNH	239-1-118rh	M	8.0	8.7	6.2
BMNH	14-7-10-4	M	8.3	7.6	5.3
BMNH	23-11-4-1	M	8.7	8.3	6.4
BMNH	31.1.11.8	M	8.8	8.2	6.9
BMNH	31.1.11.31	M	8.1	7.4	5.2
BMNH	31.1.11.32	M	7.9	8.1	5.4
BMNH	48.2.1.26	M	8.5	7.6	4.6
BMNH	31.1.11.35	M	8.7	7.9	5.1
BMNH	14.7.10.2	M	8.1	7.9	6.9
BMNH	14-7-10-1	M	8.2	7.8	5.5
BMNH	451.8.223	M	8.2	8.1	5.5
BMNH	1843.5.27.2rh	M	8.6	8.4	5.5
NMNH	35488rh	M			
NMNH	173813rh	M			
NMNH	267851rh	M			
NMNH	353186rh	M			
NMNH	63471rh	M			
NMNH	35489rh	M			
MCZ	30384rh	M	8.9	7.9	5.8
MCZ	57939rh	M			
MCZ	60629rh	M	8.2	7.8	5.9
MCZ	26478rh	M			
MCZ	26475rh	M	7.0	7.2	4.9
AMNH	7947	M			

Museum	Cat. No.	Species	mesial_distal_length_M1_M2_M3_le	mesial_distal_length_M1_M2_M3_ri
NMNH	114163	F		
NMNH	111111	F		
NMNH	123991	F		
NMNH	114506	F		
NMNH	121512	F		
NMNH	114505	F		
MCZ	35571	F	20.4	21.2
MCZ	35611	F	19.5	19.6
MCZ	35612	F	19.0	19.1
MCZ	35613	F	18.7	18.4
MCZ	35608	F	18.9	19.2
MCZ	35629	F	19.2	19.3
MCZ	35681	F	20.5	20.0
AMNH	3056	F		
AMNH	99.1/3030	F		
AMNH	99/3062	F		
AMNH	102765	F		
AMNH	103648	F		
AMNH	106283	F		
AMNH	106566	F		
AMNH	106568	F		
AMNH	106569	F		
AMNH	107099	F		
AMNH	187215	F		
AMNH	175460	F		
MCZ	37406	F	20.73	20.77
MCZ	35736	F	14.03	14.05
MCZ	35729	F	14.67	20.51
MCZ	37415	F	14.31	14.39

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MCZ	37414	F	12.5	12.5
MCZ	35673	F	13.66	14.21
MCZ	35677	F	13.27	13.01
MCZ	35656	F	13.66	14.24
MCZ	35619	F	13.01	13.27
MCZ	30384	F	17.66	18.07
BMNH	239-1-118rh	M	22.8	23.4
BMNH	14-7-10-4	M	23.7	23.8
BMNH	23-11-4-1	M	25.1	25.1
BMNH	31.1.11.8	M	24.1	23.9
BMNH	31.1.11.31	M		22.1
BMNH	31.1.11.32	M	23.1	23.8
BMNH	48.2.1.26	M	21.3	21.7
BMNH	31.1.11.35	M	24.0	23.4
BMNH	14.7.10.2	M	22.1	23.5
BMNH	14-7-10-1	M	24.0	23.6
BMNH	451.8.223	M	24.5	24.2
BMNH	1843.5.27.2rh	M	22.8	22.8
NMNH	35488rh	M		
NMNH	173813rh	M		
NMNH	267851rh	M		
NMNH	353186rh	M		
NMNH	63471rh	M		
NMNH	35489rh	M		
MCZ	30384rh	M	25.4	25.9
MCZ	57939rh	M	23.6	23.5
MCZ	60629rh	M		
MCZ	26478rh	M		
MCZ	26475rh	M	21.7	21.6
AMNH	7947	M		

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Museum	Cat. No.	Species	buc_lingual_lgth_M2_left	buc_lingual_lgth_M1_left	Inf_Superior_leth_M2_left
NMNH	114163	F			
NMNH	111111	F			
NMNH	123991	F			
NMNH	114506	F			
NMNH	121512	F			
NMNH	114505	F			
MCZ	35571	F	6.4	5.8	5.6
MCZ	35611	F	5.9	5.4	5.0
MCZ	35612	F	6.5	5.6	4.5
MCZ	35613	F	6.4	5.6	5.2
MCZ	35608	F	6.3	5.6	4.3
MCZ	35629	F	5.9	4.9	4.7
MCZ	35681	F	6.6	5.6	5.1
AMNH	3056	F			
AMNH	99.1/3030	F			
AMNH	99/3062	F			
AMNH	102765	F			
AMNH	103648	F			
AMNH	106283	F			
AMNH	106566	F			
AMNH	106568	F			
AMNH	106569	F			
AMNH	107099	F			
AMNH	187215	F			
AMNH	175460	F			
MCZ	37406	F	6.59	5.7	5.1
MCZ	35736	F	6.33	5.88	5.46
MCZ	35729	F	7.09	5.82	5.14
MCZ	37415	F	6.4	5.72	5.2

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MCZ	37414	F	6.15	5.92
MCZ	35673	F	6.12	4.4
MCZ	35677	F	6.17	4.65
MCZ	35656	F	6.84	5.36
MCZ	35619	F	6.46	4.92
MCZ	30384	F	7.67	5.54
BMNH	239-1-118rh	M	8.7	6.4
BMNH	14-7-10-4	M	7.9	5.9
BMNH	23-11-4-1	M	8.4	6.1
BMNH	31.1.11.8	M	8.3	7.4
BMNH	31.1.11.31	M		
BMNH	31.1.11.32	M	7.8	8.1
BMNH	48.2.1.26	M	8.0	5.3
BMNH	31.1.11.35	M	7.7	5.6
BMNH	14.7.10.2	M	8.9	7.8
BMNH	14-7-10-1	M	8.0	6.0
BMNH	451.8.223	M	8.3	5.9
BMNH	1843.5.27.2rh	M	8.5	5.6
NMNH	35488rh	M		
NMNH	173813rh	M		
NMNH	267851rh	M		
NMNH	353186rh	M		
NMNH	63471rh	M		
NMNH	35489rh	M		
MCZ	30384rh	M	7.7	5.5
MCZ	57939rh	M	6.9	4.7
MCZ	60629rh	M	8.0	6.0
MCZ	26478rh	M	8.1	6.1
MCZ	26475rh	M	7.5	5.2
AMNH	7947	M		

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Museum	Cat. No.	Species	Inf_Superior_lgth_M1_left	buc_lingual_lgth_M2_right	buc_lingual_lgth_M1_right
NMNH	114163	F			
NMNH	111111	F			
NMNH	123991	F			
NMNH	114506	F			
NMNH	121512	F			
NMNH	114505	F			
MCZ	35571	F	7.1	6.5	5.6
MCZ	35611	F	4.7	5.7	5.2
MCZ	35612	F	4.0	6.4	5.6
MCZ	35613	F	5.2	6.4	5.5
MCZ	35608	F	3.7	6.1	5.6
MCZ	35629	F	4.8	6.5	4.7
MCZ	35681	F	5.0	6.4	5.9
AMNH	3056	F			
AMNH	99.1/3030	F			
AMNH	99/3062	F			
AMNH	102765	F			
AMNH	103648	F			
AMNH	106283	F			
AMNH	106566	F			
AMNH	106568	F			
AMNH	106569	F			
AMNH	107099	F			
AMNH	187215	F			
AMNH	175460	F			
MCZ	37406	F	5.09	6.13	5.64
MCZ	35736	F	5.34	6.71	5.8
MCZ	35729	F	4.53	6.99	5.63
MCZ	37415	F	4.95	6.64	5.82

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MCZ	37414	F		4.26	5.71	5.46
MCZ	35673	F			6.16	5.68
MCZ	35677	F		4.02	6.27	6.56
MCZ	35656	F		4.86	7.03	5.65
MCZ	35619	F		4.88	6.43	7.07
MCZ	30384	F		5.12	8.01	8.1
BMNH	239-1-118rh	M		6.4	8.7	6.8
BMNH	14-7-10-4	M		6.1	7.9	7.5
BMNH	23-11-4-1	M		6.1	8.6	7.1
BMNH	31.1.11.8	M		6.5	8.1	6.4
BMNH	31.1.11.31	M		5.2	7.4	7.0
BMNH	31.1.11.32	M		6.9	8.1	6.4
BMNH	48.2.1.26	M		5.3	7.8	6.5
BMNH	31.1.11.35	M		5.9	7.8	8.1
BMNH	14.7.10.2	M		6.4	9.3	6.7
BMNH	14-7-10-1	M		6.0	7.8	6.3
BMNH	451.8.223	M		5.3	8.2	6.2
BMNH	1843.5.27.2rh	M		5.5	8.2	
NMNH	35488rh	M				
NMNH	173813rh	M				
NMNH	267851rh	M				
NMNH	353186rh	M				
NMNH	63471rh	M				
NMNH	35489rh	M				
MCZ	30384rh	M		5.1	8.0	7.1
MCZ	57939rh	M		4.4	6.0	6.2
MCZ	60629rh	M		5.8	7.8	6.3
MCZ	26478rh	M		5.1	8.2	6.8
MCZ	26475rh	M		4.5	7.2	6.4
AMNH	7947	M				

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Museum	Cat. No.	Species	Inf_Sup_Igth_M2_rt	Inf_Sup_Igth_M1_rt	mes_distal_Igth_M2_left
NMNH	114163	F			
NMNH	111111	F			
NMNH	123991	F			
NMNH	114506	F			
NMNH	121512	F			
NMNH	114505	F			
MCZ	35571	F	4.7	6.7	7.4
MCZ	35611	F	5.1	4.7	7.0
MCZ	35612	F	5.5	4.5	6.0
MCZ	35613	F	5.6	5.7	6.6
MCZ	35608	F	4.5	5.0	6.8
MCZ	35629	F	4.5	5.0	6.7
MCZ	35681	F	5.2	5.8	6.7
AMNH	3056	F			
AMNH	99.1/3030	F			
AMNH	99/3062	F			
AMNH	102765	F			
AMNH	103648	F			
AMNH	106283	F			
AMNH	106566	F			
AMNH	106568	F			
AMNH	106569	F			
AMNH	107099	F			
AMNH	187215	F			
AMNH	175460	F			
MCZ	37406	F	4.7	5.64	7.54
MCZ	35736	F	5.86	5.44	7.1
MCZ	35729	F	5.08	4.84	7.7
MCZ	37415	F	5.34	5.3	7.51

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MCZ	37414	F	5.8		5.62
MCZ	35673	F	4.42	4.25	7.14
MCZ	35677	F	3.82	4.72	6.77
MCZ	35656	F	5.16	5.08	7.12
MCZ	35619	F	4.66	4.66	6.41
MCZ	30384	F	5.61	4.54	8.73
BMNH	239-1-118rh	M	6.9	5.8	8.1
BMNH	14-7-10-4	M	5.6	6.1	8.4
BMNH	23-11-4-1	M	6.2	5.5	8.3
BMNH	31.1.11.8	M	7.4	7.0	8.8
BMNH	31.1.11.31	M	5.8	5.3	
BMNH	31.1.11.32	M	5.8	5.1	8.3
BMNH	48.2.1.26	M	5.8	5.3	7.7
BMNH	31.1.11.35	M	5.5	5.6	8.6
BMNH	14.7.10.2	M	7.6	6.6	8.0
BMNH	14-7-10-1	M	5.5	5.9	8.6
BMNH	451.8.223	M	6.3	5.7	8.7
BMNH	1843.5.27.2rh	M	5.9	5.4	8.1
NMNH	35488rh	M			
NMNH	173813rh	M			
NMNH	267851rh	M			
NMNH	353186rh	M			
NMNH	63471rh	M			
NMNH	35489rh	M			
MCZ	30384rh	M	5.6	4.5	8.7
MCZ	57939rh	M	4.9	4.9	7.3
MCZ	60629rh	M	5.9	5.5	8.5
MCZ	26478rh	M	6.0	5.0	8.9
MCZ	26475rh	M	5.3	5.2	7.4
AMNH	7947	M			

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Museum	Cat. No.	Species	mes_distal_lgth_M1_left	mes_distal_lgth_M2_rt	mes_distal_lgth_M1_rit
NMNH	114163	F			
NMNH	111111	F			
NMNH	123991	F			
NMNH	114506	F			
NMNH	121512	F			
NMNH	114505	F			
MCZ	35571	F	6.3	7.6	7.0
MCZ	35611	F	5.7	7.2	6.1
MCZ	35612	F	5.8	6.8	5.6
MCZ	35613	F	5.7	6.5	6.0
MCZ	35608	F	5.7	6.6	6.0
MCZ	35629	F	5.5	5.7	5.9
MCZ	35681	F	6.4	6.9	6.2
AMNH	3056	F			
AMNH	99.1/3030	F			
AMNH	99/3062	F			
AMNH	102765	F			
AMNH	103648	F			
AMNH	106283	F			
AMNH	106566	F			
AMNH	106568	F			
AMNH	106569	F			
AMNH	107099	F			
AMNH	187215	F			
AMNH	175460	F			
MCZ	37406	F	6.05	7.25	6.18
MCZ	35736	F	6.38	7.02	6.35
MCZ	35729	F	6.18	7.44	6.32
MCZ	37415	F	6.32	7.83	6.7

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MCZ	37414	F	6.26	6.01	6.16
MCZ	35673	F	5.47	7.3	5.8
MCZ	35677	F	5.84	6.67	6.08
MCZ	35656	F	5.93	7.31	5.57
MCZ	35619	F	7.69	6.91	8.18
MCZ	30384	F	6.7	8.95	7.0
BMNH	239-1-118rh	M	7.1	8.4	7.6
BMNH	14-7-10-4	M	7.3	8.5	7.0
BMNH	23-11-4-1	M	6.8	8.6	67.6
BMNH	31.1.11.8	M	6.8	8.0	6.2
BMNH	31.1.11.31	M	6.9	8.5	7.7
BMNH	31.1.11.32	M	6.2	7.7	6.3
BMNH	48.2.1.26	M	6.9	8.5	7.6
BMNH	31.1.11.35	M	5.2	8.1	5.6
BMNH	14.7.10.2	M	7.4	8.2	7.5
BMNH	14-7-10-1	M	7.0	8.8	6.9
BMNH	451.8.223	M	6.4	7.9	6.6
BMNH	1843.5.27.2rh	M			
NMNH	35488rh	M			
NMNH	173813rh	M			
NMNH	267851rh	M			
NMNH	353186rh	M			
NMNH	63471rh	M			
NMNH	35489rh	M			
MCZ	30384rh	M	7.7	9.0	8.2
MCZ	57939rh	M	6.1	7.5	6.4
MCZ	60629rh	M	7.4	8.4	7.2
MCZ	26478rh	M	7.4	8.4	7.5
MCZ	26475rh	M	6.8	7.3	6.8
AMNH	7947	M			

Appendix B:

**Extant human specimens used from the American Musuem of
Natural History**

All material studied here are from the Division of Anthropology.

Catalogue Numbers, Place of Origin, and Sex Assessment are reported.

Place of Origin	Catalogue No.	Sex Assessment
European (Bohemia)	VL/193	Male
European (Bohemia)	VL/196	Male
European (Bohemia)	VL/197	Male
European (Bohemia)	VL/1465	Male
European (Bohemia)	VL/1466	Male
European (Bohemia)	VL/193	Male
European (Bohemia)	VL/193	Male
European (Bohemia)	VL/193	Male
Eskimo (Point Barrow)	99/6853	Male
Eskimo (Point Barrow)	99/6882	Male
Eskimo (Point Barrow)	99/6858	Male
Eskimo (Point Barrow)	99/6863	Male
Eskimo (Point Barrow)	99/6851	Male
Eskimo (Tsimshian, BC)	99/4585	Male
Eskimo (Thompson, BC)	99/4308	Male
Eskimo (Skeena River, BC)	99/4647	Male
Eskimo (Baffin Bay)	99/6690	Male
Eskimo (Etah, Greenland)	99/7685	Male
San	99/8449	Male
San	99/9976	Male

San	99/8430	Male
San	VL/2464	Male
San	99/9978	Male
San	99/8436	Male
San	VL/1512	Male
San	99/8456	Male
San	99/3333	Male
San	99/8882	Male

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