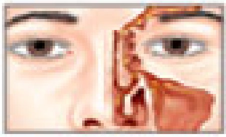

Sataloff's Comprehensive Textbook of Otolaryngology Head & Neck Surgery

Rhinology/ Allergy and Immunology

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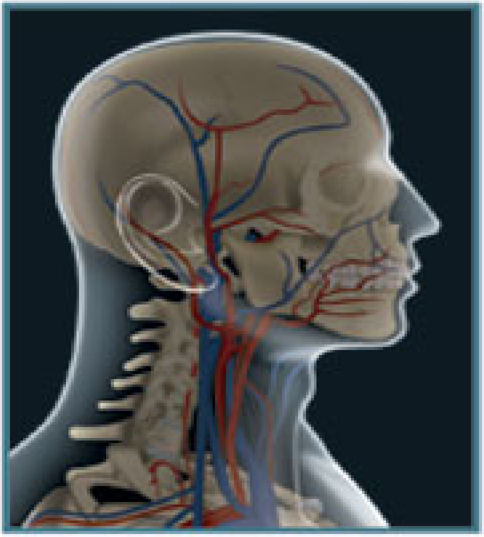

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Series Editor: **Robert T Sataloff** MD DMA FACS

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RHINOLOGY/ALLERGY AND IMMUNOLOGY

Vol. 2

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Dedication

This book is dedicated to my wife, Rita, and my daughters, Jaimie and Karen, and their families who have always been there for me. They are my foundation. To those who have taught me and have been and are my colleagues, I am truly grateful.

Marvin P Fried

It is with eternal gratitude that I dedicate this book to the nurturing guidance of my mentors, the love and support of my wife, family and friends, and most of all, to the wisdom, sacrifice and dedication of my parents. It is through their collective words and deeds that the foundations of my career and life are based.

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Foreword

Sataloff's Comprehensive Textbook of Otolaryngology: Head and Neck Surgery is a component of the most extensive compilation of information in otolaryngology—head and neck surgery to date. The six volumes of the comprehensive textbook are part of a 12-volume, encyclopedic compendium that also includes a six-volume set of detailed, extensively illustrated atlases of otolaryngologic surgical techniques. The vision for the *Comprehensive Textbook* was realized with the invaluable, expert collaboration of eight world-class volume editors. Chapter authors include many of the most prominent otolaryngologists in the world, and coverage of each subspecialty is extensive, detailed and scholarly.

Anil K Lalwani, MD edited the volume on otology/neurotology/skull base surgery. Like all six of the volumes in the *Comprehensive Textbook*, the otology/neurotology/skull base surgery volume is designed not only as part of the multivolume book, but also to stand alone or in combination with the atlas of otological surgery. Dr Lalwani's volume covers anatomy and physiology of hearing and balance, temporal bone radiology, medical and surgical treatment of common and rare disorders of the ear and related structures, occupational hearing loss, aural rehabilitation, cochlear and brainstem implantation, disorders of the facial nerve, and other topics. Each chapter is not only replete with the latest scientific information, but also accessible and practical for clinicians.

The rhinology/allergy and immunology volume by Marvin P Fried and Abtin Tabaee is the most elegant and inclusive book on the topic to date. Drs Fried and Tabaee start with a history of rhinology beginning in ancient times. The chapters on evolution of the nose and sinuses, embryology, sinonasal anatomy and physiology, and rhinological assessment are exceptional. The volume includes discussions of virtually all sinonasal disorders and allergy, including not only traditional medical and surgical therapy but also complementary and integrative medicine. The information is state-of-the-art.

Anthony P Sclafani's volume on facial plastic and reconstructive surgery is unique in its thoroughness and practicality. The volume covers skin anatomy and physiology, principles of wound healing, physiology of grafts and flaps, lasers in facial plastic surgery, aesthetic analysis of the face and other basic topics. There are extensive discussions on essentially all problems and procedures in facial plastic and reconstructive surgery contributed by many of the most respected experts in the field. The volume includes not only cosmetic and reconstructive surgery, but also information on diagnosis and treatment of facial trauma.

The volume on laryngology edited by Dr Michael S Benninger incorporates the most current information on virtually every aspect of laryngology. The authors constitute a who's who of world experts in voice and swallowing. After extensive and practical discussions of science and genetics, the volume reviews diagnosis and treatment (traditional and complementary) of laryngological disorders. Chapters on laser physics and use, voice therapy, laryngeal dystonia, cough, vocal aging and many other topics provide invaluable "pearls" for clinicians. The volume also includes extensive discussion of surgery for airway disorders, office-based laryngeal surgery, laryngeal transplantation and other topics.

For the volume on head and neck surgery, Drs Patrick J Gullane and David P Goldstein have recruited an extraordinary group of contributors who have compiled the latest information on molecular biology of head and neck cancer, principles of radiation, immunobiology, medical oncology, common and rare head and neck malignancies, endocrine neoplasms, lymphoma, deep neck space infections and other maladies. The surgical discussions are thorough and richly illustrated, and they include definitive discussions of free flap surgery, facial transplantation and other subjects.

Dr Christopher J Hartnick's vision for the volume on pediatric otolaryngology was expansive, elegantly scholarly and invaluable clinically. The volume begins with information on embryology, anatomy, genetics, syndromes and other complex topics. Dr Hartnick's contributors include basic discussions of otolaryngologic examination in a pediatric patient, imaging, hearing screening and aural rehabilitation, and diagnosis and treatment of diseases of the ear, nose, larynx, oral cavity, neck and airway. Congenital, syndromic and acquired disorders are covered in detail, as are special, particularly vexing problems such as chronic cough in pediatric patients, breathing and obstructive sleep apnea in children, pediatric voice disorders, and many other subjects. This volume will be invaluable to any otolaryngologist who treats children.

All of us who have been involved with the creation of the six-volume *Sataloff's Comprehensive Textbook of Otolaryngology: Head and Neck Surgery* and its companion six-volume set of surgical atlases hope and believe that our colleagues will find this new offering to be not only the most extensive and convenient compilation of information in our field, but also the most clinically practical and up-to-date resource in otolaryngology. We are indebted to Mr Jitendar P Vij (Group Chairman) and Mr Ankit Vij (Group President) of M/s Jaypee Brothers Medical Publishers (P) Ltd., New Delhi, India, for their commitment to this project, and for their promise to keep this work available not only online but also in print. We are indebted also to the many otolaryngologists who have contributed to this work not only by editing volumes and writing chapters, but also by asking questions that inspired many of us to seek the answers found on these pages. We also thank especially the great academic otolaryngologists who trained us and inspired us to spend our nights, weekends and vacations writing chapters and books. We hope that our colleagues and their patients find this book useful.

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Preface

The field of rhinology has undergone a dramatic evolution in the past two decades. Landmark events that have occurred during this period include the widespread adoption of advanced technologies, the expansion of endoscopic techniques to complex skull base pathologies, and a dedicated focus on clinical and basic science research. This process has been, in large part, fueled by the increasing sub-specialization of the field, including the continued growth of fellowship programs and clinician-scientists dedicated to rhinology.

As the breadth of the field has expanded, so too have our horizons. It is interesting that the trends in rhinology have moved in different directions for various aspects of the field. For example, the indications and capabilities of endoscopic approaches for skull base tumors have increasingly expanded; at the same time, there has been a greater interest in minimally invasive techniques for inflammatory sinusitis, including balloon dilation technology. Integral to the development of novel surgical techniques and technology is a greater emphasis on a more holistic approach to surgical outcome analysis, including an emphasis on patient-scored quality-of-life measures. In parallel, the striking increase in the number and quality of basic science research articles is beginning to address fundamental questions, including the pathophysiologic basis of inflammatory sinusitis. This is an exciting time in rhinology as the field collectively looks back on its recent advances and towards the future to the remaining unanswered questions.

In creating this volume, our primary goal has been to provide a comprehensive reference for the field of rhinology, including the fundamental underpinnings of anatomy, physiology, and radiology; a practical approach to the evaluation of patient with sinonasal disorders; a description of the full spectrum of rhinologic disorders, including the different subtypes of rhinitis and sinusitis; and a comprehensive approach to medical and surgical management of sinonasal disorders. Sections reviewing sinonasal malignancy, trauma, and cosmetic rhinoplasty can be found in the volumes dedicated to these disorders. Advanced surgical techniques are discussed in detail, including indications, techniques, and outcomes. We have also included thought-provoking chapters on the history and future of rhinology, current models of rhinology training, and practical aspects of practice management.

We are fortunate to have a dynamic and storied list of authors, each with an exceptional level of expertise and wisdom. Their individual contributions to this volume have helped to create a seminal reference for the field of rhinology.

Marvin P Fried MD FACS
Abtin Tabaee MD FARS FACS

Acknowledgments

The editors would like to thank Joseph Rusko, Marco Ulloa, Carol Rogers Field, Bridget Meyer, Thomas Gibbons and the rest of the Jaypee Brothers team. Without their perseverance and hard work, this volume would not have been possible. Special thanks are offered to the authors, who have shared their expertise and experience in order to improve the care of rhinology/allergy and immunology patients.

We would also like to thank Mr Jitendar P Vij (Group Chairman), Mr Ankit Vij (Group President), Ms Chetna Malhotra Vohra (Associate Director), Mr Umar Rashid (Development Editor) and Production team of Jaypee Brothers Medical Publishers (P) Ltd., New Delhi, India.

Contents

SECTION 1

History of Rhinology

CHAPTER

The History of Rhinology—From Ancient Times to the 21st Century

1

Patrick Colley, Marvin P Fried, Abtin Tabaee

Medicine is defined by a continuous stream of innovation and evolution. As such, change, often for better, at times for worse, is a fundamental feature of its history. In reviewing our collective understanding of the nose and paranasal sinuses from ancient times to the present, several general themes emerge. Advances throughout history have often reflected the cultural and disease-related needs of the civilization at that time. For example, detailed descriptions of treatment for syphilis-related ozena are prominent throughout the preantibiotic history of medicine. An additional theme is the propagation of concepts that are ultimately disproven by divergent thinkers including seminal concepts in physiology and anatomy. Further, the major diagnostic and treatment advances in medicine have had successful application to nasal and paranasal sinus disorders. This includes microscopy, anesthesia, radiography, and antimicrobial therapy. Finally, technology has been a major force in the development of rhinologic surgeries, especially over the past century. The adage that in order to know where you are going, you must first know where you came from has truth in the field of rhinology whose history is colored with innovation, misdirection, and evolution.

ANCIENT HISTORY

Interest in the nose and the diseases that affect it has puzzled human civilizations throughout history. Ancient Persian writings note that male noses with a "hawk type" appearance resembling that of King Cyrus were admired. The Huns during the age of Attila routinely used bandages to flatten the noses of their infants. The Old Testament comments on prejudices against "flat-nosed people."[1] Conditions such as nasal polyps, ozena, and epistaxis have plagued people of all civilizations since the first medical documents were written. Our knowledge about the anatomy and pathology of the nose has progressed over the centuries resulting in the current field of modern rhinology.

The ancient Egyptians were the first to demonstrate an understanding of the nasal anatomy and its surrounding structures. Egyptian papyri from 3500 BC shows that specially trained priests in charge of the embalming process were the first to access the brain through a transnasal technique; the brains of the deceased were removed through the nasal cavity using specially designed instruments. This precursor to the transnasal approach to the intracranial cavity shows the detailed anatomic knowledge of the ancient Egyptians. This civilization also provides information on the earliest historical figure who performed the role of a physician in approximately 3500 BC. Engraving on the pharaoh Sahura's tomb states that an attendant named Sekhet' enanch "healed the King's nostils."[2-4]

While the Egyptians were using the nose as a means of accessing the brain, the Hindus were also investigating the function and physiology of the nose. The Hindu document *Sushruta Samhita* provides the first detailed description of a nasal exam. It was written before the sixth century BC and notes a nasal speculum made of bamboo tree.[3,5] The Hindus developed multiple treatments for diseases of the head and neck and noted their findings in a document known as the *Sanskrit Atharvaveda*. In this document, they describe surgeries to remove nasal polyps and reconstructive techniques for nasal injury and amputation, a common form of punishment at the time. Surgeons used local flaps from the cheek and forehead to reconstruct these defects and in doing so were the first to describe several important aspects of rhinoplasty and reconstruction still in use today.[3,4]

The ancient Chinese civilizations were using traditional eastern medical practices such as acupuncture to treat many nasal conditions. The Chinese also used their pharmacologic knowledge to provide relief to individuals with nasal congestion with a small shrub endemic to their area known as ma huang. This herb was documented to be an effective stimulant and nasal decongestant during the Han Dynasty in the second century AD.[1,6] It was not until the 19th century that the active chemical in ma huang, ephedrine, was discovered and produced commercially.

Nasal ailments are even described in religious texts including the Bible. In 2 Kings 4:35, the phenomenon of sneezing is described. Treatment of epistaxis using hemlock or other plant remedies is also detailed. "Lord God formed man of the dust of the ground and breathed into his nostrils the breath of life" (Genesis 2:7) represents one of the first documented references to the respiratory function of the nose.[7]

ANCIENT GREECE AND ROME

The "Father of Medicine," Hippocrates, wrote extensively about nasal disorders in the 5th century BC including management of nasal fractures, polyps, and epistaxis. Nasal trauma was commonplace during the time of Hippocrates in both Greek athletes and soldiers. For mildly displaced fractures, Hippocrates recommended lifting the fragments of bone and cartilage back into place within the first 24–36 hours after injury and using bandages and internal stents made of leather to keep the reduced fragments in the proper position. He detailed the use of a large external splint made of olive tree branches or a leather thong that would be tied around the head and kept in place using glue in order to reduce severely displaced nasal fractures. Hippocrates also wrote detailed descriptions of his methods of removing nasal polyps. This technique consisted of tying several sponges along a string, placing them deep into the nose or nasopharynx and slowly pulling them out in the hopes of removing the polyps along with the sponges. He was also the first to describe polyp removal using a snare.[4,8] These techniques were revolutionary for their time and were practiced well into the 19th century.

The Romans played a large role in advancing medical knowledge and the study of rhinology. A Roman nobleman by the name of Aulus Cornelius Celsus is believed to have documented the extent of Roman medical knowledge during the first century AD in his eight volume encyclopedia, *De Medicina*. These eight volumes are all that survived from a much larger collection. They were discovered in the papal library in the early 15th century AD and published in 1478. His work details information regarding diet, pharmacology, and surgery practiced in the Roman Empire. Celsus is the first to note the four cardinal signs of inflammation: dolor, calor, rubor, and tumor. He translated the work of his Greek predecessor Hippocrates and became the first person to use the Latin term *cancer* to refer to a malignant lesion.[4] It is unclear whether he was a practicing physician himself, but he documented medical treatments and often provided his opinion on the subject. In his works, he described the, "two nasal passages separated by an intermediate bone." Like many other physicians or anatomists of the time, Celsus believed that, "these passages break up into two branches, one for respiration and one leading to the brain through which we get our sense of smell." His treatment for nasal polyposis involved both the use of caustic material and surgical removal. Using specially designed instruments including a spatula shaped rod and a sickle knife or hook, he located and severed the stalk of the polyp prior to removal. Celsus also made the first note of a unified airway when he discussed lung infections possibly originating from the contents of the nasal cavities.[9]

Approximately two centuries after Celsus, another Roman played a large role in the advancement of medicine and rhinology. Claudius Galenus was a physician in the 2nd century AD who advanced medical knowledge and anatomy in such a major way that many of his theories were taught in medical schools until the 18th century (Fig. 1.1). His dissections of pigs and monkeys provided detailed information regarding many areas in anatomy, in particular the upper respiratory tract. He provided anatomic descriptions of the external and internal portions of the nose and continued the theory of the nose acting as the beginning of the respiratory tract. Galen divided nasal disease into two general categories: polyps and ozena. He noted the proximity of the nose and sinuses to the brain and believed that the sinuses contained fluid and mucus produced by the brain and pituitary gland. These fluids were thought to be waste products excreted by the brain. The work of these Greek and Roman physicians provided the basis for the study of medicine and rhinology for the next 1000 years.[4,10]

Fig. 1.1: Second century AD physician, Claudius Galenus, played a large role in advancing the medical and anatomic knowledge of the nose and paranasal sinuses.
Courtesy: National Library of Medicine.

THE ITALIAN RENAISSANCE

Progress in the study of rhinology, and in medicine in general, slowed during the early Middle Ages. During this period, most physicians believed that the function of the paranasal sinuses was to store oils used to lubricate the eyes or to function as drainage space for malignant spirits. As late as the 16th century, names such as "la cloaca del cerebro" were given to the sinuses demonstrating the continuation of this belief. Although not discovered until 1901, Leonardo da Vinci drew the nasal conchae and paranasal sinuses in detail in 1489.[1] Andreas Vesalius described the anatomy of the nasal bones, nasal cartilage, choanae and maxillary, sphenoid, and frontal sinuses in his landmark publication *De humani corporis fabrica* in 1543.[11] He also notes that these sinuses are air filled and not full of humor or spirits. Bartholomeus Eustachius, another anatomist of the time, played a large role in advancing rhinology and otolaryngology by describing most of the structures within the middle ear. In his 1562 treatise *Epistola de auditus organis (Examination of the Organ of Hearing)*, he described a tube that "originates at the anterior portion of the base of the skull, and takes an anterior course towards the pterygoid process of the sphenoid bone."[12] Although the function of the Eustachian tube was not completely understood at the time, the renewed emphasis on the study of medicine and the human body during the Renaissance laid the groundwork for advancements that would take place in medicine in the years to come.

Gaspare Tagliacozzi (1545–1599) made an impact during this time period through the publication of his book *Treaty on Rhinoplasty*. In it, he detailed the "Italian method" of rhinoplasty that differed from the "Indian method" that was detailed in *Sushruta Samhita* years earlier. Tagliacozzi developed pedicled flaps from the upper extremities and shaped them to cover the nasal defects. The upper extremity was then bandaged in an elevated position for approximately 20 days before the pedicle was transected and the transferred skin was trimmed to its final shape (Fig. 1.2).[13]

Other important European anatomists and physicians of the time also played a role in advancing the treatment of diseases affecting the nose. Gabriel Fallopius wrote in detail regarding his use of a wire snare to remove nasal polyps.[14] Petrus Forestus, known as the "Hollandic Hippocrates" claims in his 1591 text *Observationum et Curationum Medicinalium Libri* to have cured a girl of ozena by copious nasal douching "with perfumed white wine in which were dissolved cypress, roses and myrrh." In this same text, Forestus also treats ozena with silver nitrate and alum rubbed up with honey and applied with a probe. He was one of the first physicians to detail the findings in patients with nasal syphilis and notes that they should be treated differently than lesions of other etiologies.[15] Another European physician practicing at the same time as Forestus was Hieronymus Fabricius. He described treatment of intranasal ulcers secondary to ozena using cautery by a "glowing hot instrument." The cautery was to be continued until the area "was thoroughly cleansed of crusts."[1]

EUROPE 17TH–19TH CENTURIES

During the 17th century, physicians and anatomists made major strides in describing the function of the nose and

Fig. 1.2: Italian surgeon Gaspare Tagliacozzi designed pedicled flaps from the upper extremities for use in reconstruction of the nose.
Courtesy: National Library of Medicine.

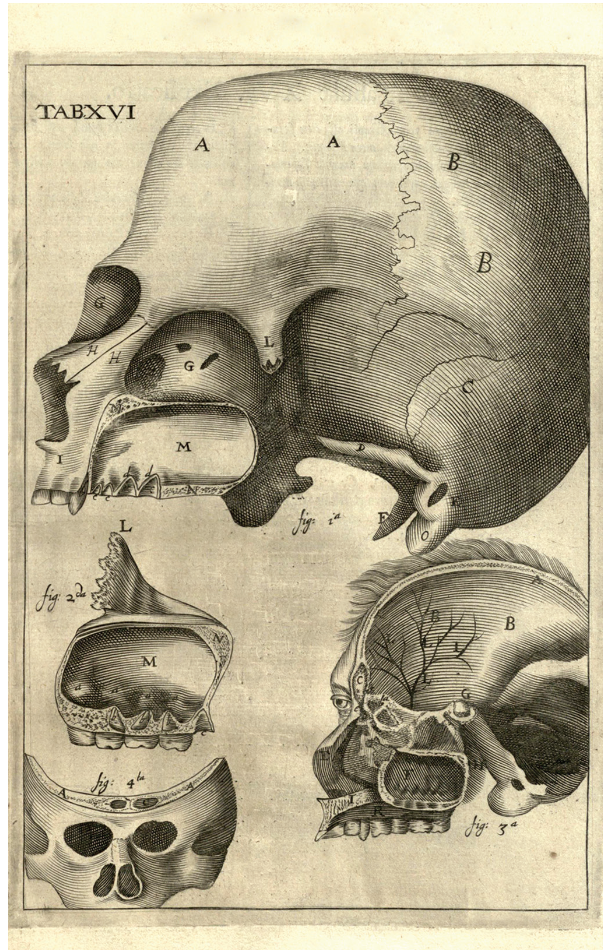

Fig. 1.3: An engraving from the British surgeon and anatomist Nathaniel Highmore's treatise *Corporis Humani Disquisitio Anatomica* detailing the anatomy of the maxillary sinus and antrum.
Courtesy: New York Academy of Medicine.

paranasal sinuses. Until this time, the belief that nasal mucus and secretions were actually "purgings of the brain" dominated most medical teachings. These secretions were believed to percolate through the bony foramina of the anterior skull base to enter the nasal cavity. Conditions such as halitosis or facial acne were associated with the nose and paranasal sinuses. The recommended treatment of such conditions was total or partial middle turbinectomy.[4]

In 1651, the British surgeon and anatomist Nathaniel Highmore published his treatise *Corporis Humani Disquisitio Anatomica* in which he described and illustrated the antrum of the maxillary sinus, a structure that later became known as Highmore's antrum (Fig. 1.3). Highmore also became the first person to use the term *ostomy* to refer to an opening made to permanently drain an organ.[16] Ten years after Highmore published his work, a German physician named Conrad Victor Schneider made the assertion that nasal secretions did not come from the cranial cavity. In his published treatise on the membranes of the nose, *De Catarrhis*, Schneider stated that nasal secretions actually originated from the mucous membranes of the nose and sinuses.[17] This change of belief would have important implications for future rhinologists.

In 1707, two English physicians named James Drake and William Cowper published a medical treatise *Antropologica Nova* in which they described multiple cases of halitosis caused by suppuration of the maxillary sinus. This suppuration was relieved by removal of maxillary teeth creating an oral antral fistula that allowed drainage of the sinus through the alveolus.[18] In 1768, French surgeon Louis Lamorier described a similar method of draining the maxillary sinuses. After its description, Lamorier's transalveolar technique remained the procedure of choice for the treatment of maxillary sinus suppuration for nearly a century.[19] An 1889 paper by Dr. Joseph H Bryam, one of the four founding physicians of the Episcopal Eye, Ear and Throat Hospital of Washington DC, notes that the best surgical method to drain an abscess of the maxillary sinus is to remove a molar tooth and perforate into the antrum through the alveolus.[20]

A new technique of accessing the maxillary sinus was developed by Charles Joseph Heath of London in 1889 and William Robertson of Newcastle–on-Tyne in 1892. It involved trephination of the anterior maxillary wall and removal of all sinus contents.[21] In 1893, George Walter Caldwell, a physician in New York, published his method of opening the maxillary sinus using trephination of the anterior maxillary wall. However, Caldwell also created an inferior antrostomy through the lateral nasal wall.[22] At roughly the same time as Caldwell described his technique, the French physician Luc independently reported his technique for opening the maxillary sinus using a nearly identical technique to Caldwell's.[23] This surgical technique became known as the Caldwell–Luc operation and remains in practice to this day.[24,25]

In addition to surgical developments in rhinology, the 19th century also heralded vast leaps in our understanding of the histology, physiology, and anatomy of the nose and sinuses. The development of the microscope in the 1830s allowed individuals like Rudolph Virchow and Friedrich Henle of Germany along with J.F.L Deschamps of France to study the epithelia of the nose and sinuses. Henle provided detailed descriptions of the different types of epithelia. He also first noted the function of the ciliated epithelium found throughout the upper respiratory tract.[4,26] In 1870, Emil Zuckerkandl of Austria published an extremely detailed anatomic and pathologic descriptions of the paranasal sinuses. Other anatomists such as L. Grunwald of Munich, M. Hajek of Austria, Adolf Onodi of Hungary, and Harris Mosher of Boston also contributed to the rapidly growing fund on rhinology knowledge.[4]

Technology was also developing rapidly during this era. The rhinologic exam became much more informative and accurate following German physician Phillip Bozzini's creation of endoscopy in 1806 (Fig. 1.4).[27] In addition to developing laryngoscopy, Czech physician Johann Czermak further improved the nasal exam by promoting the use of the nasal speculum, head mirror with reflected light, and endoscope in 1879.[28] Following the discovery of the analgesic properties of cocaine by Carl Koller of Austria in 1884, these tools contributed greatly to the surgical and anatomic teachings of physicians.[4]

Fig. 1.4: The endoscopic light source developed by German physician Philip Bozzini involved candle light reflected by a mirror into the endoscope.
Courtesy: National Library of Medicine.

With these new tools in hand, surgeons began to develop new treatments for old ailments. In 1893, Charles Henry Burnett of Philadelphia detailed a number of conditions that he believed were due to hypertrophy of the inferior turbinates and recommended inferior turbinectomy as an effective treatment. These conditions all related to "nasal stenosis" and consisted of habitual mouth breathing, rhinorrhea, excessive nasal mucous, serous otitis media, obstruction of the lacrimal duct, nasopharyngitis, laryngeal hyperemia, laryngitis, and secondary lung disease.[29] Others such as D. Braden Kyle[30] and Chevalier Jackson[31] of Philadelphia along with William Jarvis of New York supported this procedure and its benefits. As a result of the popularity of inferior turbinectomies, investigators in the United States and Europe evaluated nasal airflow patterns and developed anterior and posterior rhinomanometric methods still in use today.[32-36]

The understanding and treatment of nasal polyps improved during the 19th century as well. As far back as the times of Galen (200 AD), nasal polyps were believed to be "a constitutional disease due to the state of the humors of the body." They were treated with knotted thread, caustic agents, and snare ligation.[37-39] Deschamps was one of the first people to describe nasal polyps as a local disease of the nasal and sinus mucosa. He developed a classification system for nasal polyps consisting of "fungous and vascular, mucous and lymphatic, scirrhous, and sarcomatous."[26] The Austrian surgeon Theodore Billroth later described nasal polyps as adenomatous in nature while Virchow called them myxomata. Treatment of these lesions improved due to the use of the endoscope, nasal speculum, and topical anesthetics such as cocaine. Due to its effectiveness, the primary method of polyp removal remained the wire snare. While the design of this instrument improved during the 19th century, it still relied on principles present for hundreds of years.[4]

In 1881, Dr. Francke Bosworth of New York City published one of the first otolaryngology textbooks, *A Textbook of Diseases of the Nose and Throat*. In it, he details a multitude of pathologies affecting the nose and discusses how these can affect the entire body. He provides descriptions of thorough nasal exams and demonstrates an impressive understanding of nasal and sinus anatomy. Dr. Bosworth is often referred to as the "Father of Rhinology" in North America due to his extensive work on the subject.[40,41]

Besides Dr. Bosworth, many other American physicians of the 19th century advanced the field of rhinology. Drs. Morris Asch,[41] Fletcher Ingals,[42] Robert Weir[44], and John Rowe[43] played large roles in the development of new nasal surgery techniques. These "early rhinologists" were all part of the American Laryngological Association, a group formed in 1878 to promote knowledge "in all that pertains to the diseases of the upper air passages." This interest in rhinology as well as laryngology and otology grew to such an extent that specialty eye and ear hospitals opened in New York (1820) followed by hospitals in Philadelphia and Boston.[4]

THE 20TH CENTURY

The beginning of the 20th century continued the rapid progression of rhinology seen in the previous century. This progression was largely due to advancements in surgical techniques that allowed for more effective treatment of nasal ailments. Drs. Otto "Tiger" Freer and Gustav Kilian built on septal surgery techniques taught by Ephraim Ingals of Chicago 20 years earlier and developed the submucous resection of the nasal septum.[45] To aid in this procedure, Freer produced new surgical instruments including new nasal speculae, rasps, scissors, knives, forceps and elevators. He published extensively on this procedure and described the areas of the septum that can be safely resected, proper postoperative follow up, the proper use of cocaine, and post-operative packing. It is noteworthy that Freer's surgical teachings and instruments remain in use today.[46-48] At the same time that Freer was publishing his works in Chicago, Killian of Germany developed a similar method of submucous septal resection that yielded comparable results. Freer and Kilian's work quickly turned septal surgery into a popular procedure performed by rhinologists throughout North America and Europe.[49-51] This popularity lead others to further refine the technique, develop new instruments and decrease the operative time. During this time, most nasal surgeries were performed under local anesthesia using cocaine or epinephrine that did not allow for long procedures. Freer claimed to require 45 minutes to complete his procedure.[52] William Ballenger's invention of the swivel knife and John Mackenty's technique for application of local anesthetic reduced to average operative time for a submucous nasal septal resection to 20-30 minutes by 1908.[53]

Septal surgery was not the only rhinologic procedure that took leaps forward during this century. Surgery on the ethmoid and sphenoid sinuses was developed in the early 20th century by Albert Jansen. His transantral route to the ethmoid and sphenoid sinuses relied on the widely taught Caldwell-Luc procedure to provide access to the lateral nasal wall. Mosher, a prominent anatomist and physician in Boston, noted that this route was effective in treating "combined empyema of the antrum, ethmoid region and the sphenoid."[54] However, Jansen's procedure required removal of the majority of the lateral nasal wall including the middle and inferior turbinates that likely resulted in significant atrophic rhinitis. This led to the procedure falling out of favor among many rhinologists.[55,56]

In 1912, Mosher published one of the first descriptions of an intranasal method of performing an ethmoidectomy. The procedure required wide exenteration of the labyrinth and complete removal of the middle turbinate. This wide dissection performed through a small nasal cavity lead others to question the safety of this method of ethmoidectomy.[57] Mosher eventually became disenchanted with this procedure and in 1929 noted that "it has proved to be one of the easiest operations with which to kill a patient."[58] In response to the poor success rate of intranasal and transantral access to the ethmoid sinuses, Robert Lynch of New Orleans[59] and W. Howarth of London[60] described external approaches to these sinuses that did not leave unsightly scars or bony deformities. The Lynch frontoethmoidectomy provided a safe and relatively effective method of opening and treating the anterior ethmoid and frontal sinuses. Mucosal flaps and stents were also developed in the hopes of improving the patency of the frontoethmoid recess but none of them were used with any success.[61]

In order to treat patients who did not receive relief from their frontal sinus disease after a Lynch procedure, rhinologists of the time developed external approaches to this sinus. Originally, these procedures led to defects in the anterior table and left unsightly scars. However, a new technique developed by Howard Lothrop of Boston in 1917 allowed for treatment of frontal sinus disease with minimal aesthetic impact. Lothrop developed a method to bypass the nonfunctional frontal sinus by removing the inter-sinus septum and frontal floor to allow sinus contents to drain through the opposite side.[62,63] In 1964, Robert Goodale and William Montgomery of Boston combined the osteoplastic flap with fat obliteration of the frontal sinuses to treat chronic frontal sinus disease.[64] This technique became the treatment of choice for chronic frontal sinus disease for many years afterwards.

Another common surgical technique that developed in the early 20th century was the inferior meatus antrostomy. This procedure was promoted by Jan Mikulicz-Radecki of Austria and Lothrop for the treatment of chronic maxillary sinusitis.[65] Critics of the time did not like that it did not remove the diseased mucosa of the sinus. However, poorly controlled rabbit model studies conducted by A. C. Hilding suggested that the natural ostium of the maxillary sinus should not be surgically altered.[66] This misinformation influenced the rhinology community for over 40 years until it was finally disproven by Messerklinger.[67-70]

In addition to surgical advancements, the 20th century let to technologic advancements that benefitted the field of rhinology. The first of these was radiography. Cornelius Coakley of New York City was the first otolaryngologist to report using this new equipment. He described how he was able to diagnose frontal sinus disease using a posterior-anterior view with an exposure time of 3.5 minutes.[71] The Waters, Caldwell, and lateral views were all in use by 1915 and played a major role in the diagnosis of sinus disease before computed tomography was developed.[72,73] According to Stammberger, the lack of detail found in these early radiographs likely delayed the understanding of the complex surgical sinus anatomy.[4]

In addition to radiology, advancements in nasal endoscopy were coming about during the mid-20th century. Although the first endoscope had been invented in 1801 by Bozzini, it was not frequently used by physicians due to poor visualization and illumination. Endoscopic examinations were limited to the peritoneum and bladder. In 1853, French physician Antonin D'Esormeux demonstrated an alcohol illuminated urethroscope. Following the development of electricity, distal illumination improved significantly that led Max Nitze of Germany and Joseph Leiter of Austria to develop the Nitze–Leiter cystoscope. Using a modified version of this instrument, E. Zaufal examined the Eustachian tube orifice during the 1880s. Twenty years later, Alfred Hirschmann of Germany described the first nasal endoscopy using a special 4.0 mm diameter endoscope. He examined the middle meatus and maxillary sinus ostia through the nose as well as via the molar tooth socket. Roughly at this same time, M Reichert, also of Germany, described minor manipulation of sinus tissue using endoscopy. However, Hirschmann's and Reichert's advancements and their possible applications to the field of rhinology were ignored for the next six decades. Harold Hopkins of England designed the modern endoscope 1948. He drew influence from the work of John Baird earlier in the century who patented the transmission of images through glass fibers. Over the next two decades, Hopkins and German manufacturers improved endoscope technology to provide a precise, detailed picture. Using Hopkin's new technology, surgeons of the day slowly began performing more endoscopic examinations and eventually surgical procedures.[74-77]

Important figures in rhinology were plentiful early in the century. Arthur Proetz, an otolaryngology professor at Washington University, wrote his thesis entitled "The Displacement Method of Sinus Diagnosis and Treatment." In this thesis Proetz describes using sophisticated equipment and head positions to diagnose and treat an array of sinus conditions. For his work, Proetz was awarded the Castlebury Prize from the American Laryngological Association in 1931.[78-81] Ten years later, Professor Van Alyea of Chicago authored a legendary textbook entitled "Nasal Sinuses." In the book, he details information about nasal anatomy

Fig. 1.5: Maurice Cottle was a founding member and the first president of the American Rhinologic Society. His teaching and leadership in the field of rhinology spurred its growth that led to his nickname "the father of rhinology."

and physiology as well as the role that allergy may play in sinus disease. The book discusses newer concepts such as the mucociliary blanket, mucosal information and the role of new medications known as antibiotics in the treatment of sinusitis.[82]

Maurice Cottle of Chicago is often referred to as the "rhinologist of the century" for his work in this field and his dedication to its advancement (Fig. 1.5). He is considered to have restored rhinology to the same prominence as laryngology and otology. Dr. Cottle is known as a great educator who taught his functional approach to nasal and sinus surgery at his lecture series beginning in 1944. The series became known as "Cottle courses" and soon attracted specialists from around the country.[4] It was at one of these courses at Johns Hopkins Hospital in 1954 that the American Rhinologic Society (ARS) was formed and Dr. Cottle was elected the first president of the group. His leadership and mentoring helped the ARS flourish and grow from a somewhat small group of practitioners to a robust academic society with a strong presence in the otolaryngology community. Although the interests of the ARS originally concerned the structure and function of the nose, the advent of nasal endoscopy and surgery shifted its focus towards disease of the paranasal sinuses and skull base. The development of the ARS spurred the academic study of diseases affecting the paranasal sinuses and aided in the dissemination of effective endoscopic surgical techniques for the treatment of these conditions.[83]

In the latter half of the 20th century, pioneers such as Walter Messerklinger of Austria entered the field of rhinology and embraced the new technology and concepts introduced earlier in the century. Endoscopes developed by Hopkins were refined by German manufactures and provided significantly better visualization of the nasal cavity and sinuses than previous versions. Messerklinger was the first person to use these endoscopes to examine and treat sinus disorders.[84] He provided detailed endoscopic anatomy using this new technology and opened the gates for other pioneers to follow. David Kennedy from Johns Hopkins,[85] Heinz Stammberger of Austria,[70] and Wolfgang Draf of Germany[4] built on these concepts and further developed modern endoscopic sinus surgery. Their work showed the importance of mucociliary function and detailed the need for proper antrostomies in the treatment of chronic rhinosinusitis.

The rapid evolution of endoscopic sinus surgery also required development of new surgical instruments and other supportive technologies. The removal of only diseased mucosa and sparring of normal tissue required through cutting and power instrumentation. These instruments allowed for precise cutting of mucosal edges in order to avoid stripping mucosa and exposing the underlying bone.[86] Computed tomography, developed by Geoffrey Hounsfield in 1969 allowed for improved preoperative visualization of complex sinus anatomy and aided in the diagnosis and treatment of sinusitis. Improvements in computed tomography lead to the development of intraoperative image guidance navigation. These systems were developed to satisfy a clinical need for better intraoperative orientation and localization. Modern navigation technologies are based on stereotactic systems developed for neurosurgery.[87]

As endoscopic surgery progressed, rhinologists began pushing the boundaries of indications and pathologies for transnasal surgery. Endoscopic septoplasty and endoscopic ligation of the sphenopalatine artery for refractory epistaxis became commonly performed procedures. Transnasal endoscopic orbital procedures such as endoscopic dacryocystorhinostomy and orbital decompressions for optic neuropathy and Graves' disease were developed. Based on the work of Draf and others, frontal sinus surgery evolved from primarily an open procedure into one with multiple methods of endoscopic treatment.[4] The increase in endoscopic sinonasal surgery naturally lead some rhinologists and neurosurgeons to begin to explore the application of this new technology to the field of neurosurgery. Gerard Guiot of France with Karl Bushe and E. Halves of Germany reported the first use of a transnasal endoscope to access a pituitary lesion in 1970.[88] Over two decades later, Hae-Dong Jho and Ricardo Carrau from Pittsburgh published their first series using strictly endonasal transsphenoidal approach to resect pituitary tumors.[89] Their success led others to develop methods of accessing and treating anterior skull base, clival, and infratemporal fossa lesions.

Mirroring the paradigm shifts that have occurred throughout the history of rhinology, the past quarter of a century has refined our understanding of the pathophysiology of sinusitis. The disease began to be viewed not just as an infectious process but also the result of an inflammatory process within the mucosa itself. Mediators of inflammation such as cytokines and interleukins became targets of research and potential intervention.[90-92] The role of eosinophils in chronic sinusitis and the destructive inflammatory contents that they release became better understood.[93] Bent et al. detailed the pathogenesis of allergic fungal sinusitis.[94] Multiple research groups described the bacteriostatic role nitrous oxide plays within the paranasal sinuses.[95] Others showed that this substance that is naturally found in high concentrations within the sinuses also has antiviral properties and upregulates mucociliary activity.

The end of the 20th century and the beginning of the 21st century saw many changes in the medical management of sinusitis due to the improved understanding of its pathophysiology. Evidence supporting a polymicrobial etiology of chronic rhinosinusitis became more prevalent and the role of bacterial biofilms began to be investigated.[96] Antimicrobial therapy remained the mainstay of treatment for both acute and chronic sinus disease. However, treatment methods directed at inflammation took on a larger role in the management of chronic sinusitis.[97]

In addition to improved basic science research into the pathophysiology of chronic sinusitis, the 21st century also witnessed an emphasis on patient-centered quality of life measures in defining treatment outcomes in rhinosinusitis. Using psychometrically validated questionnaires and large patient databases, a more robust measure of treatment intervention and impact of comorbidities has become available.[98,99] As patient databases grow and researchers abilities to analyze information improve, rhinologists are sure to refine their treatments methods even further to the benefit of the millions of patients with sinus disease.

The history of rhinology can be traced back to the earliest cultures on earth. Our understanding of the anatomy and pathologies in this field has advanced steadily over the past 3 millennia leading to the fevered pace of study that has taken place in the last four decades. As more information is discovered, more questions arise. Research directed at the pathophysiology and treatment of sinus disease, collaborative dissemination of information, and technological advances will continue to advance the field of rhinology.

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SECTION 2

Embryology, Anatomy and Physiology

CHAPTER

2

Evolution of the Human Nasal Respiratory Tract: Nose and Paranasal Sinuses

Samuel Márquez, Anthony S Pagano, William Lawson, Jeffrey T Laitman

INTRODUCTION

From our humble beginnings as lobe-finned fish to our current role as the dominant species on planet Earth, the nasal cavity has been at the forefront of our evolutionary story. It is not a single unit but rather a composite structure with several developmental and evolutionary origins. These have each undergone considerable change, especially among the early mammals and during the rise of the primates. The modern human nasal cavity is thus the product of many millions of years of adaptation and preadaptation to novel functional demands. It is through the study of this evolutionary past that one may gain a deeper understanding of disease etiology and malformations of the nasal cavity and related structures. This chapter will focus on nasal evolution among humans and the non-human primates from the primitive mammalian condition to our extremely specialized anatomy.

In conceptualizing the human nasal cavity, one must understand its composite origins. That is, the external nasal vestibule, nasal cavity floor, lower and upper conchae, cribriform plate, and choanae all arose at separate times and in relation to varied functional demands. Indeed, this complicated evolutionary history is reflected in the various functions performed by the modern human nasal complex, which acts directly in the transport and conditioning of respiratory airflow, olfaction, the perception of flavor in food, production of nitric oxide gas (in the paranasal sinuses), and regulation of brain temperature via the pterygoid plexus of veins. It also serves several passive functions as the nasal cavity floor both braces against masticatory stresses and allows proper suckling by infants (achieved through complete separation of the nasal and oral cavities) while the cartilaginous Eustachian tube and soft palate attach to its posterior wall and floor, respectively.

SEGMENTATION AND THE BEGINNINGS OF THE PREOTIC HEAD

A discussion of the evolutionary origins of the various components comprising the nasal complex may best begin with head segmentation. Among the earliest to consider head segmentation was Goethe in a series of unpublished letters. His argument was later elaborated in several formally published works.[49,51,93] Early authors held that the entirety of the axial skeleton and its soft tissues, including the head, grows from iterative segments. The skull was believed to have formed from modified vertebra and, as described by Owen,[94] was derived from as many as four separate cranial vertebrae. Huxley[62] later challenged this paradigm, citing that only the anterior two thirds of the skull grow from the notochord (which is the main embryologic progenitor of the vertebral column) and that several basicranial cartilages remain unsegmented and continuous throughout vertebrate growth (reviewed by Northcutt[91]).

By the time of Goodrich,[52] discussion of head segmentation no longer centered on cranial vertebrae, but rather on series of somites and pharyngeal arches. He argued that the three anterior-most somites contribute to the preotic skull (mostly the facial skeleton) while the posterior four are successively associated with developing branchial arches and cranial nerves. This paper is important in contributing to the modern concept of skull segmentation over gastrulation and distinguishing between the preotic and periotic divisions. These roughly correspond to the division observable in the nasopharyngeal wall between the anterior and posterior portions, which are distinct in anatomy, histology, and development.

Gans and Northcutt[48] later proposed separate evolutionary origins for the pre- and postotic portions of the vertebrate skull. The former was derived from a series of sensory adaptations for active predation, developing exclusively from neural crest cells while ectodermal placodes contribute to the development of the sensory organs and some nerves. The vertebrate skull was thus an ectodermal addition to the basic protochordate body plan (with the notochord progressing only as anterior as the basicranial fenestra). The distinct origins of the elements composing the anterior and posterior nasopharyngeal walls may thus be as old as the appearance of the first vertebrates.

The developmental evidence cited by Gans and Northcutt[48] were corroborated by Couly et al.[27] who mapped the fates of neural crest, somitic, and mesodermal cells in the cranial development of the chicken. Tissue grafts were taken from quail embryos and implanted into chicken embryos between E8 and E12 (the 8th and 12th days of embryological growth, respectively). It was determined that the splanchnocranium, mandible, frontal bone, and parietal bones were all derived from neural crest cells. The sphenoid was divided into an anterior neural crest-derived half and a posterior mesoderm-derived half. The otic capsule was shown to contain elements from all three sources. These results favor the "new head" hypothesis of Gans and Northcutt[48] by confirming the neural crest origin of the prechordal skeleton and by describing the separate developmental trajectories of areas corresponding to the anterior and posterior nasopharyngeal walls.

Further evolutionary depth is given to the division of the pre- and postotic head in a synthesis by Baker and Bronner-Fraser.[4] They argue that the homologs of vertebrate neural crest cells and ectodermal placodes may be present in nonvertebrate chordates such as the cephalochordates, which are classified in the subphylum Chordata and are defined by the presence of a notochord that persists throughout the life of the organism (e.g. lancelets). These possible homologs are ectodermally derived and tend to migrate over development. It is also argued that homologs for the neural crest and placodes may be found in the neural cords of enterpneust worms, which are considered good models for the condition of the last common ancestor of all chordates.

BEGINNINGS OF THE NASAL CAVITY PROPER: IMPORTANCE OF THE CHOANAE

Fossil evidence suggests that the presence of choanae may have been among the earliest occurring synapomorphies (i.e. a shared derived trait) characterizing the tetrapods.[63] Panchen and Smithson[97] gave the first formal anatomical definition of ancestral tetrapodomorph choanae (i.e. four-limbed tetrapods) as being constrained laterally by the premaxilla and/or maxilla and medially by the vomer. The osteolepiformes, a group of fossil lobe-finned fish likely related to stem tetrapods, share synapomorphic choanal morphology with tetrapods but predated the earliest known terrestrial vertebrates by approximately 30 million years.[63] This condition is distinct from most fishes, which possess a pair of anterior and posterior nostrils on the external snout.

von Bischoff[8] first described the presence of choanae in the lungfishes and grouped them with amphibians. They were considered excellent models for the respiratory morphology of early tetrapods as they appeared intermediate in morphology between the amphibians and fishes. Lungfishes exhibit choanal morphology similar to that seen in the primitive tetrapod condition, as spaces that communicate between the nasal sac and oral cavity (Fig. 2.1). However, a nasopharynx *sensu stricto* may not be found in lungfish or ancestral tetrapods including lobe-finned fishes as no distinct airway is present. The communicative channel between the anterior and posterior nares remains, as in most fishes, an olfactory pathway lined with specialized epithelia (*see* the description by Derivot[37]). These are used specifically for olfaction in aquatic environments and are closed off during air swallowing by specialized valves.[37] As can be inferred from modern lungfish, air breathing animals that lack a means of nasal respiration may engage in an activity known as air swallowing (*see* description and review by Smith[124]) in which air is passed to the lungs through the mouth. Given the antiquity of the choanae and their function in lungfish, it appears that these apertures may not have evolved as respiratory pathways. Indeed, choanae are absent among the African lungfish (*Polypterus*), which instead exhibits a primitive nasopalatal duct.[2]

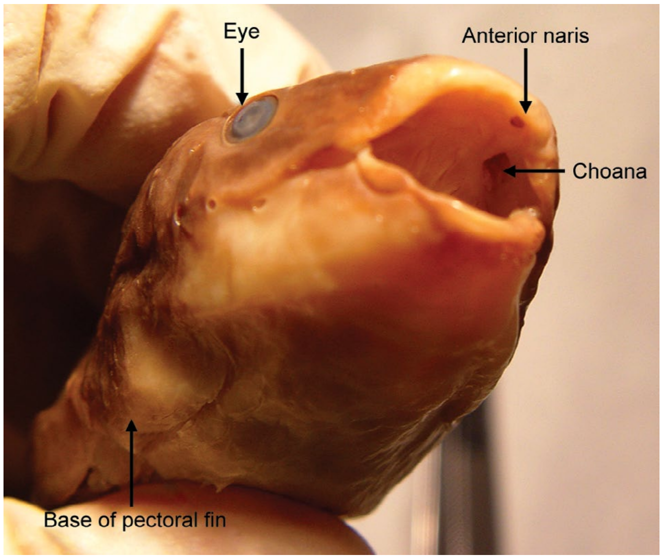


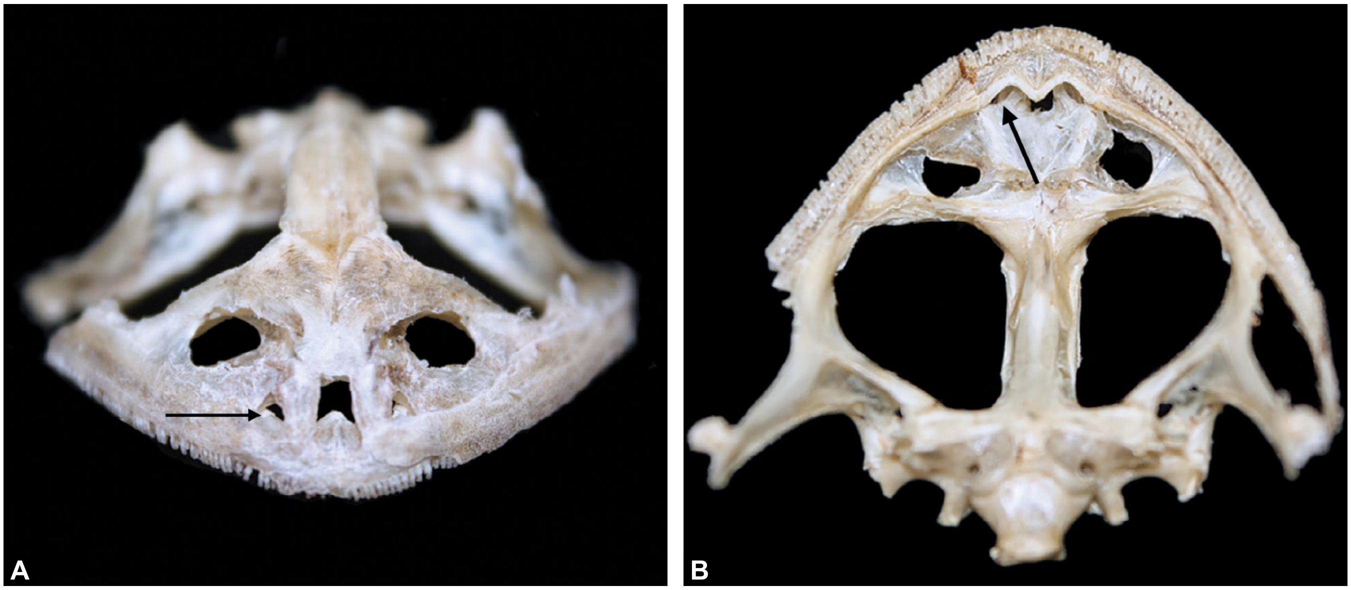
Fig. 2.1: Above is an Australian lungfish (*Neoceratodus forsteri*) exposing its oral cavity. Note that the choanae open ventrally into the hard palate. This is not a respiratory airway as the lungfish passes inspiratory air directly through its oral cavity. Rather, the nasal cavity houses specialized olfactory epithelia that function in aquatic environments. Photograph of specimen catalog # 55451, Group 7, from the Division of Ichthyology at the American Museum of Natural History, Collection of Fishes.
Courtesy: Anthony S. Pagano, Icahn School of Medicine at Mount Sinai, NY, USA.

The phylogenetic polarity of the lungfish choanae has long been debated.[142] The choanata was erected by Save-Soderbergh[112] as a taxonomic group including all tetrapods, lungfishes, and lobe-finned fishes that possessed choanae or choana-like apertures, which communicate with the palate. Similarly, Romer[108] proposed the inclusion of all choanate fishes into the taxon Choanichthyes. Rosen et al.[109] were some of the most recent authors to suggest that lungfish choanae are homologous to those of tetrapods. Yet, despite the presence of gross similarities, evidence from both the fossil record and cladistic analysis suggest that the ancestors of the modern lungfish may have homoplastically (i.e. independently) evolved choanae. Chang[22] first described *Diabolepis*, an extinct lungfish that exhibits the primitive piscine morphology of both an anterior and posterior set of nostrils that did not communicate with the oral cavity. In addition, a primitive piscine configuration of the maxillary nerve occurs in which it runs medial to the posterior nasal aperture among extant and extinct representatives of the lungfish. It has been displaced even further medially from its ancestral position by the migration of the posterior nostril into the oral cavity over lungfish evolution.[63]

Zhu and Ahlberg[142] were the first to describe a genus (*Kenichthys*) that exhibited a morphology intermediate between that of fishes and tetrapods, in which the choanae were present at the junction of the maxilla and premaxilla. It evolved as a displaced posterior external nostril, which was redirected ventrally from its primitive position on the snout to the lateral edge of the maxilla. These choanae are more laterally located than those of early tetrapods but clearly differ from the primitive piscine morphology. In addition, the maxillary nerve is located lateral to the choanae, a synapomorphy with tetrapods and their osteolepiform relatives.[63] The evidence suggests that the anatomical configuration of the tetrapod choanae (arguably the earliest aspect of the nasopharyngeal boundaries to evolve) may have resembled *Kenichthys*, first evolving from the standard posterior nostril bounding the piscine nasal sac and later migrating to a position on the palate. The palatine choanae of early tetrapods also appears similar to the condition seen during human embryologic growth, potentially serving as a resume of evolutionary history (as per Crelin[28]).

Amphibians

The earliest land tetrapods were probably amphibians.[25,77] Modern amphibians are extremely specialized relative to the first land tetrapods, which possessed dermal plates overlying the skull and lacked occipital condyles, among other primitive traits expressed in common with their piscine ancestors.[25] Nonetheless, they maintained choanae that communicate between the nasal cavity and oral cavity, which allowed them to pass air through the external nares and nasal cavity into the oral cavity via the inferiorly oriented choanae (Figs. 2.2A and B). Once air reached the oral cavity, they may have used a bucchal pump system similar to modern anurans (frogs) in which the inspired air is pumped downward toward a nearly intraoral glottis by specialized pharyngeal muscles. There is thus no nasopharyngeal airway among amphibians as they lack clear postnasal separation between the airway and alimentary tract. The nasal cavity itself is an anteroposteriorly closed sac bounded by the external nares superiorly and the choanae inferiorly in most amphibians.[99] Anurans possess the most intricate of amphibian nasal cavities; they are multichambered with at least one nasal concha and separate areas for respiratory air conditioning, olfaction, and the potential homolog of the vomeronasal organ.[92,99] The only known terrestrial tetrapod to possess completely



Figs. 2.2A and B: (A) Frontal view of a bullfrog (*Rana catesbeiana*) with the right anterior naris indicated by a black arrow. (B) Basal view of the same specimen with the right choana indicated by a black arrow. Note that the choanae exit into the oral cavity.
Courtesy: Joy S. Reidenberg, Icahn School of Medicine at Mount Sinai, New York, NY, USA.

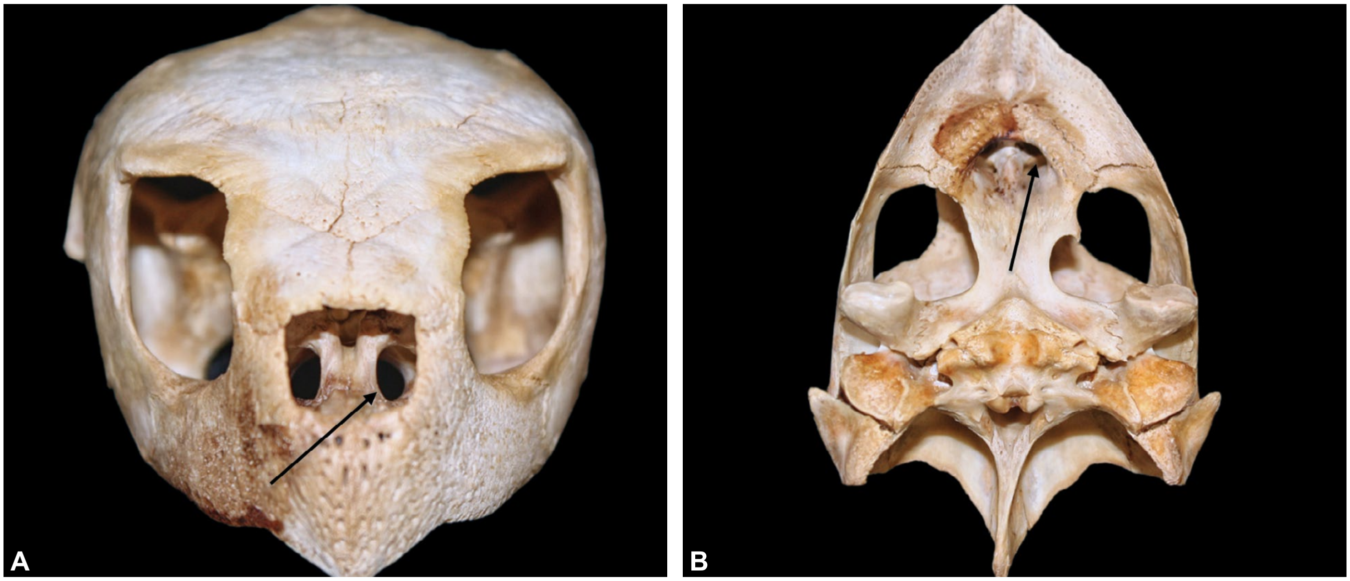
occluded choanae as part of its adult morphology is *Atretochoana eiselti*, a large lungless salamander from the cold, mountain habitats of the Andean highlands.[136] It conducts respiration solely through specialized epithelia over its skin, much like other members of the Plethodontidae (i.e. the family of lungless salamanders).

JUMPING FORWARD IN TIME: EVOLUTION OF THE SECONDARY PALATE

Among most reptiles, as in the amphibians, there is no nasopharyngeal space sensu stricto. Rather, the choanae end in the oral cavity, opening between the parasphenoid wings and epipterygoid bone at the roof of the alimentary tract.[59] The pterygoid plates are ventrally oriented and located far from the choanae, which lay anteriorly at the junction of the primary and secondary palate derivatives between the premaxilla and maxilla (Figs. 2.3A and B). As per Fuchs'[47] classic description of reptilian nasal embryology, the nasopharyngal duct is defined as the posterior ending of a space overlying a well-developed secondary palate as seen in the Crocodilia and mammals but not in most extant reptiles, which lack this structure. Parsons,[98] however, used the term more broadly to describe the area of the cavum nasi leading into the choanae in all reptiles.

The mammalian nasal cavity can arguably be identified as having arisen with the appearance of the secondary palate present among the earliest cynodonts (early mammal-like reptiles). It has been argued that a transversal ligament spanning between the tubercles of the vomer and the vomerine processes of the maxillae on either side ventrally covered the choanae to create a ligamentous precursor of the secondary palate.[5,13,15,30,79,127] Barghusen[5] and Maier et al.[79] argue that the development of this palatal precursor within the common ancestors of therocephalians and cynodonts (early, mammal-like reptiles) was tied to the development of bony choanal crests to anchor fleshy choanal folds capable of separating the nasal cavity from the oral cavity. These choanal crests were believed to be the precursor of the osseous portion of the secondary palate.[5] Maier et al.[79] suggest that this was an adaptation to carnivory, which allowed for the continued patency of the airway during deglutition of large meat boluses, which could not be reduced via mastication as no shearing or occluding postcanine dentition had yet evolved among early therocephalians and cynodonts.

In addition to alimentation, other functional demands may have influenced the evolution of the mammalian secondary palate. Our highly specialized morphology may be defined by the presence of an elongated, composite (primary and secondary) hard palate, and velum along with well-defined pharyngeal constrictor musculature.



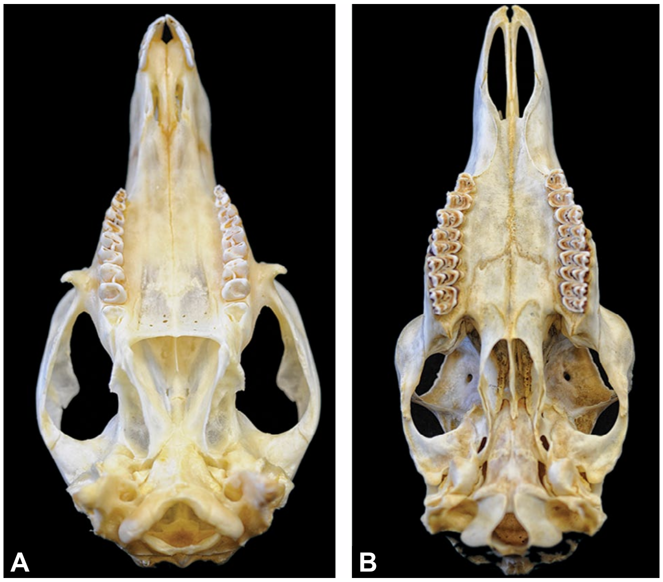
Figs. 2.3A and B: (A) Frontal view of a sea turtle (Lepidochelys sp.) with the enlarged choanal opening visible through the anterior naris (arrow on left choanal communication). (B) A basal view of the same specimen illustrating the position of the choanae opening into the oral cavity (black arrow indicating the position of the left choana).
Courtesy: Joy S. Reidenberg, Icahn School of Medicine at Mount Sinai, New York, NY, USA. Photograph by Samuel Marquez and Anthony S. Pagano.

The former trait likely evolved alongside a differentiated nasal cavity containing an olfactory recess (a probable adaptation for heightened olfactory acuity) separated from a nasopharyngeal duct inferiorly by a transverse ethmoidal lamina. In addition, this specialized morphology may have evolved to allow more efficient suckling among neonates.[79] Proper suckling is mediated by the induction of negative pressure in the oral cavity, which must be completely separated from the nasal cavity. Such separation is normally achieved via the passive action of the hard palate and active contraction of the velar and pharyngeal constrictor muscles, which can separate the nasopharynx from communication with the alimentary tract. The functional importance of this mechanism is demonstrated in cases of cleft palate infants who exhibit insufficient separation of the oral and nasal cavities, thus rendering normal suckling difficult.[24,107]

Despite the presence of choanal crests and a secondary palate among therodonts (a group of early mammals), the choanae are ventrally oriented and the pterygoid plates do not appear to border the choanae laterally. It is not until the Triassic period among early anomodont mammals such as the dicynodonts that truly posteriorly oriented choanae are observable. In *Kombuisia*, the choanae take on an elongated, funnel-shaped appearance with the pterygoid element at the caudal end of a long process of the palatine bone (see figures within Frobisch[46]). The choanae among early anomodonts are primarily bounded by the palatine bones as in the therodonts, although the position of the pterygoid element in the former group may signify a transition to the choanal morphology of extant mammals (Figs. 2.4A and B).

Distinguishing Primates—Microsmatic Versus Macrosmatic

Among mammals, primates are a decidedly derived (i.e. departing from the primitive mammalian condition) order in many aspects of cranial and postcranial anatomy. This may be reflected in the century-old debate on their proper classification and the traits that distinguish them from other archontons such as *Tupaia* (the tree shrew). However, within the order Primates, strepsirhines (i.e. lemurs and lorises) exhibit primitive morphology in aspects of the face and upper respiratory tract related to olfactory acuity, a condition called macrosmia. A major feature distinguishing macrosmatic mammalian species is the percentage of the nasal airway that is covered by olfactory epithelium (OE). In rodents, OE covers a relatively large area of the nasal cavity and confers greater olfactory acuity than among monkeys and humans, who possess



Figs. 2.4A and B: Basal views of a red kangaroo (Macropus rufus) (A) and whitetail deer (Odocoileus virgineanus) (B). Note the location of the choanae is posterior and superior to the hard palate, even among distantly related mammals. This creates a separation of oral and nasal cavities not present among reptiles. *Courtesy*: Joy S. Reidenberg, Icahn School of Medicine at Mount Sinai, New York, NY, USA.

OE only on the superior-most reaches of the nasal cavity walls.[55] In a histological examination of the nasal region of F344 rats (i.e. Fischer laboratory rodents that exhibit good reproductive performance, big litters, and low level of aggression toward their handlers) Gross et al.[54] found OE covering about 50% of their nasal cavity. In contrast, Sorokin[125] found that neuropeithelium covered 500 mm^2 in the human nasal cavity, comprising only 3% of its total surface area. Primates, such as the haplorhines (tarsiers, monkeys, apes, and humans), lack these specializations and are thus considered microsmatic. This division has long been discussed in relation to morphological variation in the primate nose.[18,19,20,120,132] Although there is currently no reliable histological criterion for distinguishing macrosmatic primates from microsmatic ones,[119,121] certain soft tissue and skeletal features of the nasal cavity tend to distinguish these two groups.

Morphologically, macrosmats often possess a rhinarium (i.e. wet nose), a patent nasopalatine duct serving as the entrance to the vomeronasal organ, greater cover of the lateral nasal wall by OE, and a greater number of ethmoturbinals that are vertically arrayed and separated from respiratory air flow by a posterior transverse lamina or lamina transversalis posterior,[20,120] otherwise known as the "schlussplatte" of Zuckerkandl.[143] At the end of this recess lies the vertically oriented cribriform plate. A "nasopharyngeal duct"[123] is created in the space between the posterior transverse lamina and the hard palate, which ends in a vertically reduced (compared with haplorhines) choanal opening. The medial pterygoid plates usually take on an elongated, funnel-shaped appearance as in other nonprimate mammals, which may be a structural consequence of a long, narrow rostrum, and nasopharyngeal duct. These features are shared among most placental mammals and suggest that the earliest representatives of the order Primates exhibited skeletal traits related to the enhancement of olfactory acuity, which are absent among most haplorrhines. However, some haplorhines have been shown to exhibit a high degree of olfactory acuity, necessitating caution when inferring sensorial abilities from gross anatomy.[18,120]

Relative to most generally macrosmatic strepsirhines, microsmatic haplorhines are characterized by a dry external nose covered in skin, an anteroposteriorly shorter hard palate and nasal cavity, a reduced lamina transversalis posterior, a weakly defined or absent olfactory recess, fewer ethmoturbinals (usually two), reduction of the nasoturbinal (the agger nasi of humans), and choanal apertures not bounded anteriorly by a nasopharyngeal duct.[120] Accompanying relative foreshortening of the rostrum and nasal cavity, the medial pterygoid plates reach laterally at a relatively obtuse angle with the posterior hard palate. The choanae take on a tall, narrow appearance and are variably angled anteroinferiorly.

Accompanying these traits is orbital convergence, frontation, and retraction of the nasal cavity under the forebrain, which characterizes anthropoids relative to other primates (discounting the highly specialized orbital morphology of *Tarsius*). Ross and Ravosa[110] argue that orbital convergence among haplorhines renders facial, nasal, orbital, and anterior cerebral morphology part of a single functional unit so that, when any of these structures undergoes morphologic change, it influences basicranial flexion to a greater degree than among the strepsirhines. They measured internal basicranial flexion (angle made at the intersection of the lines connecting the planum sphenoideum with the occipital clivus) from lateral plain-film radiographs of a diverse sample of nonhuman haplorhine and strepsirhine primate crania. It was found that, among haplorhines, basicranial flexion was positively and significantly ($p < 0.05$) correlated with angle of facial kyphosis (the angle made between the intersection of the lines connecting the palatal plane and the occipital clivus) and orbital axis orientation (angle made at the intersection of lines passing through the midpoint of the orbital cavity and the occipital clivus). It was also shown to be negatively correlated with encephalization (the cube root of endocranial volume scaled over the length of the basicranial axis). Thus, a pattern emerges in which the anthropoids exhibit a reduction of conchal complexity and the recessus olfactorius alongside changes in brain size, orbital orientation, basicranial flexion, and facial orientation from their more primitive ancestors. The nasal cavity may also be seen as one of several cranial functional units, which may exhibit integration with other such units.

Differences Among Anthropoids

The skeletally microsmic haplorhines are conventionally divided into platyrrhines (New World monkeys) and catarrhines (Old World monkeys, apes, and humans) based, in part, on nasal morphology. The former group may be characterized by widely separated, anteriorly facing nares, whereas the latter possess closely approximated, inferiorly directed nares. The fetal growth of the external nose has been studied by Maier[78] who traces this difference to morphology of the cupulae nasi, or the cartilage-lined, anterior-most extent of the nasal capsule. Platyrrhines express primitively broad nasal cupulae during fetal growth, which result in the widely separated, anteriorly oriented nares observable in postnatal life. Catarrhines, however, exhibit narrow nasal cupulae as fetuses, eventually resulting in narrow, inferiorly facing nares.[78]

Differences between the platyrrhines and catarrhines may also be found in the internal nasal cavity. The former have a more strongly expressed olfactory recess and a better expressed (albeit reduced from the strepsirhine condition) vomeronasal organ.[61,80,122] They also retain primitively (relative to catarrhines) well-expressed marginoturbinals and atrioturbinals. As among the more primitive insectivores, the marginoturbinal of strepsirhines begins at the nasal roof and communicates between the piriform aperture margin and maxilloturbinal via the atrioturbinal. These were described by Maier[78] as anchoring a muscle that attaches it to a posterior (cartilaginous) alar process, ultimately dividing inspiratory airflow at the nasal cavity entrance between a superior olfactory area and an inferior, strictly respiratory area. Among Old World monkeys, the marginoturbinal is not in contact with the maxilloturbinal but rather appears as a separate turbinal bone. Hominoids (i.e. apes and humans) appear to exhibit a remnant of a marginoturbinal during fetal life, which may persist as a weakly expressed protrusion into adulthood. Maier[80] argues that the possession of well-expressed atrioturbinals and marginoturbinals during fetal life followed by loss or reduction in adulthood is a defining trait of catarrhines.

Hominoids (apes and humans) are distinct from most Old World monkeys in the orientation of the ethmoturbinals, which are horizontally arrayed rather than the vertical orientation characterizing most other primates.[80] This may be related to reduction in prognathism and a trend in shifting the facial skeleton farther under the forebrain. Indeed, the superior-most extent of the pre-maxillary-maxillary suture is located at the distal-most boundary of the nasal bone or at the piriform aperture rim among hominoids, whereas Old World monkeys exhibit a contact point more superiorly by the frontal bone articulation or midway on the lateral edge of the nasal bone.[102] The hominoid configuration suggests a reduction in the premaxilla and overall facial length, which is observable even among the earliest fossil apes who still exhibited primitive, monkey-like postcranial skeletal traits.[102] Horizontal orientation of the ethmoturbinals may thus accompany a large-scale change in nasal cavity architecture and airflow dynamics.

Unlike most other anthropoid taxa, nearly all Old World monkeys lack any true paranasal sinuses, instead exhibiting recesses that have not undergone secondary pneumatization by nasal epithelia (sensu[19,80]). The one exception is the genus *Macaca*, which has been argued to have independently evolved the expression of maxillary sinuses.[103] Most hominoids (humans and apes) and platyrrhines do exhibit true paranasal sinuses with at least a maxillary sinus.[19,21,89,111] However, Rossie[111] argues that some platyrrhines exhibit sinuses that, based on apomorphic (unique to that species) developmental patterns, are not homologous (that is, not inherited from a common ancestor).

Although the processes and patterns of hominoid skull pneumatization are not fully understood, the presence and extent to which these air-containing spaces invade the bony elements of the cranium has been an important consideration of hominoid phylogenetic analysis. As is well known, modern humans exhibit all four paranasal sinuses: the maxillary, frontal, sphenoid, and ethmoid (Figs. 2.5 and 2.6). It should be noted that the human ethmoid sinus system is composed of 2 to 12 distinct air

Fig. 2.5: Frontal view of a 3-D computed tomography reconstruction of an adult male human (author SM) showing the topographical relationship between frontal sinus (seen in green) and maxillary sinus (seen in purple) to the nasal cavity proper (seen in red); note the characteristic asymmetry in frontal sinus morphology. The maxillary sinus is the largest of the four paranasal sinuses exhibited by humans and dominates the midfacial architectural space. Sphenoid sinuses are not visible in this coronal plane.

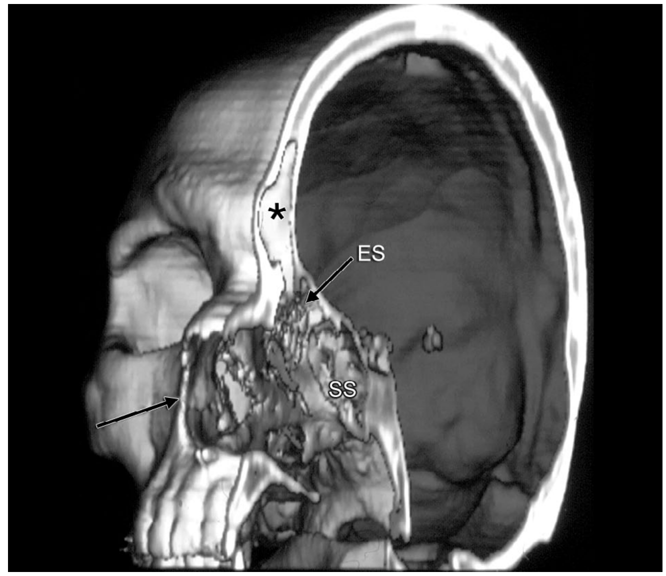


Fig. 2.6: A 3-D computed tomography reconstruction of the same individual in Figure 2.5 shown in oblique parasagittal view where ethmoid (ES) and sphenoid air sinuses (SS) can be viewed. The black asterisk indicates the frontal sinus and the black arrow is pointing to the piriform aperture rim where, just posterior to it, is the site of attachment of the inferior turbinate.

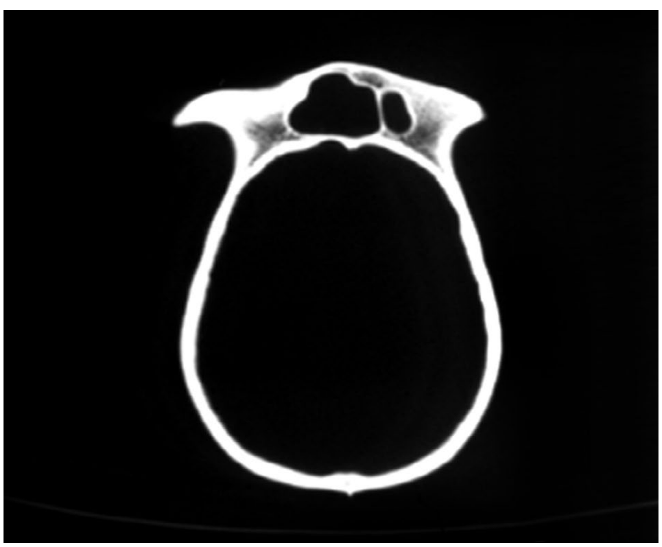


Fig. 2.7: An axial computed tomography scan showing the asymmetric frontal sinuses of the chimpanzee. This individual exhibits an enlarged right frontal sinus.

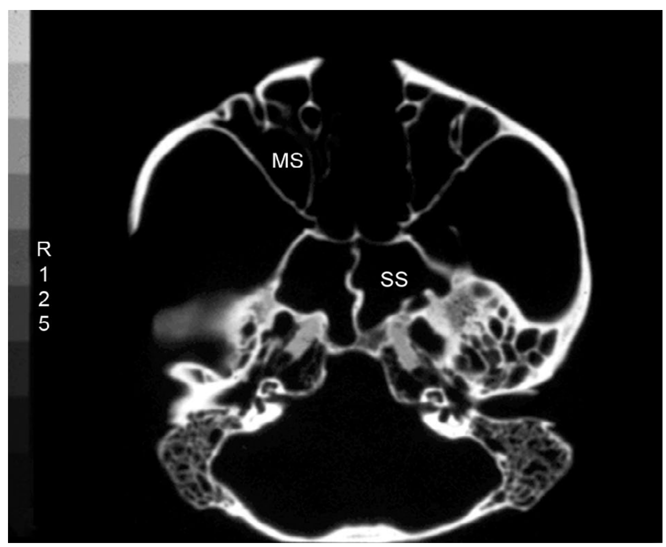


Fig. 2.8: An axial computed tomography scan of a chimpanzee cranium demonstrating distinct maxillary sinuses (MS) and sphenoid sinuses (SS).

cells on each side, making it somewhat distinct from the other paranasal sinuses.[82,83,86] A CT examination of living ape skulls selected from the Division of Anthropology of the American Museum of Natural History found a maxillary sinus present in all three genera of chimp, gorilla, and orangutan (*see* Figs. 2.7 to 2.10). These findings corroborate previous reports on ape sinonasal anatomy.[21,68] The ethmoid sinus system is well developed among

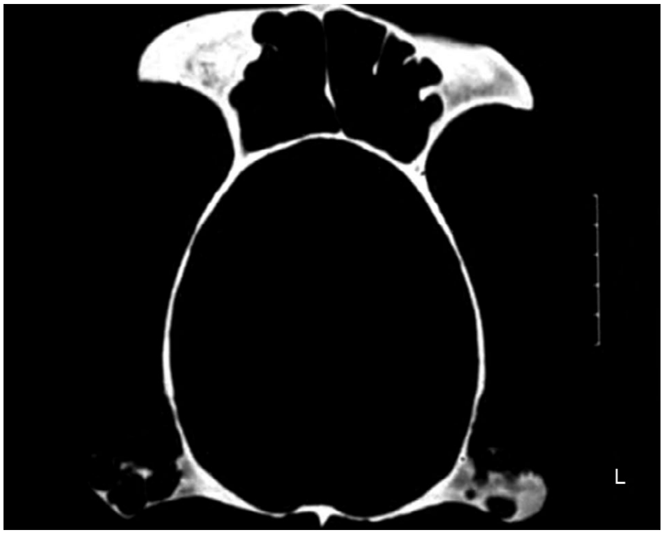


Fig. 2.9: An axial computed tomography scan through a gorilla cranium revealing enlarged, septated frontal sinuses.

Fig. 2.10: An axial computed tomography scan of a gorilla cranium. Note the distinct, two-celled ethmoid sinus (ES) and the extensive sphenoid sinus (SS), which may be seen invading the greater wing of the sphenoid (asterisk).

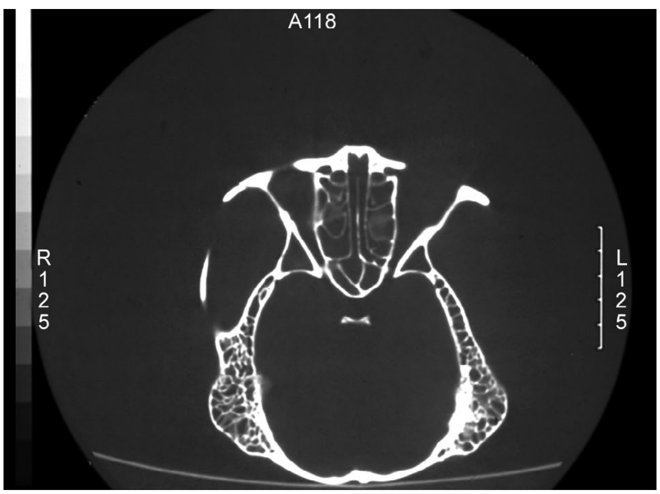


Fig. 2.11: An axial computed tomography scan of a chimpanzee cranium. Note the extensive system of ethmoid air cells. This anatomic pattern is similar to the human condition.

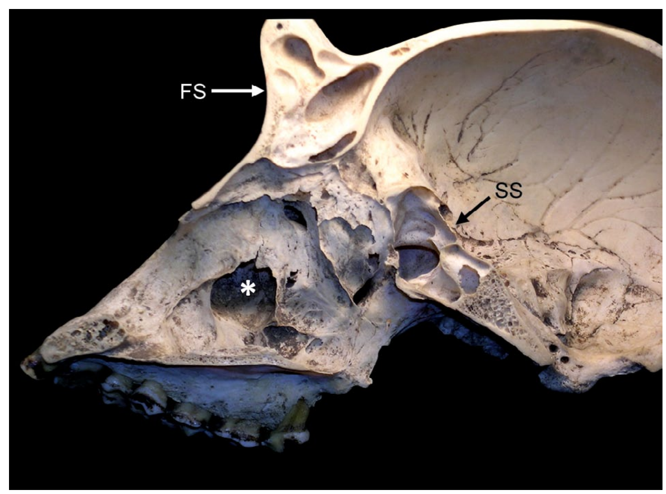
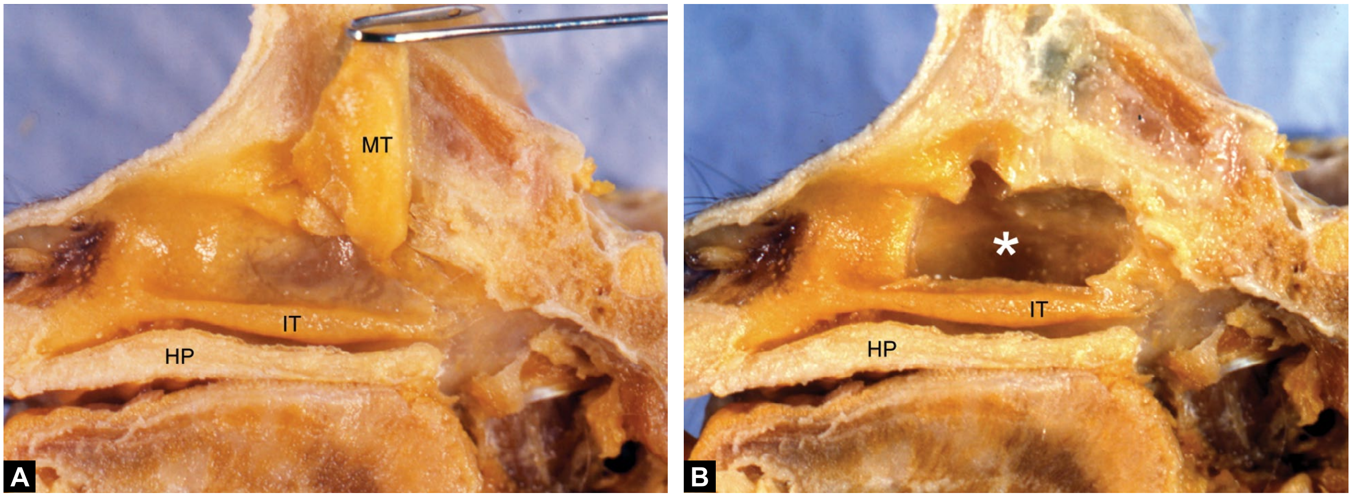


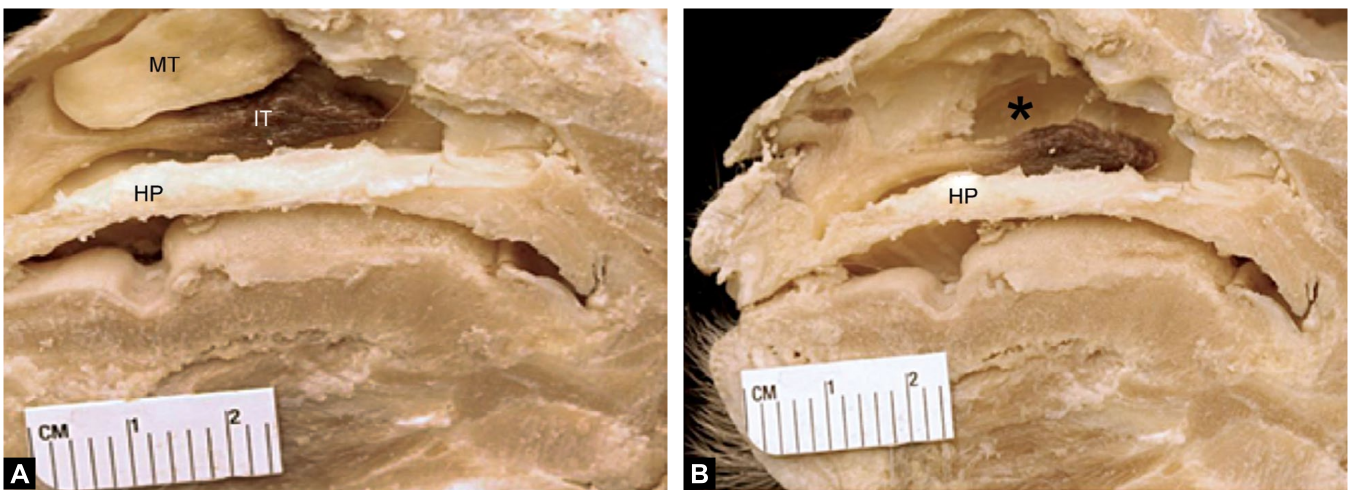
Fig. 2.12: A midsagittally sectioned gorilla cranium. Note the extensive pneumatization of the maxillary sinus (asterisk), frontal sinus (FS), and sphenoid sinus (SS).

both gorillas and chimpanzees, with 1–2 and 4–5 air cells in adults, respectively (Fig. 2.11). Frontal and sphenoid sinuses are confirmed to be restricted to the living African great apes (Fig. 2.12). Sphenoidal development is particularly extensive within the gorilla, involving the pterygoid plates and even the greater wing of the sphenoid (*see* Fig. 2.10).

Given the presence of only a maxillary sinus in *Macaca* (the one genus representative of the Old World Monkeys), it appears that development of any other sinus cavity is a derived character state among catarrhines – the group that includes humans, apes, and monkeys (Figs. 2.13 to 2.15). Orangutans are conservative morphologically but exhibit a dominantly enlarged MS that can expand to other cranial bony elements. The diverticula of the maxillary sinus (i.e. the mucosal evaginations, which are the developmental precursors of the paranasal sinuses) can greatly invade the frontal and/or sphenoid bones to create the appearance of frontal and sphenoid sinuses.[114] However, due to the origins of these spaces as extensions of the maxillary sinus,



Figs. 2.13A and B: (A) Right lateral view of nasal cavity wall of adult male *Macaca fascicularis* showing hard palate (HP), inferior turbinate (IT), and middle turbinate (MT). (B) The middle turbinate has been removed revealing the internal morphology of the maxillary sinus (white asterisk is within the sinus). Note the margin of the sinus cavity has been cut away.



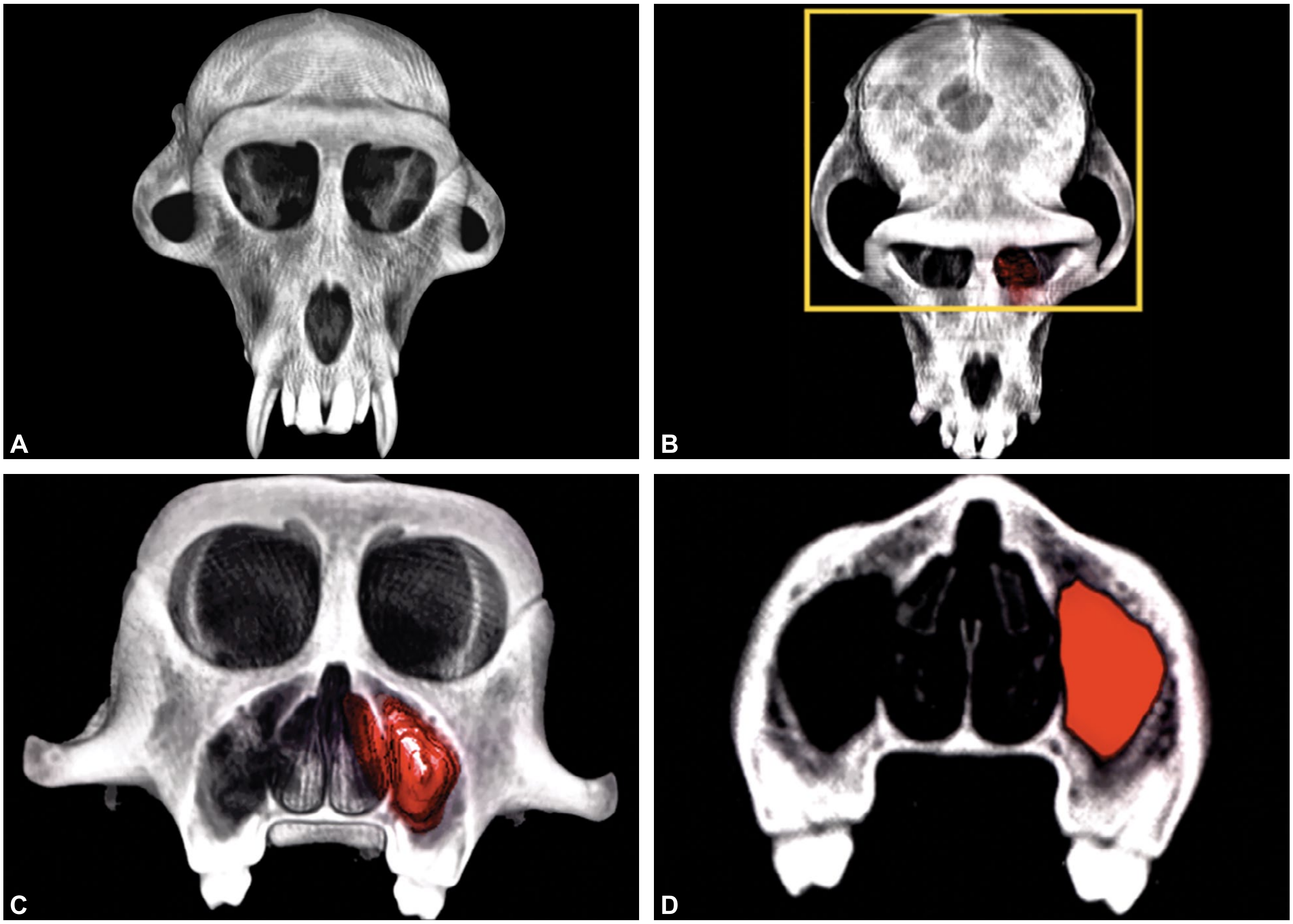
Figs. 2.14A and B: (A) Right lateral view of nasal cavity wall of adult male *Macaca mulatta* showing hard palate (HP), inferior turbinate (IT), and middle turbinate (MT). (B) The maxillary sinus (black asterisk) appears smaller than in *M. fascicularis*.

they may not be identified as distinct sinuses according to Cave's[19] definition (Figs. 2.16 and 2.17).

Among the African apes, distinctions may be made between the nasal morphology of chimpanzees and gorillas, there being a number of derived (i.e. evolutionarily novel) traits among the former. The nasal conchal configurations and larger number of ethmoid air cells of chimpanzees appear more human-like (Figs. 2.18A and B). These may constitute synapomorphies (shared derived traits) of the chimpanzee-human lineage, corroborating the close genetic relationship found between these groups. Furthermore, the presence of these synapomorphies allows for the reconstruction of nasal morphology within the most recent common ancestor of humans and chimpanzees, a valuable tool for assessing the evolutionary importance of traits observed among fossil humans.

EVOLUTION OF NASAL COMPLEX FROM EARLY HUMAN ANCESTORS TO *HOMO ERECTUS*

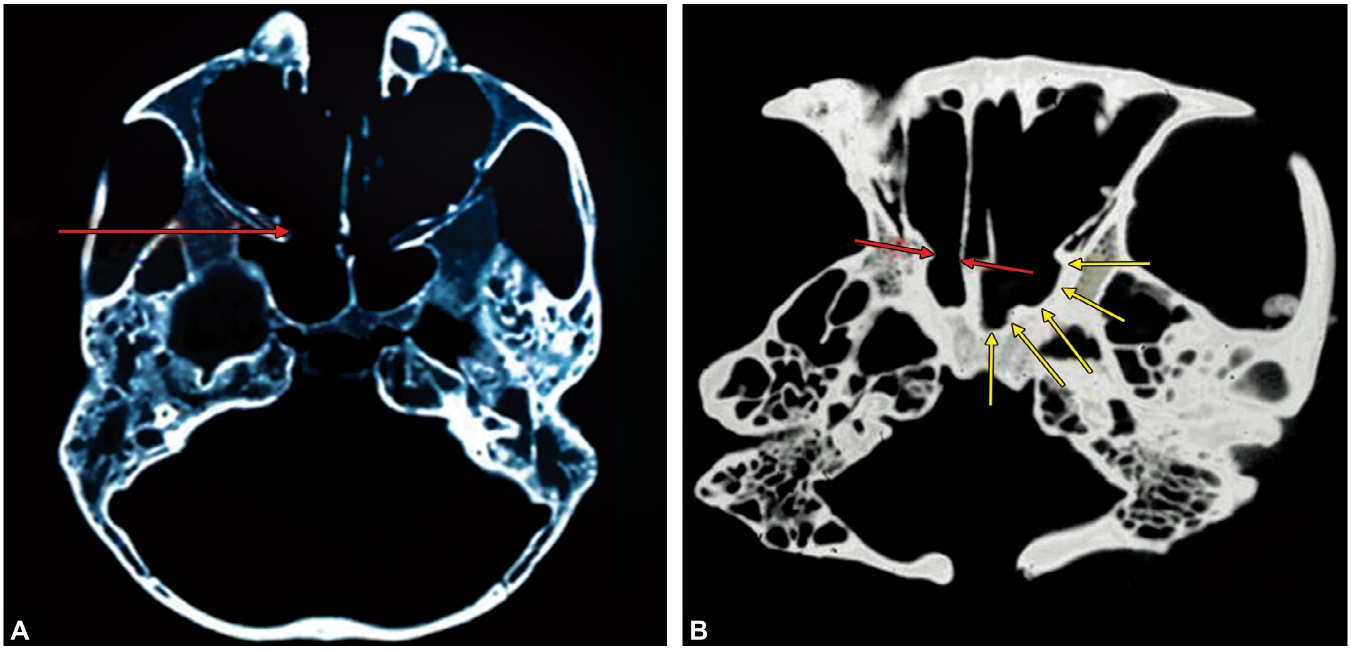
The osseous boundaries of the nasal cavity have an extremely long evolutionary history. However, aspects of the piriform aperture, external nose, and nasal vestibule have



Figs. 2.15A to D: A composite plate showing: (A) a 3-D computed tomography reconstructed skull of an adult male *Macaca fascicularis* viewed anteriorly and (B) a reference coronal slice transection line (seen in yellow) viewed superiorly. The coronal slice can be reconstructed 3-D or presented in 2-D (D). Such reconstructions allow quantitative and qualitative sinus assessments.

undergone relatively recent evolutionary changes so that the anterior nasal complex of humans differs markedly from that of the great apes as well as early fossil humans. For example, otolaryngologists would routinely see an anterior nasal spine in their human patients but such a structure is absent within the apes. Indeed, many aspects of the human skeleton can be reliably traced to between 2.5 and 1.8 million years before present (m.a.), whereas our most recent common ancestor with the chimpanzee, our closest living relative, likely existed over 6 m.a. with some potential interbreeding still occurring after this initial speciation event.[100] As can be seen from aspects of the postcranial skeleton, our ancestors appeared to have locomoted equally among terrestrial and arboreal substrates (*see* the classic study of *Australopithecus afarensis* by Stern and Susman[126]) until the appearance of the oldest member of our genus, *Homo habilis*, approximately 2.6 m.a.,[117] when the earliest stone tools were produced for butchering animal carcasses and (at least in some locations) utilizing more open environments.[38,76,101]

The facial skeleton also remained ape-like during this nearly four million year interval with only moderate reduction in hard palate length and canine dentition. The piriform aperture and surrounding nasal skeleton also retained primitive characteristics. Rather than exhibiting an anterior nasal spine, a nasoalveolar clivus was instead present so that the nasal floor sloped into the alveolar process of the premaxilla. When considered alongside flat nasal bones, location of the internasal suture in the same coronal plane as the nasomaxillary suture, and coronal orientation of the lateral piriform aperture margin, these early "australopith-grade" human relatives may not have



Figs. 2.16A and B: An axial scan of a subadult orangutan (A) showing what appears to be a sphenoid sinus but is actually the maxillary sinus invading the sphenoid bone. An adult orangutan (B) exhibiting clearly patent communication between the left maxillary sinus and the evacuated sphenoid bone (in yellow arrows); red arrows illustrating the path of the right maxillary sinus in its intrasphenoidal encroachment.

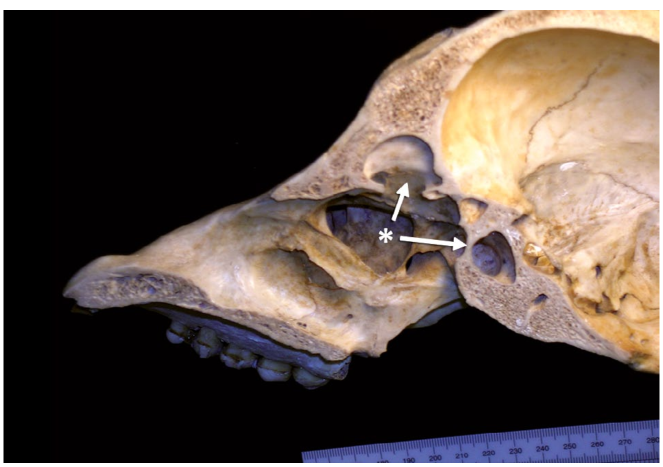
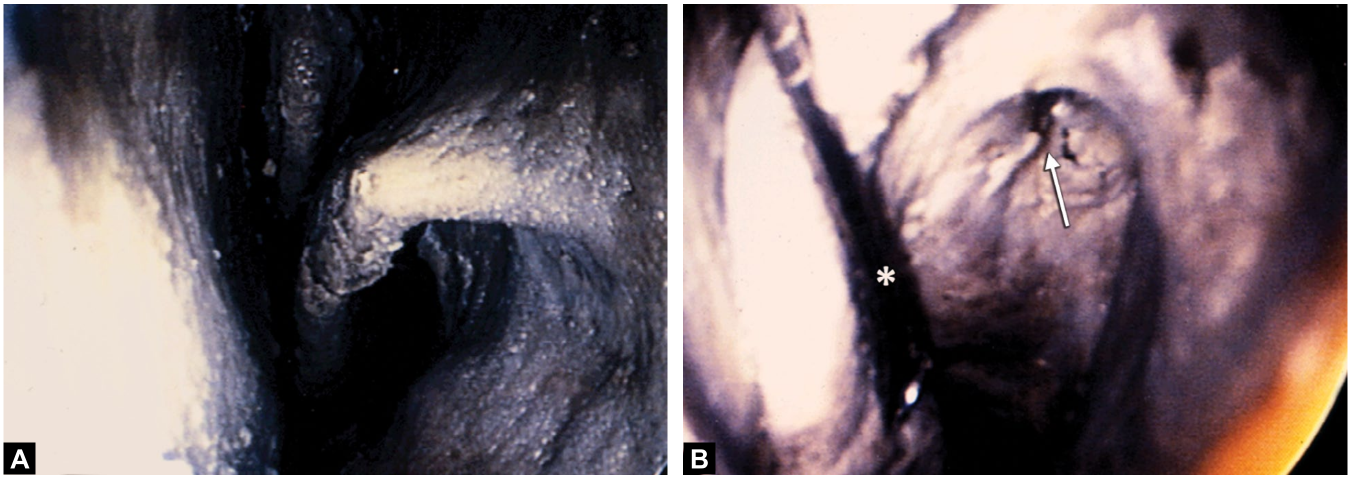


Fig. 2.17: A midsagittally sectioned orangutan cranium. Note that the maxillary sinus (asterisk) is in communication with both the frontal and sphenoid bones (illustrated by arrows) to create the appearance of separate frontal and sphenoid sinuses thus nullifying their status as “true” paranasal sinuses.
Courtesy: Anthony S. Pagano.

had external noses as modern humans but rather the appearance of the great apes, who lack a nasal vestibule.[45] Many also exhibit an apelike piriform aperture outline,[31] which is short and broad relative to the modern human condition.[113]

Arguably, the first fully committed biped in our evolutionary history was *Homo erectus*. This species exhibited a human-like postcranial skeleton and was the first to leave Africa and eventually colonize Asia. Its fossils may be found in locations as varied as South Africa, Kenya, Israel, Georgia, China, and Indonesia. *Homo erectus* likely operated in conditions far more arid than its predecessors, requiring more human-like patterns of nasal projection. These include elevation of the internasal suture above the plane of the nasomaxillary sutures, eversion of the lateral piriform aperture margins, and a more acute nasoalveolar angle despite the absence of an anterior nasal spine.[45]

Relatively few studies have focused on cranial pneumatization among *Homo erectus*. Márquez et al.[87] described an Asian *Homo erectus* calvaria from Indonesia’s Sambungmacan region (designated Sm 3; Fig. 2.19), dated around 1.0 m.a.[87] Unfortunately, the ethmoid, sphenoid, and maxillary bones were missing due to poor preservation. However, the frontal bone remained intact and was assessed for pneumatization. This analysis was inconclusive at the time of its publication as the frontal sinus was filled with rock matrix, obfuscating its boundaries. It was not until the return of Sm 3 to Indonesia that the mineral infill was removed. What remained was



Figs. 2.18A and B: Endoscopic imaging of a chimpanzee nasal cavity. (A) The inferior turbinate is visible in situ. (B) When it is protracted away from the nasal wall (white asterisk on the Freer elevator instrument), the ostium of the nasolacrimal duct becomes visible (black arrow).

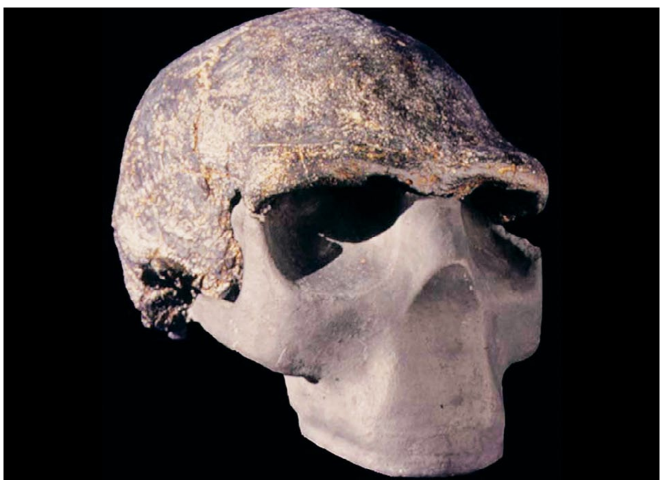


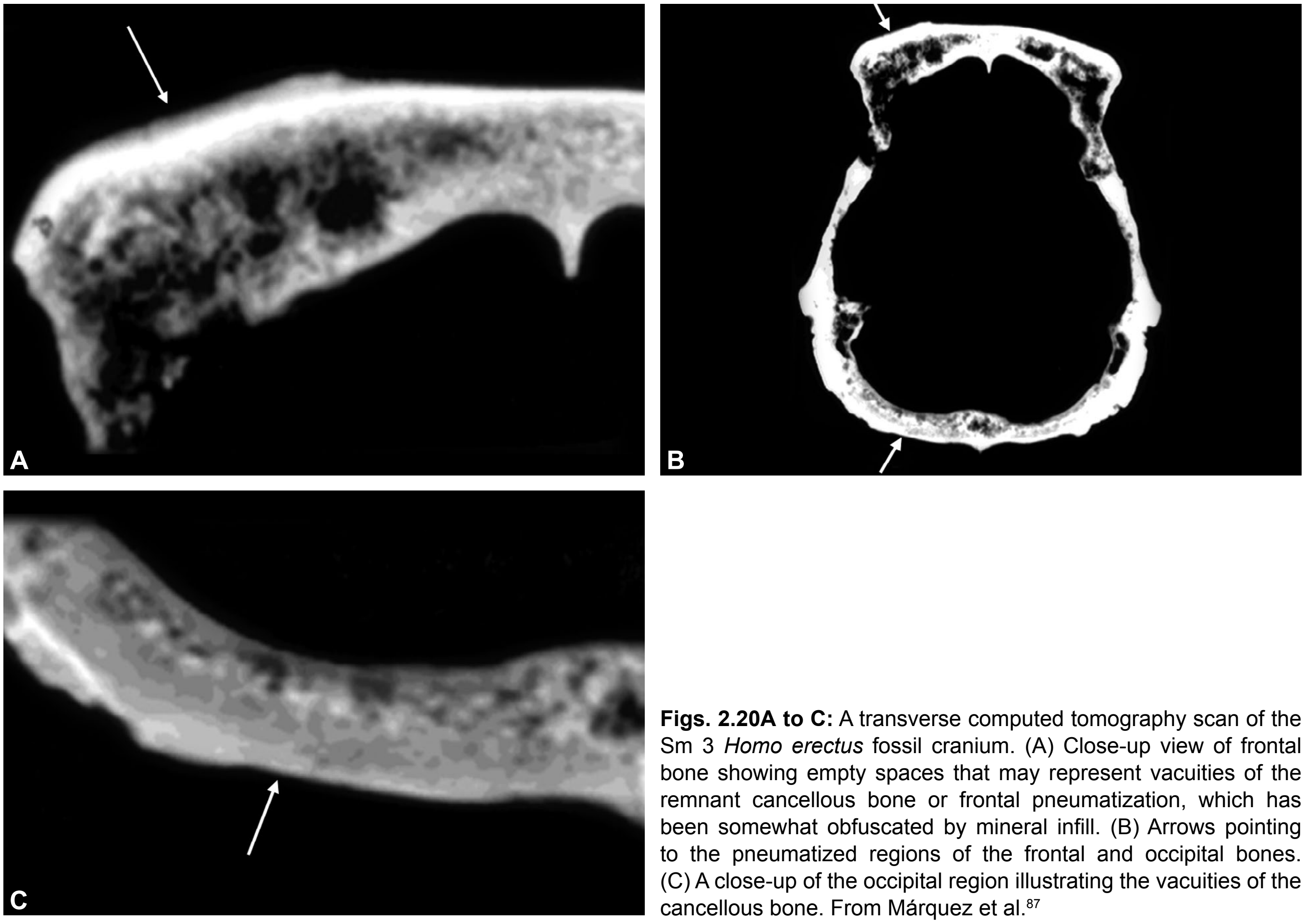
Fig. 2.19: A one-third frontal view of the Sm 3 *Homo erectus* calvarium from Sanbungmacan, Indonesia. Note that the bar-like supraorbital torus (brow ridge) is well developed and protrudes far anteriorly to the short, sloping frontal bone.
Courtesy: Samuel Márquez, SUNY Downstate Medical Center, Brooklyn, NY, USA.

a marked cavitation area indicating the frontal sinus. Despite exhibiting massive supraorbital tori (bony brow ridges), these structures were not invaded by the frontal sinus, which was smaller than expected (Figs. 2.20A to C).

The Evolutionary Relationship between the Nasal Complex and Climate

When anatomically modern humans migrated out of Africa approximately 50,000 years ago, they were able to populate arctic climates despite having evolved in tropical African ecogeographic conditions. Today, humans are able to shift from one extreme environment to another over relatively short periods of time without injuring the upper or lower respiratory systems. Such a useful ability is afforded by the nasal cavity, which equilibrates inspired air with interior body conditions with remarkable efficiency to protect the internal *milieu* of the lung. The nasal cavity apparatus can air condition inspiratory airflow by fully saturating it into water vapor and modify its temperature close to core body temperature, ideal conditions for gas exchange in the alveolae of the lungs. These dual processes are performed in the mucosal and submucosal layers of the nasal cavity walls, respectively.

Humidification of inspiratory air occurs largely via the action of goblet cells in producing mucin, a substance that also protects the epithelia from desiccation and traps particulate matter from inspiratory air flow. Heating of air takes place at the submucosal layer where corpora cavernosa carry venous blood and drain into the pterygoid veinous plexus. The warmth of the venous blood is transmitted through the mucosal layer to the inspiratory airflow. Thus, cool, dry ambient air requires greater contact with nasal epithelia to warm and humidify. Population differences in human nasal morphology have long been studied as adaptations to climatic stresses, in which groups from cold, dry regions exhibit features promoting increased contact between inspiratory air and nasal mucosa. These include increases in nasal surface area and reorientation of the external nasal vestibule to promote greater turbidity as inspiratory airflow is redirected to contact the nasal walls.



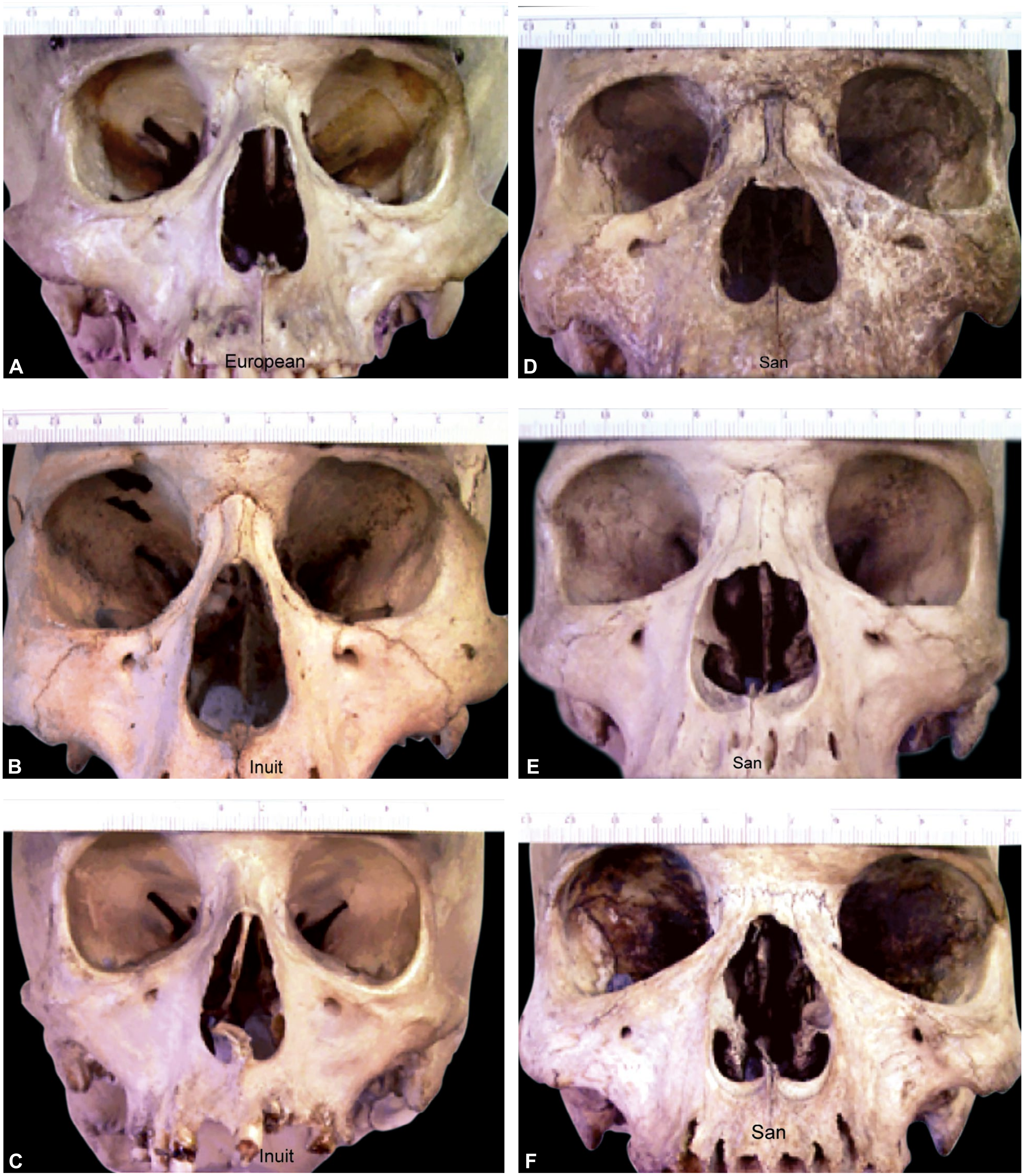
Figs. 2.20A to C: A transverse computed tomography scan of the Sm 3 *Homo erectus* fossil cranium. (A) Close-up view of frontal bone showing empty spaces that may represent vacuities of the remnant cancellous bone or frontal pneumatization, which has been somewhat obfuscated by mineral infill. (B) Arrows pointing to the pneumatized regions of the frontal and occipital bones. (C) A close-up of the occipital region illustrating the vacuities of the cancellous bone. From Márquez et al.[87]

Variation in piriform aperture dimensions has been the most extensively studied aspect of human upper respiratory tract variation. As early as the 18th century, data had been collected on the piriform aperture dimensions of a wide range of human populations. These were often monographs (e.g.[14,130]) that offered descriptions of varied biological phenomena without offering deeper analyses of specific hypotheses or their physiologic/evolutionary implications. Specifically, nasal index (defined as [maximum nasal breadth/nasal height] × 100) has been widely used in anthropology for distinguishing human "races" since the 18th century (e.g.[14,12,131]).

It was not until the study of Hrdlicka's[60] on the cranial morphology of the Inuit that a relationship was considered between piriform aperture shape and climate. In his publication on the craniology of the Eskimo, he suggested that the narrow nasal aperture of this population was directly related to the effects of the Arctic cold.[60] Although Hrdlicka did not discuss the functional significance of this narrowing, a comparison between a group of Eskimo and West Africans clearly illustrates piriform breadth differences (Figs. 2.21A to F).

Osteological changes of the nasal region as seen in Figure 2.5 may reflect an adaptation that serves as a protective mechanism for the respiratory mucosa. Many later studies focused on the functional relationship between nasal morphology and climate (e.g.[34,128,135,137]). For example, Endler[40] cited the action of natural selection, as there exists an association between the variation in a single trait, or set of traits, and specific environments. Thomson and Buxton[128] were among the earliest workers to specifically study the relationship between the nasal index and climatic factors among geographically diverse populations.

Weiner[135] suggested that the critical variable determining nasal shape (i.e. the nasal index) was not temperature/relative humidity but rather absolute humidity. According to Weiner,[135] correlations among the nasal index



Figs. 2.21A to F: 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. VL/1466), (B) Inuit (Cat. No. 99/6690), (C) Inuit (Cat. No. 193), (D) San (Cat. No. 99/8449), (E) San (Cat. No. 99/9976), (F) San (Cat. No. 9978). Specimens courtesy of Division of Anthropology, American Museum of Natural History.

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 critical operative factor in determining nose form. Later studies[6,29,44] concluded that differences among populations from cold, dry and warm, wet climates in the nasal index (nasal width/height ×100) were related to an increased area of nasal mucosa for warming and moisturizing airflow. However, Wolpoff[137] questioned the use of piriform aperture height as it did not correspond to internal nasal cavity height. He instead argued that external nasal width was a better indicator of climatic adaptation as it bears a closer relationship with nasal cavity width among Inuits and Aboriginal Australians, estimated by hard palate width. Carey and Steegman[17] later proposed that nasal projection is related to humidity using data from Woo and Morant.[138]

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 and foreshortening of the splanchnocranium caused by brain expansion.[75] Bergland[7] 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 nares (choanae), even though the nasal cavity communicates with the nasopharynx via this portal. Its potential importance as a functional determinant warrants investigation of this region.

Glanville[50] has suggested that there is a direct relationship between nasal shape, prognathism, and the shape of the maxillary dental arch. He found a strong correlation between nasal height and the length of the cranial base and also between nasal breadth and the distance that separates the upper canines. Such relationships can lead to inferences about functional relationships as Laitman and others.[70,71,72,73,74] have suggested 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, comparing these results with nasal complex dimensions could potentially uncover functional relationships between the accessory cavities of the nose and climate.

Most recently, Noback et al.[90] applied geometric morphometrics to the study of nasal morphology. They used 21 externally accessible landmarks to estimate the boundaries of the nasal cavity. Specifically, the ethmoid foramina were used as a proxy for the nasal cavity roof and the piriform aperture and choanal margins were, respectively, considered two areas in which steep dimensional changes could promote greater turbidity in inspiratory air. They also collected landmark coordinate data on the basicranium to model the nasopharyngeal boundaries, which they consider a part of the nasal cavity given its predominantly respiratory function.[129] A geographically diverse group of pooled sex crania representing populations from cold and wet, cold and dry, warm and wet, and warm and dry environments of known temperature and vapor pressure (i.e. humidity) was used. They found that, when expressed as a function of temperature, the nasal cavity grows longer at the piriform aperture and narrower between the left and right ethmoid foramina. Anterior displacement at the anterior ethmoid foramina suggests that elongation occurs at the middle of the nasal cavity roof as well. They also express a heightened and elongated nasopharynx, paradoxically suggesting a smoother transition from cavum nasi with less postnasal turbidity. However, when expressed as a function of vapor pressure, the nasal cavity appears vertically lower with posteriorly located ethmoid foramina to create a stronger "tapering" from posterior to anterior. There is also a more abrupt difference between choanal height and posterior nasal cavum height measured at the posterior ethmoid foramen. These results suggest that the overall nasal cavity dimensions may be more closely related to temperature while nasopharyngeal dimensions are influenced more by vapor pressure.

Few studies have directly examined aspects of the internal nasal cavity as potential sites for climatic adaptation. Charles[23] analyzed internal nasal morphology among a group of African and European American crania and found that the latter group exhibited a longer nasal cavity, but there was little difference in the height or width of the internal nasal fossa. However, Franciscus[42] collected many of the same measures on a diverse group of Old World crania spanning from Northern Europe to Sub-Saharan Africa and concluded that nasal fossa breadth, especially at its superior-most extent, was narrower among Supra-Saharan populations of both modern human and archaic *Homo*. Yokley and Franciscus[141] later combined measures from both of these studies to perform a principal components analysis. On both the first and second principal components vectors, the data indicated a separation of Supra- and Sub-Saharan groups (including African and European Americans) where the former is characterized