11

Evolution of the Mammalian Nose

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Introduction

Endothermy requires an integrated set of morphological and physiological features (Kemp 2006) that evolved independently in birds and mammals (Ruben 1996). Morphologic evidence for the evolution of endothermy has partially been based upon the presence of the intranarial respiratory turbinals or conchae that act as temporal countercurrent exchange sites (Bennett and Ruben 1986). Since endotherms have a higher respiratory rate than ectotherms, evolution of the temporal countercurrent exchange mechanism allowed them to control the temperature of expired air when at rest and during mild exercise, and afforded them significant savings of heat and water (Owerkowicz et al., this volume). Birds achieved this by evolving cartilaginous nasal conchae (Bang 1961; Geist 2000), while mammals developed ossified maxillary turbinals (Macrini 2012; Rowe et al. 2005). Both mechanisms warm and humidify inhaled air, and cool exhaled air (Schmidt-Nielsen 1981), and both require a firm temporary seal between the nasal cavity and the trachea, so that inspired and expired air passes through the nose and bypasses the oral

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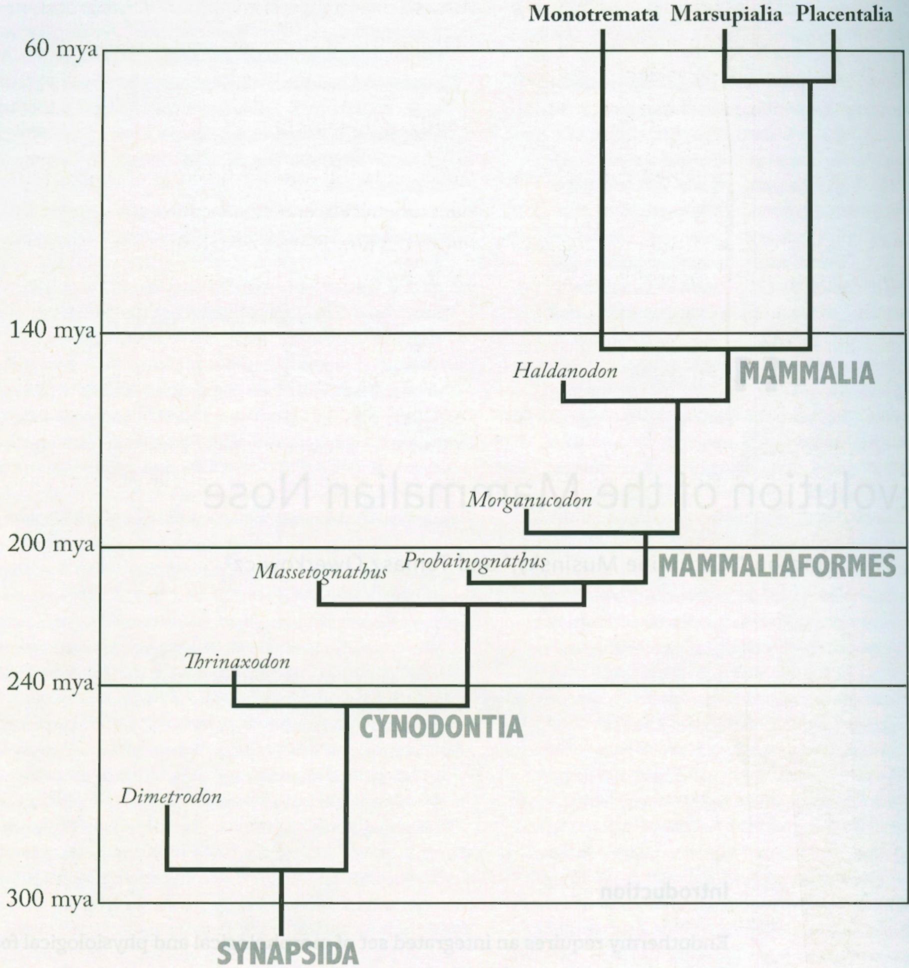

FIG. 11.1 Relationships and timeline of the specimens discussed in this chapter.

cavity. Conchae and maxilloturbinals also provide sites for evaporative cooling during exercise and high ambient temperatures (Taylor 1977).

Evolution of these countercurrent exchange sites was likely gradual and probably involved considerable reorganization of the skull skeleton. In this chapter, we focus on the evolutionary changes to the synapsid skull, which may have housed the incipient respiratory turbinates.

Within the nonmammalian therapsids (mammal-like reptiles) spanning more than 100 million years from the mid-Permian to the Early Jurassic (fig. 11.1) (Kemp 1982; Rowe and Gauthier 1992), some of the progressive changes leading to the mammalian skull—for example, the three-boned middle ear, precise dental occlusion, determinate growth, and an enlarged braincase—are well documented. The evolution of the mammalian nose, however, remains relatively uncertain. Hillenius (1992, 1994), Hillenius and Ruben (2004), Ruben (1996), and Ruben et al. (2012) have pointed to ridges found on the inner surface of the nasal and maxillary bones to suggest that ossified turbinates were present in nonmammalian therapsids. On the basis of these characters—the purported maxillary ridges, the presence of a bony secondary palate, and an enlarged nasal respiratory chamber—the authors concluded that several groups of nonmammalian therapsids were either partially or fully endothermic.

In extant mammals the embryonic cartilaginous nasal capsule ossifies to form the mesethmoid and ethmoid bones. The latter include ossified maxilloturbinals. But such ossifications have never been found in the nasal region of nonmammalian synapsids, suggesting that the nasal capsule remained cartilaginous throughout life.

To understand the structure of the cartilaginous nasal capsule of nonmammalian synapsids, it is necessary to determine the shape of the space enclosed by the membrane bones that would have surrounded it. MicroCT scans contribute new insights to the findings of Hillenius (1994), Ruben (1996), and Ruben et al. (2012). Based on such scans, we offer suggestions as to the structure and function of some cartilaginous nasal capsules of Triassic nonmammalian cynodonts and Jurassic mammaliaforms, and review important steps in the development of the mammalian nose.

Reptiles: Squamata

Olfaction is the primary function of the reptilian nose: olfactory nerves enter the posterodorsal region that lies above the flow of air through the nasal capsule. In typical living reptiles (Bellairs and Kamal 1981; Malan 1946; Parsons 1959; Pratt 1948), a cartilaginous nasal cavity opens directly into the oral cavity through primary choanae, or internal nares (fig. 11.2A, B); thus all air breathed through the nose must also pass through the oral cavity. The route of air through the nasal capsule between the nares and the primary choana is short (as indicated by the arrow in fig. 11.2C), limiting the space

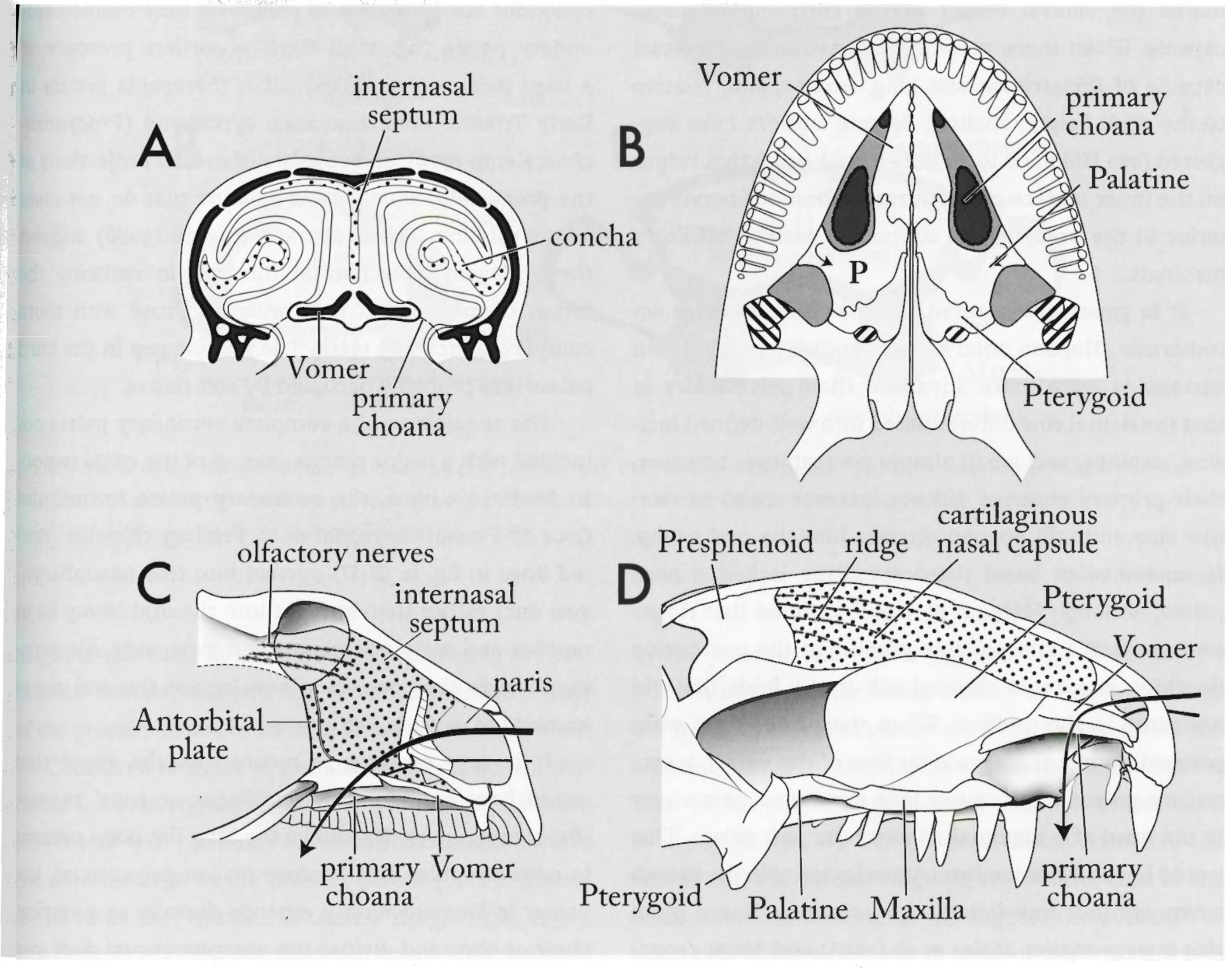

FIG. 11.2 Nasal region of an extant *Amblyrhynchus cristatus* (A–C) and an extinct *Dimetrodon limbatus* (D). A, Transverse section; B, ventral view of the palate; C, sagittal section; D, sagittal section through the nasal region.

for structures that might support respiratory epithelium. A tall, cartilaginous internasal septum between the vomer and the nasal roof separates the two sides of the nasal cavity (fig. 11.2A).

Early Nonmammalian Synapsids

In primitive nonmammalian synapsids, such as the pelycosaur *Dimetrodon* (fig. 11.2D), the nasal capsule remained cartilaginous. As in reptiles, the primary choanae open directly into the oral cavity (Hillenius 1992; Hillenius 1994; Romer and Price 1940), which limits the space available to house structures supporting respiratory epithelium. The posterior extent of a cartilaginous nasal capsule is constrained by the presphenoid bone. The presphenoid is Y-shaped in cross-section, its ventral keel forms an interorbital septum and its expanded dorsal area (Kemp 1980) encloses the olfactory nerves. The dorsal edge of the tall pterygoid bone probably marks the ventral extent of the cartilaginous nasal capsule. Given these volumetric constraints, the nasal capsule of *Dimetrodon* was long, narrow, and, relative to the skull height, shallow. Several authors have suggested (see Hillenius 1992; Ruben et al. 2012) that ridges on the inner surface of the intramembranous bones anterior to the presphenoid supported ossified olfactory turbinals.

It is generally accepted that pelycosaurs were ectothermic (Hopson 2012; Kemp 2006). Therocephalian therapsids were more advanced than pelycosaurs in that the dental row differentiated into well-defined incisors, canines, and small simple postcanines; however, their primary choanae did not increase much in relative size and still opened directly into the oral cavity. Nonmammalian basal therocephalians lacked a hard palate, although Maier et al. (1996) claimed that ridges on the maxilla and palatine parallel to the postcanine dentition supported choanal soft tissue folds that did not meet in the midline. When their free edges were pressed against the ventral surface of the vomer, a secondary palate was created that continued posteriorly in the form of a mammalian muscular soft palate. This would have allowed uninterrupted activity in the mouth cavity without interfering with breathing. Based upon this interpretation, Maier et al. (1996) and Maier (1999) claimed that nonmammalian therocephalians and more advanced nonmammalian therapsids suckled their young, possessed hair, and were endothermic. However, this conclusion invites reexamination because nonmammalian therocephalians had multiple generations of tooth replacement throughout life, rather than the diphyodont dentition of mammals, which correlates with rapid growth and early dependence on maternal milk for nourishment (Hopson 1973).

Nonmammalian Cynodonts

The description of the nasal capsule of nonmammalian cynodonts given here is based upon MicroCT scans of *Massetognathus* and *Probainognathus* the description of the skull of *Thrinaxodon* upon a reconstruction from serial grinding (Fourie 1974); and that of several cynodonts upon manually prepared cynodont skulls (Brink 1955; Estes 1961; Hillenius 1992; Kemp 1980; Sues 1986).

Advanced nonmammalian synapsids, such as the cynodont *Massetognathus*, possess a fully ossified secondary palate (fig. 11.3B–E). The earliest presence of a hard palate in nonmammalian therapsids occurs in Early Triassic nonmammalian cynodonts (*Procynosuchus*; Kemp 1979), and consists of medial projections of the premaxilla, maxilla, and palatine that do not meet in the midline. Thomason and Russell (1986) suggest these played a mechanical function in resisting the forces of mastication that probably arose with more complex postcanine teeth. The median gap in the hard palate was probably occupied by soft tissue.

The acquisition of a complete secondary palate coincided with a major reorganization of the nasal region. In *Massetognathus*, the secondary palate formed the floor of a nasopharyngeal duct. Primary choanae (dotted lines in fig. 11.3B–D) opened into this nasopharyngeal duct rather than straight into the oral cavity as in reptiles and early nonmammalian synapsids. Air passing through the nose could now bypass the oral cavity en route to or from the larynx.

It is now possible to reconstruct the space that would have contained the cartilaginous nasal capsule (fig. 11.4; fig. 11.5A, B). Unlike the long flat bone present in extant reptiles and nonmammalian pelycosaurs, the vomer in *Massetognathus* extends dorsally as a vertical sheet of bone and divides the nasopharyngeal duct into left and right regions (figs. 11.3B, C, 11.5A). The increase in

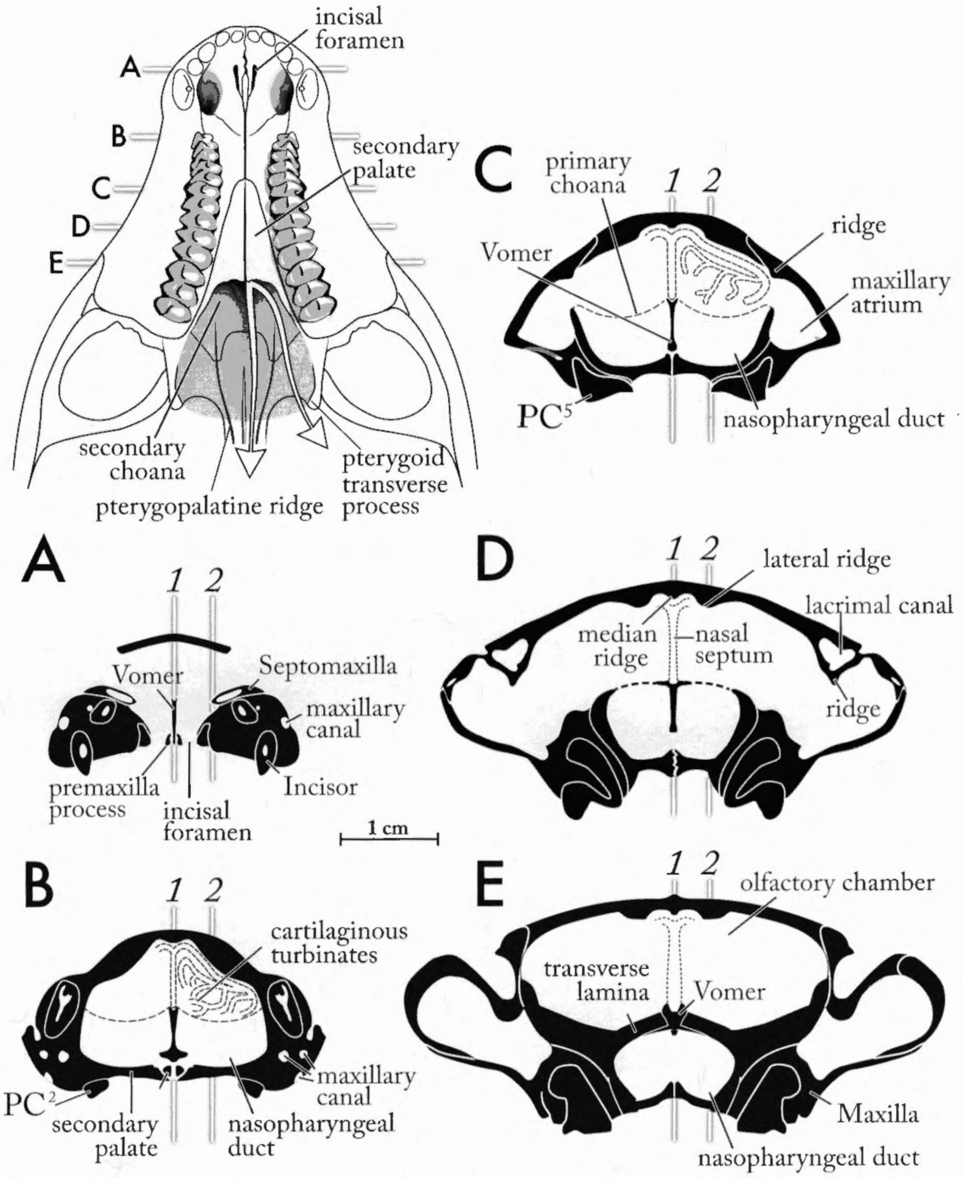

FIG. 11.3 Nasal region of a nonmammalian cynodont (*Massetognathus*). Ventral view of the palate (left) and transverse sections of the nasal cavity (A–E). Capital letters to the left of the palate indicate the position of the transverse sections shown in A–E. The two vertical lines labeled 1 and 2 indicate the planes shown in figure 11.5A and B.

height of this bone appears to have occurred as the premaxilla, maxilla, and palatine extended below the floor of the primary palate to form the hard secondary palate.

Compared to those of primitive nonmammalian therapsids, *Massetognathus* and *Probainognathus* have longer and wider primary choanae that extend back to the anterior edge of the primary palate (heretofore referred to as the "transverse lamina") (figs. 11.3E, 11.5B). The primary choanae are bordered laterally by the maxilla and palatine, medially by the vomer, and posteriorly by the palatine and vomer (fig. 11.3B–D). The posterior portion of the vomer forms a strut that, together with the medially directed plates of the palatines, forms the anterior part of the transverse lamina (fig. 11.3E) and the floor to the posterior (olfactory) chamber of the nasal cavity (fig. 11.5A, B). The grooved dorsal border of the vomer and the medial ridge on the ventral side of the nasal bone in *Massetognathus* suggest the presence of a tall cartilaginous internasal septum (figs. 11.3B–E and 11.6D). The posterior extension of the primary choanae

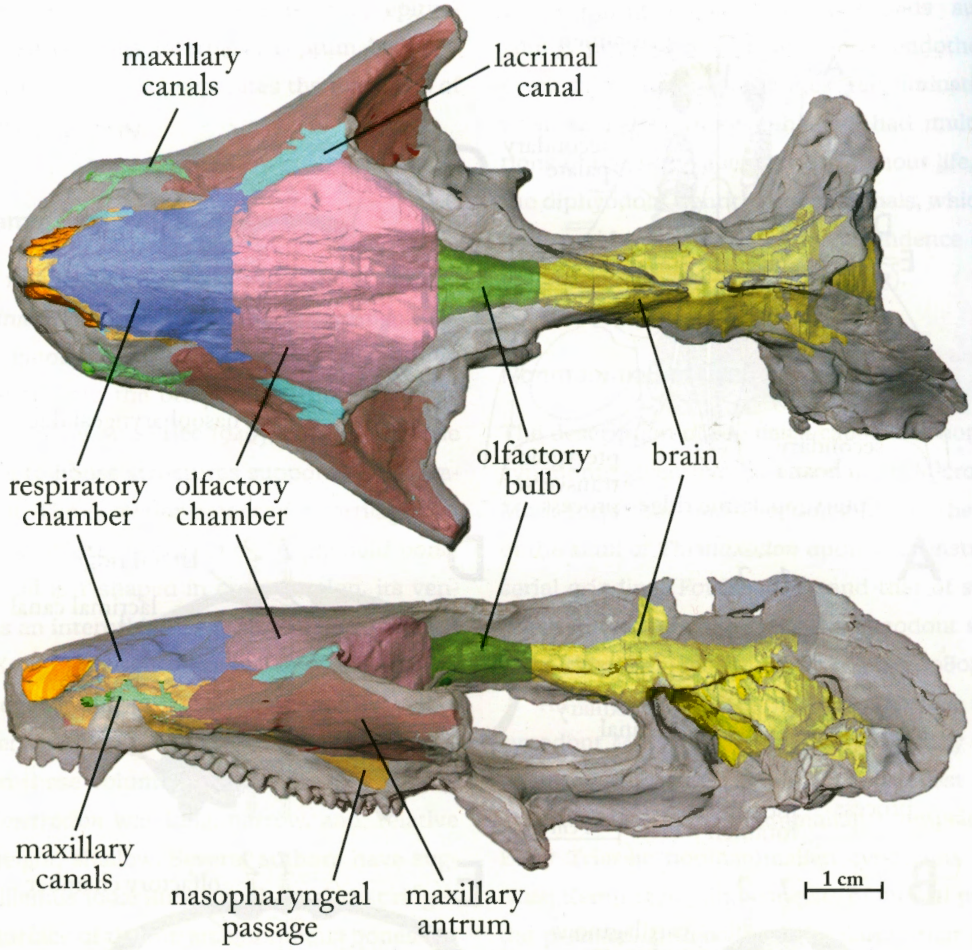

FIG. 11.4 Division of the nasal cavity as seen in dorsal and lateral views (see also supplementary video, Musinsky 2012, http://vimeo.com/43930404).

greatly increases the volume of a respiratory chamber through which inhaled and exhaled air pass. Arrows in figure 11.5B indicate airflow through the primary choana into the nasopharyngeal duct.

The internal surfaces of the membrane bones surrounding the nasal cavity of *Massetognathus* have a series of ridges: a median ridge, two lateral ridges—one on either side (fig. 11.3C–E)—and one ridge on each inner surface of the lacrimals and maxillae (figs. 11.3C, D and 11.5A, B). These and some additional ridges have been described in several nonmammalian synapsids (Brink 1955, 1957; Fourie 1974; Hillenius 1994; Kermack et al. 1981). All these authors described these ridges as the remnants of the bases of either ossified olfactory or respiratory turbinals. In modern mammals when the maxilloturbinals are lost due to damage in dried skulls, a ridge terminated by a fracture line remains, indicating the presence of maxilloturbinals. In nonmammalian cynodonts the ridges have a smooth surface, and no such fracture line is present. It is likely that the ridge on the ventral edge of the nasal bone that Hillenius (1992) claimed supported a respiratory turbinate in *Massetognathus* is an artifact of dorsoventral compression before fossilization (Hopson 2012 contra Hillenius 1994). The medial ridge on the inner surface of the nasal bone in *Massetognathus* almost certainly lay above a cartilaginous internasal septum (fig. 11.3C, D). This supports the view that the ridges on the inner surfaces of bones in the nasal region may, in fact, indicate the presence of cartilaginous structures. Similarly, the lateral ridges parallel to the median ridge may point to the presence of cartilaginous nasal turbinals. However, we could find no ridges in the CT scans of *Massetognathus* that could indicate the number or orientation of cartilaginous ethmoturbinals; so no attempt to reconstruct them has been made in figure 11.3D or E. The long ridge that forms the base for the maxilloturbinals in mammals lies close to the opening of the nasolacrimal duct (fig. 11.6E). The posterior edge of a similar ridge in *Massetognathus* (fig. 11.5B) lies above the internal opening of the nasolacrimal duct, suggesting that this ridge lies proximal to the base of a cartilaginous maxilloturbinal (figs. 11.3C, D and 11.6D). In reptiles, the nasal capsule does not extend below the level of the dorsal border of the vomer (fig. 11.2A) (Malan 1946); likewise, in *Massetognathus* and other cynodonts the cartilaginous capsule probably lay above the dorsal border of the tall vomer. Respiratory turbinals may have filled the respiratory chamber

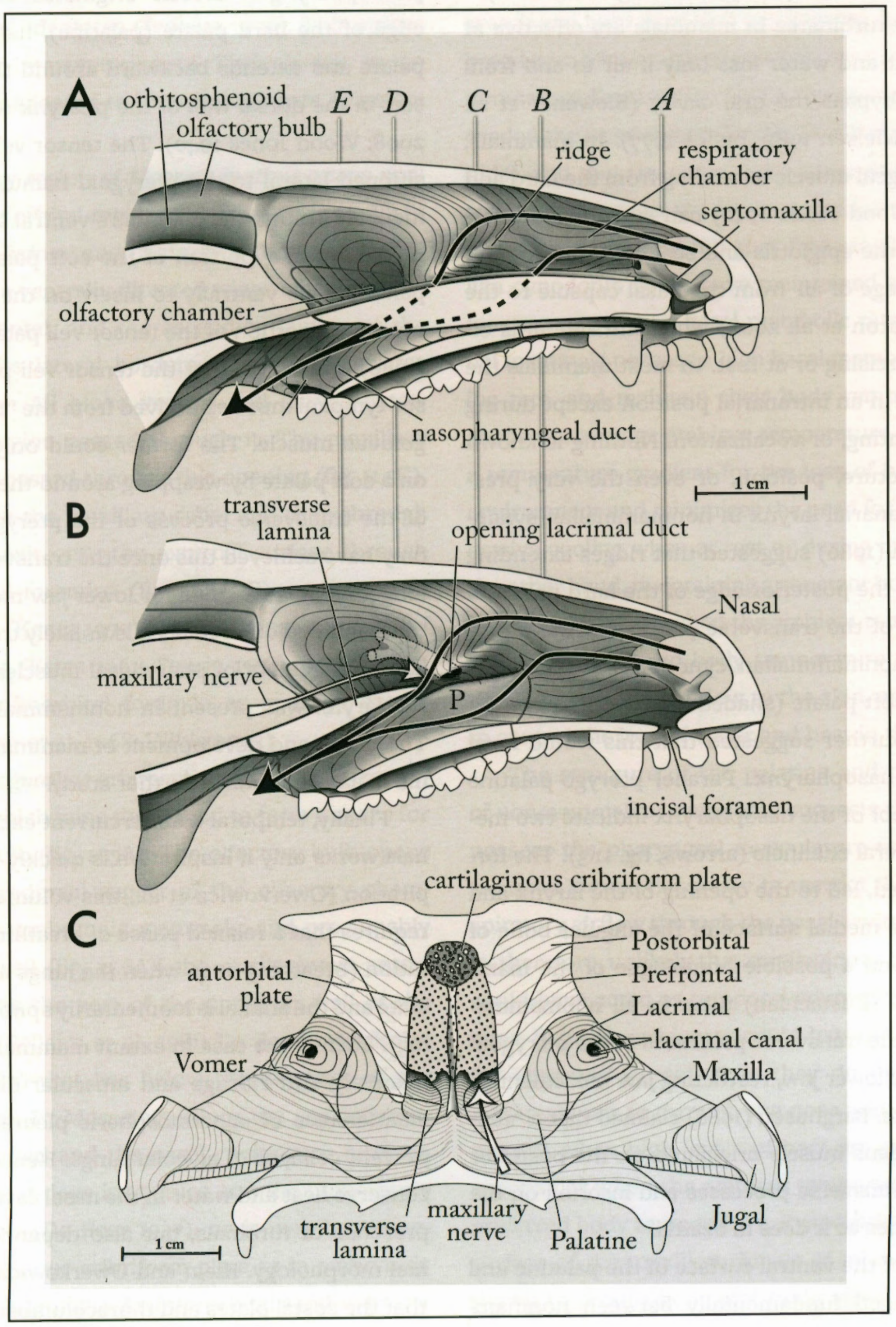

FIG. 11.5 A, Sagittal and B, parasagittal sections through the snout of *Massetognathus pascuali*. C, Posterior view of the nasal region of the same specimen. Vertical lines labeled A through E indicate the position of the sections included in figure 11.3. The two vertical lines in figure 11.3 indicate the planes shown here in A and B.

above the large primary internal choana (fig. 11.6D), but they may have extended ventrally into the nasopharyngeal duct. We cannot calculate the surface area of hypothetical respiratory turbinals, if they were in fact present, but since cartilaginous laminae tend to be thicker than ossified turbinals, it is unlikely that their surface area could have approached that of the highly branched respiratory turbinals in many terrestrial and some aquatic mammals (Van Valkenburgh et al. 2011).

Respiratory turbinates in mammals are effective at controlling heat and water loss only if air to and from the lungs can bypass the oral cavity (Biewener et al. 1985; Schmidt-Nielsen 1981; Taylor 1977). In mammals, a palatopharyngeal muscle extending from the hard and soft palates (Wood Jones 1940) can surround the larynx and tip of the epiglottis and seal off from the oral cavity the passage of air from the nasal capsule to the trachea (Crompton et al. 2008) while the animal is either mildly exercising or at rest. In most mammals the larynx remains in an intranarial position except during swallowing, panting, or vocalization. Nothing is known about the structure, position, or even the very presence of an intranarial larynx in nonmammalian synapsids. Barghusen (1986) suggested that ridges extending backward from the posterior edge of the hard palate to the outer edge of the transverse process of the pterygoid bone in nonmammalian cynodonts supported a non-muscular soft palate (shaded area in fig. 11.3). Barghusen (1986) further suggested that this would form the floor of a nasopharynx. Parallel pterygo-palatine ridges on the roof of the nasopharynx indicate two medial and two lateral channels (arrows, fig. 11.3). The former, he proposed, led to the opening of the larynx and the latter to the medial surface of the angular bone of the lower jaw and a possible homologue of the mammalian auditory (Eustachian) tube. In all nonmammalian cynodonts the transverse processes of the pterygoid abut against the lower jaw, restricting jaw movement to the sagittal plane. Barghusen (1986) claimed that a "reptilian" pterygoideus muscle originated on the posterior surface of the transverse processes and inserted on the postdentary bones as it does in lizards.

The shape of the ventral surface of the palatine and pterygoid changed fundamentally between nonmammalian cynodonts and mammals. The transverse process of the pterygoid reduced in size and lost contact with the lower jaw, thus permitting more complex jaw movements (Crompton 1995). The pterygoid hamulus could be either a remnant of the large transverse process of the pterygoid of nonmammalian therapsids or a modification of the ectopterygoid (Barghusen 1986). In mammals, the palatine and the pterygoid hamulus form the roof and sidewall of a dome-shaped nasopharynx with a muscular soft palate as its floor. The palatopharyngeal muscle originates on the posterior edge of the hard palate (palatine), hamulus, and soft palate and extends backward around the larynx to insert in the dorsal wall of the pharynx (Crompton et al. 2008; Wood Jones 1940). The tensor veli palatini is positioned lateral to the pterygoid hamulus and extends medially around the hamulus's ventral surface to insert in the anterior portion of the soft palate. The levator palatini runs ventrally to insert on the soft palate behind the insertion of the tensor veli palatini. Barghusen (1986) has shown that the tensor veli palatini and tensor tympani muscles derived from the "reptilian" pterygoideus muscle. The former could only have inserted on a soft palate by wrapping around the ventral margin of the transverse process of the pterygoid, and could only have achieved this once the transverse process no longer acted as a guide for lower jaw movement. Given these marked differences it is unlikely that the mammalian arrangement of pharyngeal muscles or an intranarial larynx was present in nonmammalian cynodonts. The origin and development of mammalian pharyngeal musculature requires further study.

Finally, temporal countercurrent exchange on turbinals works only if inspiration is quickly followed by expiration (Owerkowicz et al., this volume). This rhythm requires that a relaxed phase of breathing follows expiration (breathing out), when the lungs are in a deflated state and the animal is momentarily apnoeic (not breathing). Such is the case in extant mammals, in which the relatively stiff ribcage and muscular diaphragm allow maintenance of subatmospheric pleural pressure and prevent collapse of alveolar lungs. Hence, the ability to conserve heat and water in the nasal cavity required the presence of turbinals, but also depended on postcranial morphology. Klein and Owerkowicz (2006) argued that the costal plates and thoracolumbar differentiation in *Thrinaxodon* point to the presence of a muscular diaphragm before the origin of mammals, as originally suggested by Brink (1955). We now find this scenario unlikely, because other cynodonts do not show such postcranial morphology (Jenkins 1971; Kemp 1982), and the earliest record of a complex metameric sternum (with sternebrae) is in the Early Jurassic tritylodontids *Oligokyphus* (Kühne 1956) and *Kayentatherium* (Sues and Jenkins 2006). The costal plates of *Thrinaxodon* have previously been interpreted to allow the animal to brace the trunk against external forces (Jenkins 1971), similar to extant edentates (Jenkins 1970). This agrees with a current interpretation of *Thrinaxodon* as an adept burrower, adapted to fossorial habitats (Damiani et al. 2003).

The olfactory region of *Massetognathus* opens posteriorly into the orbital region through a wide foramen (fig. 11.5C). The frontal and postorbital form the roof of the foramen; the ventrally directed wings of the postorbital, the prefrontal, and the ascending lamina of the palatine form its lateral borders; and the transverse lamina, its floor. All blood vessels and nerves entering the nasal region passed through it. The maxillary nerve probably passed through this opening (fig. 11.5C), forward through the maxillary canal and then through the maxilla to exit onto the external surface through numerous small foramina (fig. 11.3A, B), as it does in *Procynosuchus* (Kemp 1979), *Thrinaxodon*, and several therocephalians (Estes 1961; Fourie 1974), rather than from a large infraorbital foramen as in most extant mammals (Miller et al. 1968; Wible 2003).

The *Massetognathus* orbitosphenoid is a long trough-shaped bone, which joins the frontal to form a space for the olfactory bulb (fig. 11.5A). The olfactory bulb opens into the posterodorsal aspect of the olfactory chamber. In reptiles, embryonic mammals, and presumably cynodonts as well (fig. 11.6A), the cartilaginous antorbital plate forms the part of the posterior wall of the nasal capsule (Bellairs et al. 1981; De Beer 1937; Kuhn 1971; Zeller 1987) that lies below the entrance of the olfactory nerves. In *Massetognathus*, the gap between the orbitosphenoid and the nasal cavity may have remained open as it does in reptiles and the monotreme *Ornithorhynchus* (De Beer 1937); or it may have contained a cartilaginous cribriform plate as in embryonic *Tachyglossus* (Kuhn 1971). An interorbital septum below the orbitosphenoid, ossified in some other nonmammalian synapsids (Kemp 1972, 1969), appears to have remained cartilaginous in *Massetognathus* and other cynodonts.

The climate of the Middle to Late Triassic included arid to semiarid environments, as well as wet temperate conditions with cool winters and warm summers (Preto et al. 2010). Fauna included numerous diurnal nonmammalian cynodonts and early archosaurs. Hopson (2012) has characterized most nonmammalian cynodonts as "widely foraging" (WF), enabling carnivorous forms to search and hunt prey, and herbivorous forms to search a broad area for suitable vegetation. He concludes that WF nonmammalian cynodonts' low basal metabolic rate exceeded the basal metabolic rate of WF reptiles (e.g., varanids), and that they possessed a high maximum aerobic metabolism necessary for sustained activity over long distances. It is doubtful that free-ranging nonmammalian cynodonts could have maintained a constant body temperature if their basal metabolic rate was low. Diurnal mammals possess a high basal metabolic and breathing rate, and maintain their body temperature slightly above the average ambient temperature. This maintains a temperature gradient for the loss of body heat to the environment and minimizes the need for excessive evaporative cooling when at rest or during mild exercise. On the other hand, maintaining a constant body temperature and breathing rate when the ambient temperature drops below the preferred body temperature requires insulation, control of blood flow to the skin, and a mechanism to control the loss of water and heat in the expired air.

The structure of the palatine and pterygoid bones of nonmammalian cynodonts suggests that they did not possess the pharyngeal musculature to support an intranarial larynx, necessary to restrict the passage of respiratory airflow through the nasal cavity when at rest. It is, therefore, unlikely that cartilaginous maxilloturbinals could have acted as temporal countercurrent exchange sites. Instead, turbinates could have provided a surface for evaporative cooling as they do during panting in mammals (air in through the nose and out through the mouth) when high levels of heat are generated during exercise or when the ambient temperature exceeds the preferred body temperature. Evaporative cooling on the surface of the maxilloturbinals of mammals have been shown to reduce body and brain temperatures (Taylor and Lyman 1972). We conclude that cartilaginous respiratory turbinals arose initially to aid in cooling and only later were co-opted to act as countercurrent exchangers when an intranarial larynx arose. Although adult humans have lost the intranarial larynx, lips can seal the entrance to the oral cavity and cause both inhaled and exhaled air to pass instead through the nasal cavity.

Mammaliaformes

Mammaliaforms such as the Late Triassic/Early Jurassic *Morganucodon* show several more mammalian nasal features. We MicroCT scanned the *Morganucodon* specimen (Institute of Paleontology and Paleoanthropology, Beijing, #V8682) referred to in Rowe et al. (2011). The individual bones of this specimen are displaced and a reconstruction is currently being undertaken, but the scans show a vomer dramatically reduced in height, almost to mammalian levels, compared to nonmammalian cynodonts. The much-flattened vomer no longer divides the nasopharyngeal duct; consequently the respiratory chamber of the nasal capsule is much larger than in nonmammalian cynodonts. Kermack et al. (1981) reconstructed the internal structure of the nasal capsule of *Morganucodon* to include maxillary turbinals, a cribriform plate and a mesethmoid bone. No evidence of any of these ossified structures appear in our MicroCT scans of *Morganucodon*. Perhaps the turbinals were too fragile to have remained intact before fossilization, but if the bulkier parts of the nasal capsule such as the cribriform plate or the mesethmoid had ossified in *Morganucodon*, surely some part of these bones would have been fossilized, especially as the remaining bones of the skull are so well preserved. It appears, therefore, that in mammaliaforms the nasal capsule remained cartilaginous.

The orbitosphenoid and the olfactory bulb were, relative to skull size, considerably larger in *Morganucodon* than in *Massetognathus* (Rowe et al. 2011). It is generally agreed that some of the smaller mammaliaforms such as *Morganucodon* and *Kuehneotherium* had a diphyodont dentition and definitive growth (Hopson 1973; Luo et al. 2004). Van Nievelt and Smith (2005) suggested that this indicated that these animals suckled their young because "the period of lactation which requires no teeth eliminates the need for functional replacement early during growth or at a small size." These animals were considerably smaller than their nonmammalian ancestors. It has been suggested that they were nocturnal (Kemp 1982; Kielan-Jaworowska et al. 2004). If this is true and they retained a combination of a low basal metabolic rate and high aerobic metabolism, they may have been capable of maintaining a low constant body temperature, as several nocturnal mammals such as tenrecs and hedgehogs do, by combining a low basal metabolic rate and resting body temperatures (Crompton et al. 1978). We agree with Kemp (2006) that these extant species secondarily modified their metabolic rates to enter a nocturnal environment, but suggest that low basal metabolic and high maximum metabolic rates could have also been a strategy adopted by small nocturnal mammaliaforms and early mammals.

The vacant space in the nasal cavity of *Massetognathus* (fig. 11.6A, D) resembles the space that contains an ossified nasal capsule in the marsupial *Didelphis* (fig. 11.6B–C, 11.6E–F). The embryonic nasal septum in mammals ossifies to form the mesethmoid (fig. 11.6B, E) (Moore 1981). The compression of the vomer from a tall bone in nonmammalian cynodonts to a thin splint of bone lying below the mesethmoid increases the relative size of the respiratory chamber, possibly allowing for increased space for ossified maxilloturbinals (fig. 11.6).

The posterior region of the embryonic cartilaginous nasal capsule in mammals ossifies to form the ethmoid bone that includes the ossified ethmoturbinals, nasoturbinals, and cribriform and lateral plates (Macrini 2012; Miller et al. 1968; Rowe et al. 2005).

The ethmoturbinals occupy the chamber that forms a blind alley above the transverse lamina, above and beyond direct airflow from the nares to the nasopharyngeal passage (fig. 11.6C). This space in cynodonts undoubtedly also included olfactory turbinals that formed in the same way as they do in mammals—that is, as medial extensions of the nasal capsule's cartilaginous side wall—except that they remained cartilaginous. In embryonic mammals the cartilaginous anterior region of the nasal capsule appears close to the inner surface of the maxilla. During development, the ventral edges of the nasal capsule extend into the nasal cavity. These and membranous extensions later ossify to form maxilloturbinals, which in turn fuse directly to the maxillary bones (fig. 11.6E).

Maxilloturbinals branch repeatedly to create a large surface area, and are organized so as to reduce resistance to the airflow to and from the nasopharyngeal

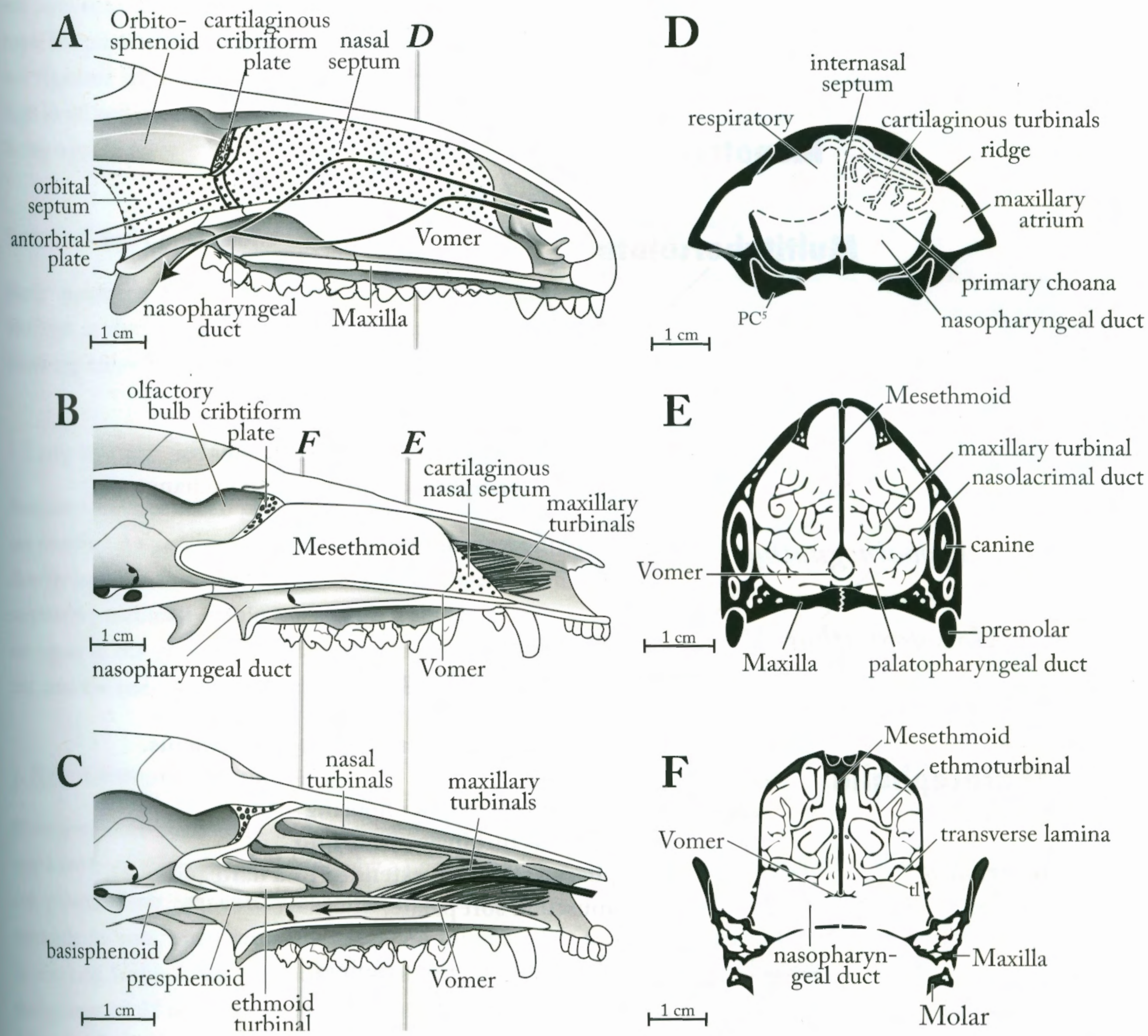

FIG. 11.6 Comparison of the nasal region of a nonmammalian cynodont, *Massetognathus*, and an extant basal mammal, *Didelphis*. A, Sagittal section through the nasal region of *Massetognathus*. Vertical line shows the position of the section shown in D; B, sagittal section through the nasal region of *Didelphis*; C, parasagittal section through the nasal region of *Didelphis*, slightly lateral of B. Vertical lines indicate the position of the sections shown in E and F.

duct. The long ridge that forms the base for the maxilloturbinals in mammals lies close to the opening of the naso-lacrimal duct (fig. 11.6E).

The first suggestion of ossified turbinals and a mesethmoid bone appear in the late Jurassic mammaliaforms docodont *Haldanodon*, as described by Lilligraven and Krusat (1991). Although their paper does not distinguish between olfactory and respiratory turbinals, its authors claim that turbinals filled the nasal cavity and that the foundations of some of these turbinal scrolls are preserved as ridges on the maxillae.

The pterygoid bones of multituberculates are, as in all mammals, widely separated from the lower jaw. The structure of the palatal region behind the hard palate in the multituberculate, *Paulchoffatia delgao* (Hahn 1987) is essentially mammalian, and suggests the presence in mid-Jurassic mammals of pharyngeal muscles and an intranarial larynx. Fragments of bone have been described in the nasal cavities of the Late Cretaceous multituberculates, *Nemegtbataar* and *Chulsanbaatar* (Hurum 1994). Hurum claims that these are the remnants of ossified turbinates. All three groups of living mammals—

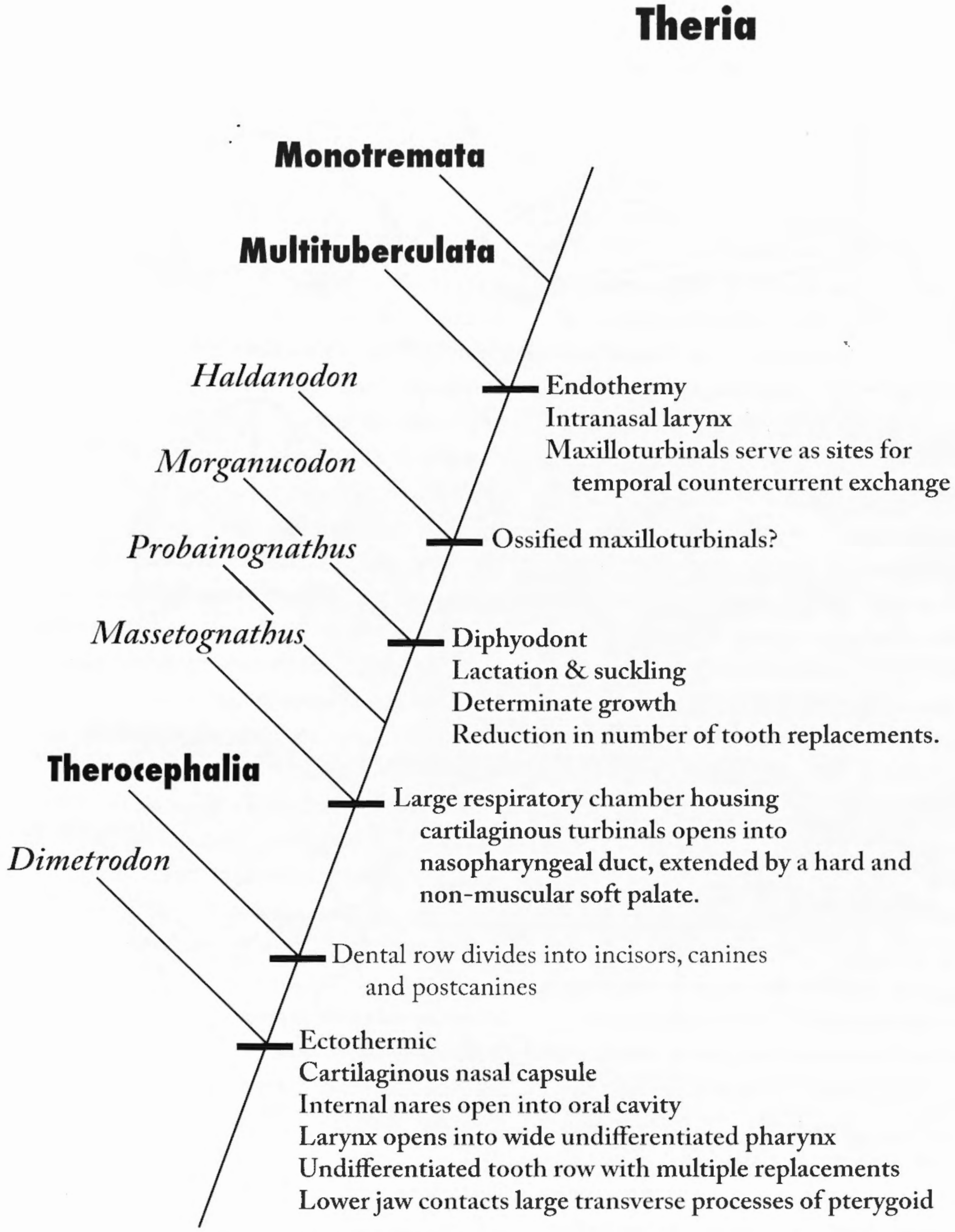

FIG. 11.7 Progressive changes in the nasal, oral, and pharyngeal regions in nonmammalian synapsids.

monotremes, marsupials, and placentals (fig. 11.1)—possess ossified maxilloturbinals, so it is probable that their common ancestor, which dates back to the Middle Jurassic (Luo 2007), and probably existed alongside some mammaliaforms (e.g., *Haldanodon*), also possessed ossified maxilloturbinals and an intranarial larynx.

Diurnal mammals have constant body temperature, high basal and maximum aerobic metabolic rates, decreased compliance of the chest matching an increased volume of the nasal cavity, an intranarial larynx, and ossified maxilloturbinals that can function either for cooling or as temporal countercurrent exchange sites. Conservation of water and heat represent only one feature necessary to support endothermy, but, we argue, maintaining constant body temperature in an environment with significant shifts in daily and seasonal ambient temperatures would only have been possible when nasal temporal countercurrent exchange sites were present together with other features necessary to support high basal and maximum metabolic rates (Hopson 2012; Kemp 2006).

Summary and Conclusions

Many questions remain about the successive changes involved in the evolution of the mammalian nose. The following steps are proposed (fig. 11.7):

1. Early Nonmammalian Synapsids

Permian nonmammalian pelycosaurs and therocephalians possessed a cartilaginous nasal capsule that opened directly into the oral cavity. This limited the space for respiratory turbinals within the airflow from the external nares to the primary choanae. They were ectothermic, and the nose was designed primarily for olfaction.

2. Nonmammalian Cynodonts

Nonmammalian cynodonts added a hard palate that may have been extended posteriorly by a non-muscular soft palate. Their respiratory chamber increased dramatically in size. They probably lacked an intranarial larynx, and, if this is so, the path of respiratory airflow during rest could not have been temporarily restricted to the nasal cavity. Consequently, they lacked temporal countercurrent exchange sites for the conservation of water and heat, necessary to maintain a constant body temperature and rhythmic breathing rate. However, their cartilaginous maxilloturbinals and oral cavity provided surfaces for evaporative cooling during panting.

3. Mammaliaformes

The structure of the nose in mammaliaforms appears to have been the same as in cynodonts, but the olfactory bulb was larger. A reduction in the height of the vomer increased the relative volume of the respiratory chamber. Their diphyodont dentition suggests determinate growth and suckling of their young.

4. Mammalia

The common ancestor of Mammalia probably had a muscular soft palate and a palatopharyngeal muscle that could hold the larynx in an intranarial position. The embryonic cartilaginous nasal capsule, including respiratory turbinates, completely ossifies in the adult. This animal had a higher basal metabolic and breathing rate than in typical reptiles and its maxilloturbinals, operating as temporal countercurrent exchange sites, controlled the loss of water and heat. Mammalian endothermy arose when these changes in nasal structure combined with a host of other specializations necessary to support a high resting metabolic rate and constant body temperature.

Future Directions

The conclusions reached in this paper are of necessity speculative due to the spotty fossil record upon which they are based, an incomplete analysis of the internal and external structures of critical regions in known fossils, and the difficulty of relying on bony structures alone for the reconstruction of soft tissues. Such shortcomings can be ameliorated in the future by using advanced imaging techniques to reexamine existing material, and continuing field work to fill in gaps in the fossil record, especially from the Early to Middle Jurassic, when the final steps in the evolution of mammals occurred. Understanding the morphology of new specimens will still require classic comparative anatomical and physiological approaches aided by the study of the function and development of comparable regions in extant animals.

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References

Bang, B. G. 1961. The surface pattern of the nasal mucosa and its relation to mucous flow—a study of chicken and herring gull nasal mucosae. J. Morphol. 109:57.

Barghusen, H. R. 1986. On the evolutionary origin of the therian tensor veli palatini and tensor tympani muscles. P. 253 in The Ecology and Biology of Mammal-Like Reptiles. Washington, DC, and London: Smithsonian Institution Press.

Bellairs, A. d. A., and A. M. Kamal. 1981. The chondrocranium and the development of the skull in recent reptiles. P. 1 in C. Gans and T. S. Parsons, eds., Biology of the Reptilia: Morphology. Toronto: Academic Press.

Bennett, A. F., and J. A. Ruben. 1986. The metabolic and thermoregulatory status of therapsids. P. 207 in The Ecology and Biology of Mammal-Like Reptiles. Washington, DC, and London: Smithsonian Institution Press.

Biewener, A. A., G. W. Soghikian, and A. W. Crompton. 1985. Regulation of respiratory airflow during panting and feeding in the dog. Respir. Physiol. 61:185.

Brink, A. S. 1955. A study on the skeleton of *Diademodon*. Palaeontol. Afr. 3:3.

Brink, A. S. 1957. Speculations on some advanced mammalian characteristics in the higher mammal-like reptiles. Palaeontol. Afr. 4:77.

Crompton, A. W. 1995. Masticatory function in nonmammalian cynodonts and early mammals. P. 55 in J. Thomason, ed., Functional Morphology in Vertebrate Paleontology. Cambridge: Cambridge University Press.

Crompton, A. W., R. Z. German, and A. J. Thexton. 2008. Development of the movement of the epiglottis in infant and juvenile pigs. Zoology (Jena), 111:339.

Crompton, A. W., C. R. Taylor, and J. A. Jagger. 1978. Evolution of homeothermy in mammals. Nature (London) 272:333.

Damiani, R., S. Modesto, A. Yates, and J. Neveling. 2003. Earliest evidence of cynodont burrowing. Proc. R. Soc. Lond. Biol. 270:1747.

De Beer, G. 1937. The Development of the Vertebrate Skull. Oxford: Clarendon Press.

Estes, R. 1961. Cranial anatomy of the cynodont reptile *Thrinaxodon liorhinus*. Bull. Mus. Comp. Zool. Harvard College 125–26.

Fourie, S. 1974. The cranial morphology of *Thrinaxodon liorhinus*. Ann. South Afr. Mus. 65:337.

Geist, N. R. 2000. Nasal respiratory turbinate function in birds. Physiol. Biochem. Zool. 73:581.

Hahn, G. 1987. Neue Beobachtungen zum Schadel- und Gebiss-Bau der Paulchoffatiidae (Multituberculata, Ober-Jura). Palaeovertebrata (Montpellier) 17:155.

Hillenius, W. J. 1992. The evolution of nasal turbinates and mammalian endothermy. Paleobiology 18:17.

Hillenius, W. J. 1994. Turbinates in therapsids: evidence for Late Permian origins of mammalian endothermy. Evolution 48:207.

Hillenius, W. J., and J. A. Ruben. 2004. The evolution of endothermy in terrestrial vertebrates: who? when? why? Physiol. Biochem. Zool. 77:1019.

Hopson, J. A. 1973. Endothermy, small size, and the origin of mammalian reproduction. Amer. Nat. 107:446.

Hopson, J. A. 2012. The role of foraging mode in the origin of therapsids: implications for the origin of mammalian endothermy. Fieldiana Life Earth Sci. 5:126.

Hurum, J. H. 1994. Snout and orbit of Cretaceous Asian multituberculates studied by serial sections. Acta Palaeontol. Pol. 39:181.

Jenkins, F. A., Jr. 1970. Anatomy and function of expanded ribs in certain edentates and primates. J. Mammal. 51:288.

Jenkins, F. A., Jr. 1971. The postcranial skeleton of African cynodonts. Bull. Peabody Mus. Nat. Hist. 36:i.

Kemp, T. S. 1969. On the functional morphology of the gorgonopsid skull. Philos. Trans. R. Soc. Biol. 256:1.

Kemp, T. S. 1972. Whaitsiid Therocephalia and the origin of cynodonts. Philos. Trans. R. Soc. London Biol. 264:1.

Kemp, T. S. 1979. The primitive cynodont *Procynosuchus*: functional anatomy of the skull and relationships. Philos. Trans. R. Soc. London Biol. 285:73.

Kemp, T. S. 1980. Aspects of the structure and functional anatomy of the Middle Triassic cynodont *Luangwa*. J. Zool. (Lond.) 191:193.

Kemp, T. S. 1982. Mammal Like Reptiles and the Origin of Mammals. London and New York: Academic Press.

Kemp, T. S. 2006. The origin of mammalian endothermy: a paradigm for the evolution of complex biological structure. Zool. J. Linn. Soc. 147:473.

Kermack, K. A., F. Musset, and H. W. Rigney. 1981. The skull of *Morganucodon*. Zool. J. Linn. Soc. 71:1.

Kielan-Jaworowska, Z., R. Cifelli, and Z.-X. Luo. 2004. Mammals from the Age of Dinosaurs: Origins, Evolution, and Structure. New York: Columbia University Press.

Klein, W., and T. Owerkowicz. 2006. Function of intracoelomic septa in lung ventilation of amniotes: lessons from lizards. Physiol. Biochem. Zool. 79:1019.

Kuhn, H. J. 1971. Die Entwicklung und Morphologie des Schädels von *Tachyglossus aculeatus*. Abh Senckenb. Naturf. Ges. 528:1.

Kühne, W. G. 1956. The Liassic Therapsid *Oligokyphus*. London: Order of the Trustees of the British Museum.

Lillegraven, J. A., and G. Krusat. 1991. Cranio-mandibular anatomy of *Haldanodon exspectatus* (Docodonta; Mammalia) from the Late Jurassic of Portugal and its implication to the evolution of mammalian characters. Contrib. Geol. Univ. Wyoming, 28:39.

Luo, Z. -X. 2007. Transformation and diversification in early mammal evolution. Nature 450:1011.

Luo, Z. -X., Z. Kielan-Jaworowska, and R. L. Cifelli. 2004. Evolution of dental replacement in mammals. Bull. Carn. Mus. Nat. Hist. 36:159.

Macrini, T. E. 2012. Comparative morphology of the internal nasal skeleton of adult marsupials based on x-ray computed tomography. Bull. Am. Mus. Nat. Hist. 365:1.

Maier, W. 1999. On the evolutionary biology of early mammals—with methodological remarks on the interaction between ontogenetic adaptation and phylogenetic transformation. Zool. Anzeiger 238:55.

Maier, W., J. van den Heever, and F. Durand. 1996. New therapsid specimens and the origin of the secondary hard and soft palate of mammals. J. Zool. Sys. Evol. Res. 34:9.

Malan, M. E. 1946. Contributions to the comparative anatomy of the nasal capsule and the organ of Jacobson of the Lacertilia. Ann. Univ. Stellenbosch 24A:69.

Miller, M. E., G. C. Christensen, and H. E. Evans. 1968. Anatomy of the Dog. Philadelphia: W. B. Saunders.

Moore, W. J. 1981. The Mammalian Skull. Cambridge: Cambridge University Press.

Musinsky, C. 2012. Evolution of the Mammalian Nose. Vimeo .com/43930404.
Parsons, T. S. 1959. Nasal anatomy and the phylogeny of reptiles. Evolution 13:175.
Pratt, C. W. M. 1948. The morphology of the ethmoidal region of *Sphenodon* and lizards. Proc. Zool. Soc. London 118: 171.
Preto, N., E. Kustatscher, and P. B. Wignall. 2010. Triassic climates—state of the art and perspectives. Palaeogeog. Palaeoclim. Palaeoecol. 290:1.
Romer, A. S., and L. I. Price. 1940. Review of the Pelycosauria. Geol. Soc. Am. Washington Spec. Pap. 28:18.
Rowe, T. B., T. P. Eiting, T. E. Macrini, and R. A. Ketcham. 2005. Organization of the olfactory and respiratory skeleton in the nose of the gray short-tailed opossum *Monodelphis domestica*. J. Mamm. Evol. 12:303.
Rowe, T., and J. Gauthier. 1992. Ancestry, palaeontology, and definition of the name Mammalia. Syst. Biol. 41:372.
Rowe, T. B., T. E. Macrini, and Z.-X. Luo. 2011. Fossil evidence on origin of the mammalian brain. Science 332:958.
Ruben, J., 1996. Evolution of endothermy in mammals, birds and their ancestors. P. 349 in I. A. Johnston and A. F. Bennett, eds., Animals and Temperature: Phenotypic and Evolutionary Adaptation. Cambridge: Cambridge University Press.
Ruben, J. A., W. J. Hillenius, N. R. Geist, A. Leitch, T. D. Jones, P. J. Currie, J. R. Horner, and G.E. Espe III. 1996. The metabolic status of some Late Cretaceous dinosaurs. Science 273:1204.
Ruben, J. A., W. J. Hillenius, T. S. Kemp, and D. E. Quick. 2012. The evolution of mammalian endothermy. P. 272 in A. Chinsamy-Turan, ed., Forerunners of Mammals: Radiation—Histology—Biology. Bloomington: Indiana University Press.
Schmidt-Nielsen, K. 1981. Countercurrent systems in animals. Sci. Am. 244:100.
Sues, H.-D. 1986. The skull and dentition of two tritylodontid synapsids from the Lower Jurassic of western North America. Bull. Mus. Comp. Zool. 151:217.
Sues, H.-D., and F. A. Jenkins Jr. 2006. The postcranial skeleton of *Kayentatherium wellesi* from the Lower Jurassic Kayenta Formation of Arizona and the phylogenetic significance of postcranial features in tritylodontid cynodonts. P. 114 in M. T. Carrano, T. J. Gaudin, R. W. Blob, and J. R. Wible, eds., Amniote Paleobiology: Perspectives on the Evolution of Mammals, Birds, and Reptiles. Chicago: University of Chicago Press.
Taylor, C. R. 1977. Exercise and environmental heat loads: different mechanisms for solving different problems? Int. Rev. Physiol. 15:119.
Taylor, C. R., and C. Lyman 1972. Heat storage in running antelopes: independence of brain and body temperatures. Am. J. Physiol.—Legacy Content, 222:114.
Thomason, J. J., and A. P. Russell 1986. Mechanical factors in the evolution of the mammalian secondary palate: a theoretical analysis. J. Morphol. 189:199.
van Nievelt, A. F. H., and K. K. Smith 2005. To replace or not to replace: the significance of reduced functional tooth replacement in marsupial and placental mammals. Paleobiology 31:324.
Van Valkenburgh, B., A. Curtis, J. X. Samuels, D. Bird, B. Fulkerson, J. Meachen-Samuels, and G. J. Slater 2011. Aquatic adaptations in the nose of carnivorans: evidence from the turbinates. J. Anat. 218:298.
Wible, J. R. 2003. On the cranial osteology of the short-tailed opossum *Monodelphis brevicaudata* (Didelphidae, Marsupialia). Ann. Carnegie Mus. 72:137.
Wood, Jones, F. 1940. The nature of the soft palate. J. Anat. 74: 147.
Zeller, U. 1987. Morphogenesis of the mammalian skull with special reference to *Tupaia*. P. 17 in H. J. Kuhn, D. A. N. Hoyte, and U. Zeller, eds., Morphogenesis of the Mammalian Skull. Göttingen: Paul Parey.