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STRUCTURE OF THE NASAL REGION OF NON-MAMMALIAN CYNODONTS AND MAMMALIAFORMS: SPECULATIONS ON THE EVOLUTION OF MAMMALIAN ENDOTHERMY

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ABSTRACT—Nasal regions of the non-mammalian cynodonts *Massetognathus, Probainognathus*, and *Elliotherium* were reconstructed from micro-computed tomography scans and compared with scans and published accounts of more derived forms, including *Brasilitherium, Morganucodon, Haldanodon*, and extant mammals. The basic structure of the modern mammalian nose, already present in non-mammalian cynodonts of the Early Triassic, underwent little modification during the Triassic. A respiratory chamber opened into a nasopharyngeal passage through an enlarged primary choana bordered posteriorly by a transverse lamina that formed the floor to a more posterior olfactory chamber. Cartilaginous respiratory turbinals initially provided a surface for evaporative cooling during periods of increased activity in the exceptionally high ambient temperatures of the Triassic. A similar mechanism for heat loss is present in extant crocodilians, squamates, and mammals. In the Late Triassic and Early Jurassic non-mammaliaform cynodonts (*Elliotherium*) and mammaliaforms (*Morganucodon*), the pterygopalatine ridges behind the hard secondary palate extended ventrally and formed the lateral walls to a narrow nasopharynx, as pterygoid hamuli do in extant mammals. Ridges in this position suggest the presence of a palatopharyngeus muscle in late non-mammaliaform cynodonts that could hold the larynx in an intranarial position during rest or low activity levels to prevent inhaled air from entering the oral cavity, thus allowing cartilaginous respiratory turbinals to assume an additional role as temporal countercurrent exchange sites for heat and water conservation. Ossification of respiratory turbinals in mammals enhanced their efficiency for conserving heat and water at rest, as well as their ability to dissipate heat during thermal stress.

INTRODUCTION

External features of the nasal region in therapsids are well documented, but with the exception of a few brief descriptions (Brink, 1955; Fourie, 1974; Kemp, 1979; Hillenius, 1994, 2000), the internal structure remains poorly understood. The relatively recent advent of micro-computed tomography (micro-CT) and neutron tomography imaging allows detailed descriptions of the internal morphologies of rare fossils without destroying them in the process as previous methods (e.g., serial grinding or sectioning) required. Despite these advantages, reconstruction of the internal structure of the nasal region in non-mammalian cynodonts remains difficult because cartilage is not preserved and, as in amphibians and sauropsids, non-mammalian cynodonts' nasal capsule remained cartilaginous throughout life (De Beer, 1937; Bellairs and Kamal, 1981). In adult mammals, in contrast, parts of the embryonic cartilaginous nasal capsule ossify to form bony turbinals and ethmoid bones, whereas the rest is either replaced by appositional bone or resorbed (De Beer, 1937; Moore, 1981; Zeller, 1987; Maier, 1993). With the possible exception of *Brasilitherium* (Ruf et al., 2014), no ossified portions of the nasal

capsule have been identified in therapsids. Speculations on the structure of the cartilaginous nasal capsule must therefore rely upon the internal sculpture of the nasal cavity. Ridges on the internal surface of the membrane bones of the snout in non-mammalian cynodonts have been interpreted as evidence for the presence of respiratory turbinals (Hillenius, 1994); for example, midline and lateral ridges on the ventral surface of the nasal bone suggest the attachment of a cartilaginous nasal septum and nasoturbinals, respectively.

It is widely accepted that the evolutionary history of therocephalians and non-mammalian cynodonts included a progressive increase in the level of sustained aerobic activity and a corresponding increase in the levels of resting and maximum aerobic rates. Numerous changes in the skeleton support this view (see Bennett and Ruben, 1986; Kemp, 2005; Hopson, 2012, for reviews of these features). A progressive increase in aerobic activity implies a gradual increase in lung ventilation and the potential for greater loss of heat and water in expired air. Several authors have claimed that therocephalians and non-mammalian cynodonts possessed either cartilaginous or bony respiratory turbinals (Brink, 1957; Crompton, 1958; Fourie, 1974; Bennett and Ruben, 1979, 1986; Bennett, 1991; Hillenius, 1992; Ruben, 1995, 1996; Hillenius and Ruben, 2004; Kemp, 2005, 2006; Ruben et al., 2012). Ruben et al. (2012) suggest that fully developed

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respiratory turbinates are an unequivocal anatomical correlate of endothermy.

Terrestrial mammals are characterized by continuous rhythmic breathing, with inspiration preceding exhalation. They breathe exclusively through the nose at rest and during mild exercise. In mammals, respiratory turbinals—primarily maxilloturbinals, lateral surfaces of nasoturbinals, and rostral ethmoturbinals—act as sites of temporal countercurrent exchange (TCCE). During inspiration, a stream of cold ambient air is progressively warmed and humidified, whereas the respiratory turbinal epithelium is cooled. During expiration, moisture in the warm and humid air from the lungs condenses on the cool turbinal epithelium, rewarming it to the core body temperature and preparing it for the next respiratory cycle. In this way, respiratory turbinals recoup most of the heat and water from the expired air (Schmidt-Nielsen and Jackson, 1964; Schmidt-Nielsen, 1981). The time interval between inhalation and exhalation must be short enough to prevent blood flowing through the nasal mucosa from warming and humidifying the respiratory turbinals before exhalation (Johansen and Bech, 1983; Owerkowicz et al., 2015).

Temporal countercurrent exchange requires that inhaled air travel the same path as exhaled air. This is achieved when the palatopharyngeal muscle holds the larynx in an intranarial position and respiratory air bypasses the oral cavity (see dotted line showing the palatopharyngeal arch extending backwards around the larynx from the tip of the palatopharyngeus in Fig. 1A). Even in humans, with the uniquely derived condition of a descended larynx, an airtight seal between the soft palate and the posterior tongue allows for strictly nasal breathing (Rodenstein and Stanescu, 1984). In mammals, the pterygoid hamuli form lateral walls to a relatively narrow nasopharynx. The palatopharyngeal muscles originate from the posterior end of the hard palate and on the medial surface of the hamuli. The tensor veli palatini muscles form a floor to the nasopharynx between the ventral edges of the hamuli and the palatopharyngeal muscles. A narrow Eustachian tube connects the nasopharynx to the middle ear.

Mammalian maxilloturbinals usually form thin and delicate bony plates, often with elaborate branching patterns (Negus, 1958; Moore, 1981; Rowe et al., 2005; Van Valkenburgh et al., 2011, 2014; Owerkowicz et al., 2015). The surface area of the mucosa covering the respiratory turbinals correlates with an animal's habitat: the turbinals of mammals living in cold or relatively dry climates (e.g., camels, reindeer, carnivores, kangaroos, seals) have correspondingly greater surface areas. Animals inhabiting warm and humid tropical environments (e.g., primates) where selective pressures to conserve water and heat are relaxed, or mammals with low metabolic rates and body temperatures (e.g., the echidna, wombat, naked mole-rat), have respiratory turbinals with a smaller surface area. An analysis of residuals found that the surface area of respiratory turbinals is a strong predictor of the field metabolic rates in extant mammals (Owerkowicz et al., 2015). Avian cartilaginous respiratory conchae have, relative to volume, three times less surface area than those of mammals, but their trachea also participates in temporal countercurrent exchange (TCCE; Owerkowicz et al., 2015).

Respiratory turbinals, however, do more than retain water and heat in expired air. They can also facilitate heat loss, especially because most mammals tend to maintain a constant body temperature (Tb) above ambient temperatures, which creates a gradient for heat loss. During heat stress (e.g., activity), many mammals augment evaporative heat loss from their upper respiratory tract by panting—a breathing pattern of rapid but shallow breaths that do not affect alveolar ventilation or acid-base balance because of their small tidal volume (Taylor, 1977; Robertshaw, 2006). During panting, the larynx is withdrawn from the palatopharyngeal arch, allowing inspired air to enter the oral cavity (Fig. 1B; see also Biewener et al., 1985). Inspired air is warmed as it passes over the maxilloturbinal while it simultaneously cools the blood flowing through the mucosa. Because panting involves small tidal volumes, flow of inspired air is restricted to the trachea and the oropharynx. During expiration, some of the air is exhaled through the nose, but most of the air that is fully saturated and at body temperature exits through the mouth (Schmidt-Nielsen, 1970; Goldberg et al., 1981). Increasing aqueous secretions from the lateral nasal glands in the maxillary recesses increases evaporative cooling from the respiratory turbinals during panting in the dog (Blatt et al., 1972; Rossie, 2006). Dissociation of inspired and expired pathways prevents operation of the temporal countercurrent exchange in the nasal cavity and augments evaporative heat loss (Schmidt-Nielsen, 1970; Taylor, 1977). Cooling of venous blood in the respiratory turbinals reduces total body heat content (Fuller et al., 2004) and may specifically help to maintain a constant brain temperature (Taylor and Lyman, 1972).

Claims as to the existence of respiratory turbinals within therapsids usually rely upon ridges on the internal surface of the bones surrounding the nasal cavity. Fourie (1974) described such a longitudinal ridge on the inner surface of the maxilla in the non-mammalian cynodont, *Thrinaxodon*, and claimed that it denoted the presence of rudimentary maxilloturbinals and the possibility of 'incipient homoiothermy' in this and other cynodonts. Hillenius (1994) claimed that ridges on the internal ventral edge of the nasal bones in therocephalians and cynodonts had also supported maxilloturbinals. There are different views on the nature and development of respiratory turbinals in therapsids. Hillenius (1992) suggested that maxilloturbinals were cartilaginous in the early stages of their evolution as are the conchae of living reptiles. In 1994, he pointed out that maxilloturbinals developed ontogenetically from a cartilaginous precursor and turbinals could attach to either the nasal or maxillary bones (Hillenius, 1994). Ossified turbinals have not been observed in any non-mammalian cynodont. It is not clear whether the ridges represent the only portion of ossified turbinals preserved or whether they are extensions of the surrounding membrane bones. Bennett (1991) suggested that respiratory turbinals were ossified, whereas Kemp (2005) and Hopson (2012) doubted that respiratory turbinals even existed in non-mammalian cynodonts. Hopson (2012) suggested that the ridge that was purported to have supported a maxilloturbinal, figured by Hillenius (1994: figs. 13 and 14), actually resulted from diagenetic compression of the nasal bone forcing its ventral edge away from the maxillary bone and into the nasal cavity.

Hillenius (1992, 1994) and Ruben (1995, 1996) proposed that endothermy developed gradually within therapsids; that progressive increases in ventilation rates matched the increased complexity of the maxilloturbinals; and that this progression was largely complete in the early mammals. The development of a large respiratory region of the nasal cavity and a secondary palate in non-mammalian cynodonts (Hillenius, 1994) suggests an increase of ventilation through the nose. If respiratory turbinals were present, they lay within the path of respiratory airflow.

Most published discussions on the evolution of endothermy focus on the role that respiratory turbinals played in controlling the loss of water and heat. Less attention has been given to the role that respiratory turbinals may have played in reducing body temperature. Crompton et al. (2015) suggested that the original role of cartilaginous maxilloturbinals in Early to Middle Triassic non-mammalian cynodonts was to reduce body temperature rather than to conserve heat and water.

The aim of this paper is to support this hypothesis through descriptions of the internal structure of the nasal region of four non-mammalian cynodonts (*Thrinaxodon, Massetognathus, Probainognathus*, and *Elliotherium*). We compare these with published accounts of the nasal regions of a Late Triassic/Early
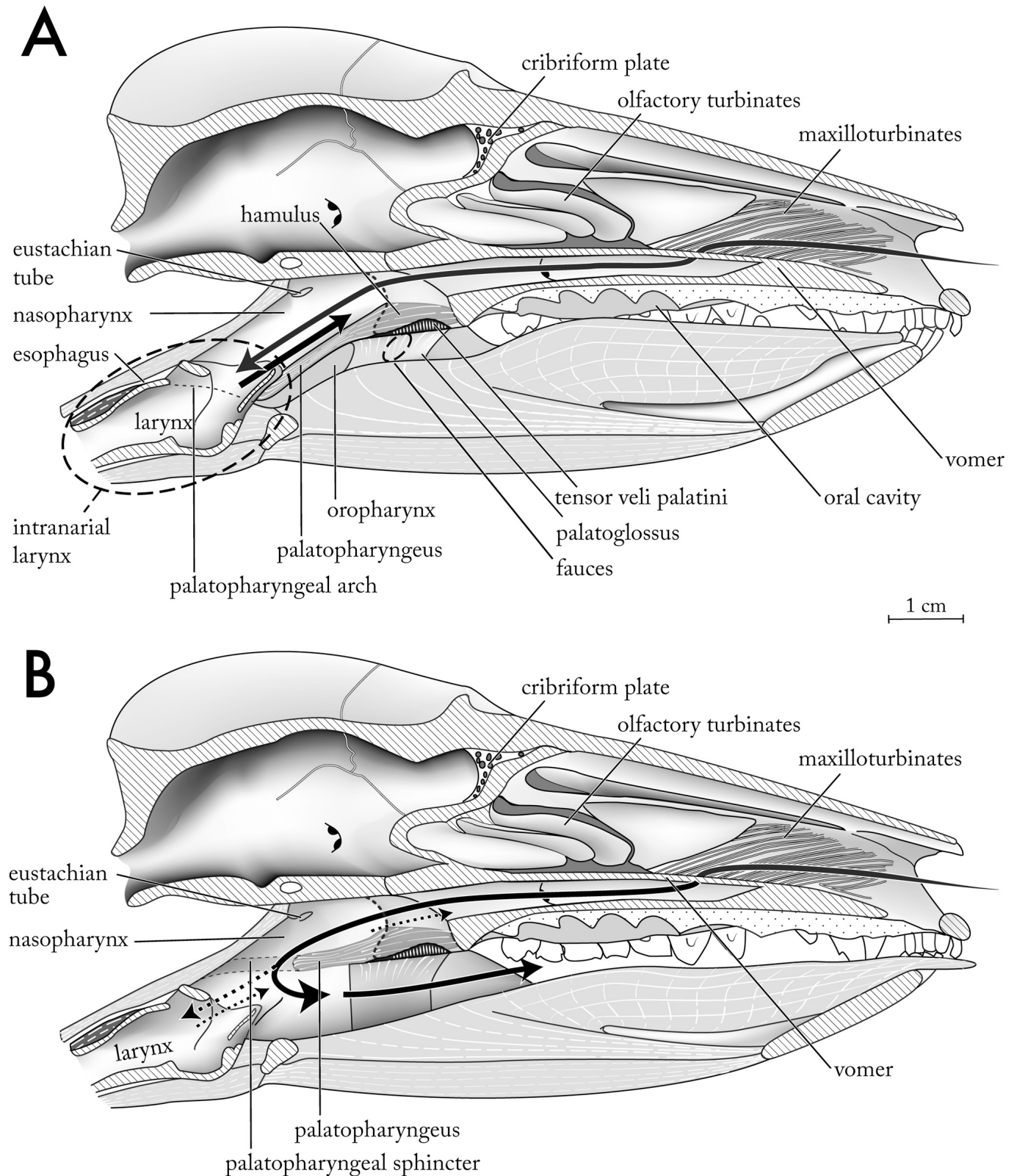
FIGURE 1. Mid-sagittal section of *Didelphis virginiana*. **A**, the larynx is held in an intranarial position by a sphincter in the palatopharyngeal muscle. Inspiratory and expiratory airflows (bold arrows) occur through the nasal cavity. The respiratory turbinals (maxilloturbinal and nasoturbinal) act as a temporal countercurrent exchange site, by recapturing most of the heat and water from expired air. This allows for considerable heat and water conservation from expired air. **B**, the larynx is withdrawn from an intranarial position. Inspiration is through the nose, and expiration largely through the mouth (bold arrows). Small tidal volume ensures mostly the tracheal dead space is ventilated (dotted arrows). The respiratory turbinals act to warm inspired air but do not recapture latent heat of evaporation. This serves to dissipate heat and simultaneously cool cranial venous blood.

Jurassic non-mammaliaform cynodont (*Brasilitherium*), a mammaliaform (*Morganucodon*), and extant mammals. The interrelationships of non-mammalian cynodonts are well known (Hopson and Kitching, 2001; Abdala, 2007; Liu and Olsen, 2010; Martinelli and Bento Soares, 2016). It is generally accepted that non-mammaliaform cynodonts form a sister group to mammaliaformes, but the interrelationships of the former are poorly documented and controversial (Sidor and Hancox, 2006; Luo, 2007; Martinelli and Rougier, 2007; Liu and Olsen, 2010; Ruf et al., 2014; Martinelli and Bento Soares, 2016).

Finally, we speculate on the structural innovations necessary for cartilaginous respiratory turbinals to assume the additional role of conserving heat and water.

MATERIALS AND METHODS

We scanned five specimens of the skulls of *Massetognathus pascuali* (MCZ 3785, 3790, 3798, 4012, 4214); five of *Probainognathus jenseni* (MCZ 4019, 4280, 4004, 4281, 4287); a snout of a non-cataloged specimen of *Elliotherium kersteni* (collected at Diepgesicht, Ladybrand, South Africa, on loan from Dr. J. Hopson); *Morganucodon* sp. (IVPP V8682); and a non-cataloged specimen of the Virginia opossum, *Didelphis virginiana*. We used an Xtek HMXST Micro-CT X-ray imaging system at the Center for Nanoscale Systems at Harvard University. Slice thickness/resolution ranged from 26.8 to 67.2 μm, voltage from 62 to 190 kV, and current from 45 and 175 μA.

With the aid of VGStudio MAX (Volume Graphics) and Amira (Visage Imaging), we then prepared three-dimensional (3D) reconstructions of various internal and external views of the skulls. Postmortem deformations to the fossil specimens (e.g., a slight dorsoventral compression to MCZ 3785 and lateral compression in MCZ 4019) were corrected in Figures 5C and 11A.

Computed tomography (CT) scanning produces a digital matrix of cubic pixels, or voxels. A gray-scale value stored in each voxel represents the specimen's radio-opacity, or density, at the corresponding point in the specimen. VGStudio MAX's reconstruction tools enabled us to reconstruct bone by rendering transparent the gray-scale values that corresponded to lower-density matrix surrounding it. Although it often proves difficult to view bones with lower, matrix-level density, because they are rendered transparent along with the matrix, such bones show up clearly in individual slices from the image stack.

The voxel matrix can be serially sliced along any axis to create a stack of images, each image representing at least a 1-voxel-thick slice from the specimen. We refer to these individual images as 'image slices.' In addition, portions of the 3D reconstructions can be cleanly removed as if by cutting the volume with a knife. Such virtual sections, to which we refer as 'cutaways,' can be made at any angle and enable us to examine the internal structures. Due to variable density in the bone, some regions are ill defined in the stereo cutaways. The same structures, however, show up well in transverse and sagittal slices, so we have included them in the line-drawn reconstructions.

To view the reconstructions, we used stereo images on printed materials, or anaglyphic 3D images onscreen, with corresponding glasses. These 3D methods of visualization, together with the examination of the internal structures of the fossils, provided excellent detail of the nasal region.

In addition, 15-μm-thick serial transverse and longitudinal sections of two paraffin-embedded heads of *Didelphis virginiana* pouch neonates were included to document the early stages of the development of the nasal cavity in modern mammals. Attachment of a cartilaginous maxilloturbinal to the membrane bones of the snout was based on an adult short-beaked echidna, *Tachyglossus aculeatus*, whose head was embedded in methylmethacrylate, sectioned serially at 1-mm intervals, and hand-ground to approximately 100 μm.

Institutional Abbreviations—IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; **MCZ**, Museum of Comparative Zoology, Cambridge, Massachusetts, U.S.A.

Anatomical Abbreviations—BS, basisphenoid; **C**, canine; **c**, unerupted canine; **cc**, cranial cavity; **ccp**, cartilaginous cribriform plate; **cet**, cartilaginous ethmoturbinal; **cmxt**, cartilaginous maxilloturbinal; **cnt**, cartilaginous nasal turbinal; **cns**, cartilaginous nasal septum; **co**, concha; **cp**, cribriform plate; **cr**, canine root; **crt**, cartilaginous respiratory turbinals; **ep**, ethmoid plate; **et**, ethmoturbinals; **exn**, external nares; **F**, frontal; **I**, incisor; **if**, incisive foramen; **infn**, foramina for infraorbital nerve; **inp**, intranarial process; **ioc**, infraorbital canal; **ios**, interorbital septum; **J**, jugal; **LAC**, lacrimal; **lc**, lacrimal canal; **ld**, lacrimal duct; **lon**, lamina orbitonasalis; **lr**, lateral ridge; **lw**, lateral cartilaginous wall of the nasal capsule; **lwv**, lateral wing of the vomer; **M**, molar; **ME**, mesethmoid; **mr**, median ridge; **MX**, maxilla; **MX-P**, maxillary-palatine suture; **mxc**, maxillary canal; **mxr**, maxillary recess; **mxt**, maxilloturbinal; **nc**, cartilaginous nasal capsule; **np**, nasopharyngeal passage; **ns**, nasal septum; **nt**, nasoturbinal; **ob**, olfactory bulb location; **olc**, opening of lacrimal canal; **o-mxr**, opening of maxillary recess; **omxt**, ossified maxilloturbinal; **on**, foramina for olfactory nerve; **op**, orbital plate of palatine; **or**, olfactory region; **OS**, orbitosphenoid; **P**, palatine; **PC**, postcanine; **pch**, primary choana; **PF**, prefrontal; **pm**, premolar; **pmp**, premaxillary process; **PMX**, premaxilla; **PO**, postorbital; **pr**, pterygopalatine ridge; **PS**, presphenoid; **PT**, pterygoid; **r**, ridge; **rpc**, replacing postcanine; **rr**, respiratory region; **sch**, secondary choana; **SM**, septomaxilla; **smc**, septomaxillary canal; **spc**, septal crest; **spf**, sphenopalatine foramen; **tl**, transverse lamina; **tppt**, transverse process of the pterygoid; **V**, vomer; **vn**, vomeronasal capsule; $\mathbf{V_2}$, maxillary nerve.

RESULTS

Nasal Region of *Massetognathus pascuali*

We begin this review of therapsid nasal regions with a description of *Massetognathus*, the best preserved of the fossils we have examined. The nasal region of the skull of *Thrinaxodon* (Fourie, 1974) closely resembles that of *Massetognathus*. Although little is known about the internal snout structure of one of the earliest known non-mammalian cynodonts, *Procynosuchus* (Broom, 1938; Kemp, 1979) from the Late Permian of South Africa, Germany, and Zambia, similarity of external features suggests the same basic internal organization as that of the Middle Triassic *Massetognathus*.

A deep keel-shaped vomer (Figs. 2A, 3B, 4, 5A, 6:sections 1–6), also observed in *Diademodon* (Brink, 1955) and *Thrinaxodon* (Fourie, 1974), divides the deep and wide nasopharyngeal passage (Figs. 2A, 3A, 6:sections 2–4). The anteroventral edges of the vomer extend laterally to form shallow ledges, whose grooved dorsal surfaces likely supported a pair of vomeronasal organs that opened into the oral cavity through the incisive foramina, as is the case in mammals and basal lepidosaurs such as *Sphenodon* (Wible et al., 1990; Hillenius, 2000). The palatal processes of the premaxilla (Figs. 5A, 6:section 1, 7B) underlie the anteroventral edges of the vomer for a short distance. Posteriorly, the vomer decreases in height, and the dorsal edge projects laterally in both directions to form a plate between and under the medially directed flanges of the palatines. Together, the vomerine plate and palatine flanges form a transverse lamina (a low-density structure not clear in the cutaway reconstruction of Fig. 2A, but readily seen in slices), which in turn forms the posterior border of a long primary choana. The internal choanae extend the length of the vomer and open into the nasopharyngeal passage, itself divided into two by the tall vomer (see dashed
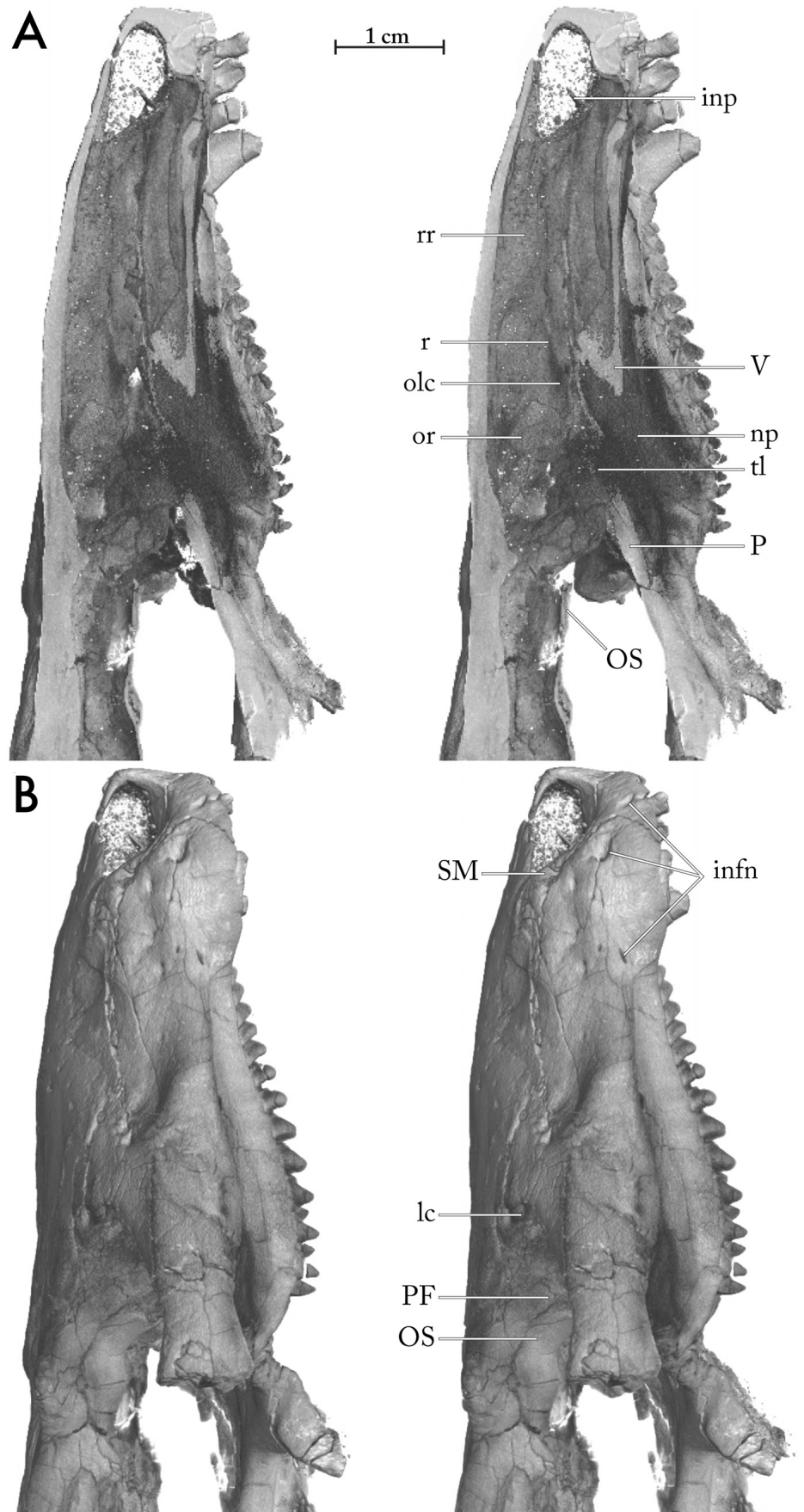
FIGURE 2. *Massetognathus pascuali* (MCZ 3798). Stereo pairs of **A**, mid-sagittal section and **B**, external views of the snout.
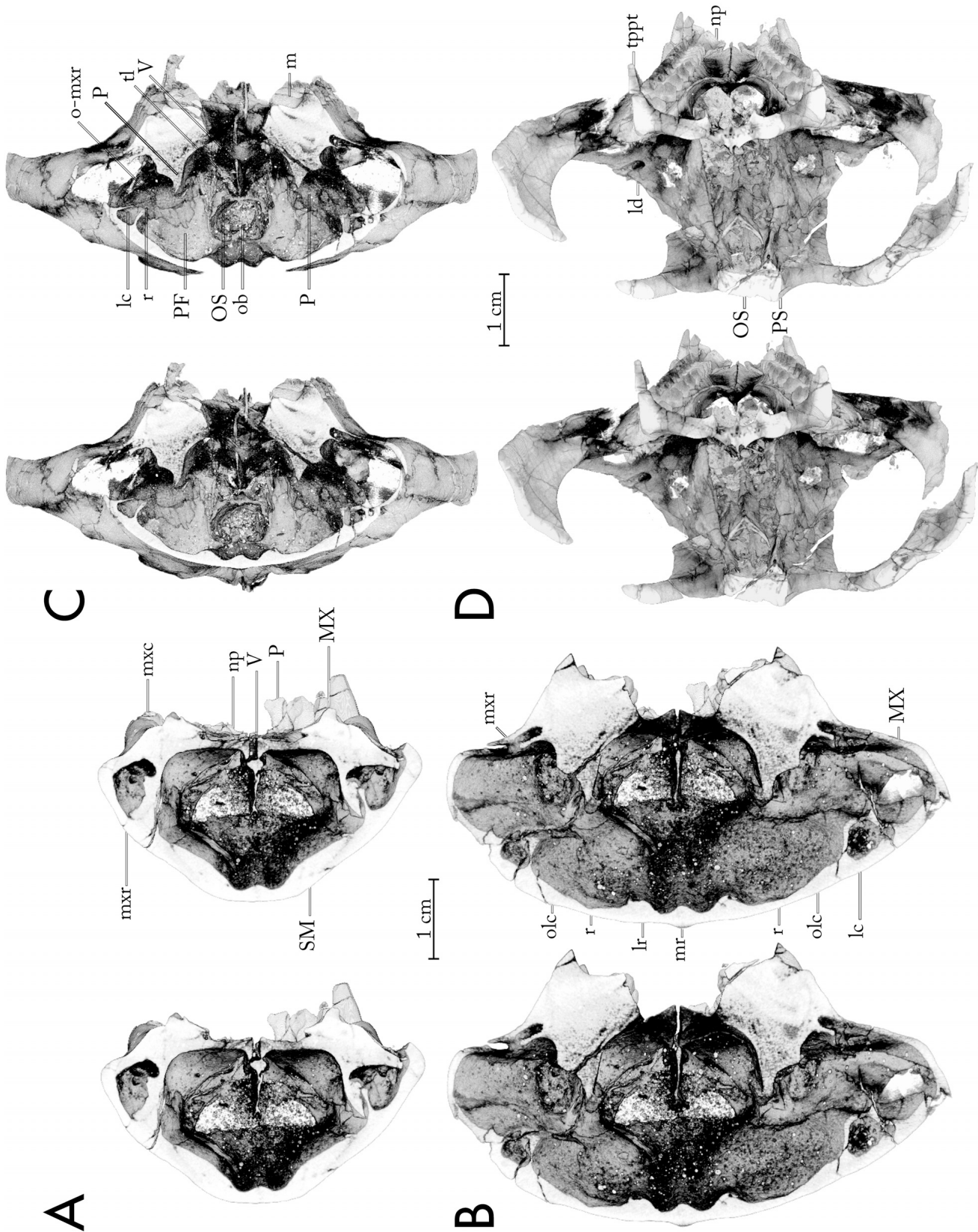
FIGURE 3. *Massetognathus pascuali* (MCZ 3798 and MCZ 3790). **A–C**, stereo pairs of cross-sections of MCZ 3798: **A**, rostral view at the position of Figure 5C, line 2; **B**, rostral view at the position of Figure 5C, line 4; **C**, caudal view at the position of Figure 5C, line 5. **D**, MCZ 3790: posterior view of nasal region.
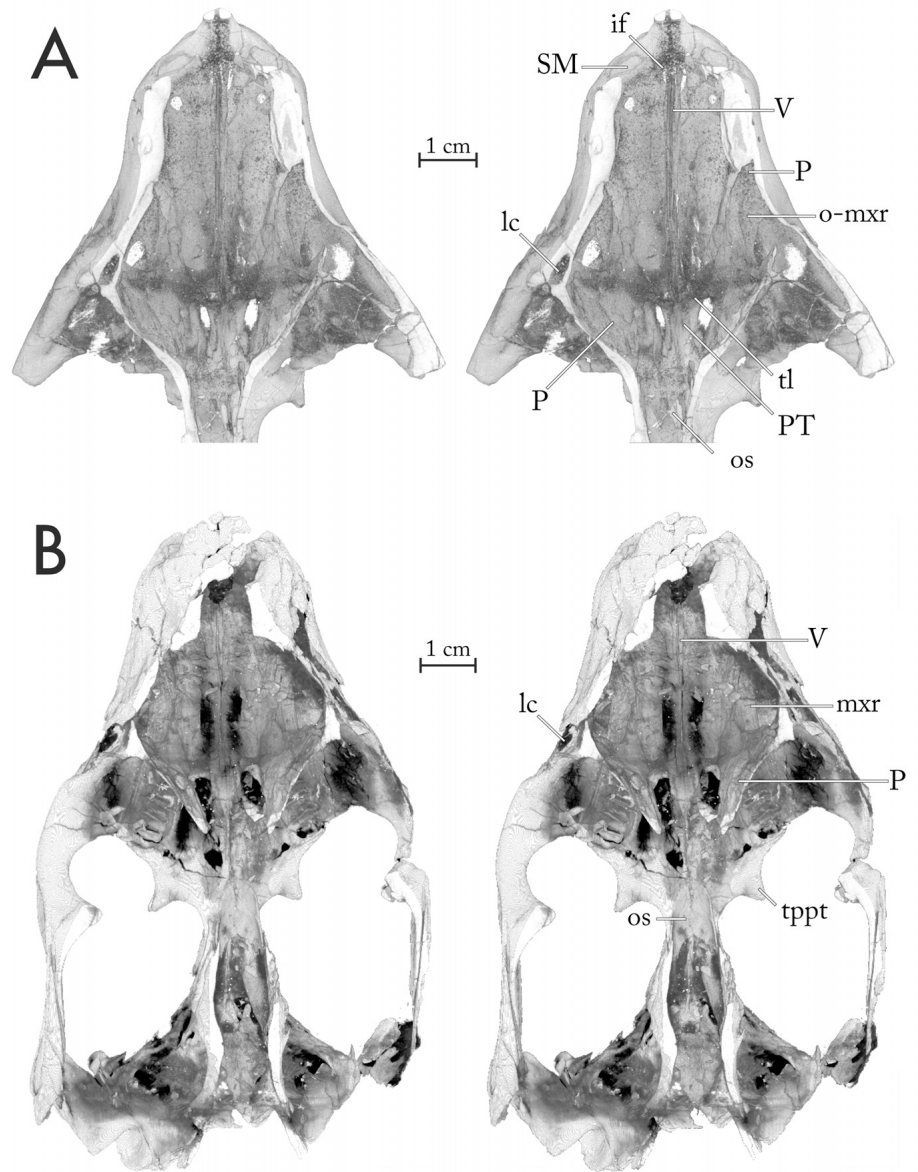
FIGURE 4. *Massetognathus pascuali.* **A**, MCZ 3798: stereo pair images of internal view of snout; **B**, MCZ 3790: stereo pair of whole skull with dorsally positioned cranial bones removed.

line in Fig. 6). The primary choana has no clearly defined anterior boundary. We concur with Hillenius (1994) that space dorsal to the transverse lamina provided an olfactory chamber, and the large space anterior to the transverse lamina contained a respiratory chamber probably filled with cartilaginous respiratory turbinals. These were likely attached to the ridge that runs forward from the opening of the lacrimal canal.

In *Massetognathus*, the grooved dorsal edge of the tall vomer would have supported the ventral edge of a cartilaginous nasal septum, as it does in extant reptiles (Bellairs and Kamal, 1981). In mammals, the mesethmoid bone ossifies within a cartilaginous nasal septum, its ventral border fitting into the forked dorsal border of the vomer. In many mammals (Moore, 1981) and most reptiles (Malan, 1946; Bellairs and Kamal, 1981), the ventral surface of the nasal capsule does not extend far below the nasal septum-vomer contact. It is likely that in non-mammalian cynodonts, the nasal capsule and attached cartilaginous respiratory turbinals were similarly restricted to the space above the dorsal edge of the vomer (Fig. 6: sections 2–3, left halves of each cross-section) and did not extend into the nasopharyngeal

passage. Admittedly, maxilloturbinals in mammals with an unusually tall vomer (e.g., *Daubentonia*) extend ventrally below its dorsal edge (Maier and Ruf, 2014). This suggests that branching of maxilloturbinals is not necessarily constrained to the space dorsal to the vomer. If such a condition were present in non-mammalian cynodonts (Fig. 6:sections 2–3, right halves of cross-sections), the volume of their respiratory chambers would have been considerably increased. Thus, in *Massetognathus*, inhaled air could flow either directly into the nasopharyngeal passage or through the respiratory chamber, reaching the nasopharyngeal passage via the primary choana (upper curved arrow in Fig. 5A–B). The route taken by the bulk of respiratory airflow would have depended on air velocity (low at rest, high during activity), as well as relative resistance offered by respiratory turbinals. Without further evidence on the extent and density of maxilloturbinals, it is hard to speculate on the preferred airflow route, but it would have varied with relative resistance offered by respiratory turbinals.

The palatine has a complex shape. It forms much of the lateral wall, roof, and floor of the nasopharyngeal passage, and part of
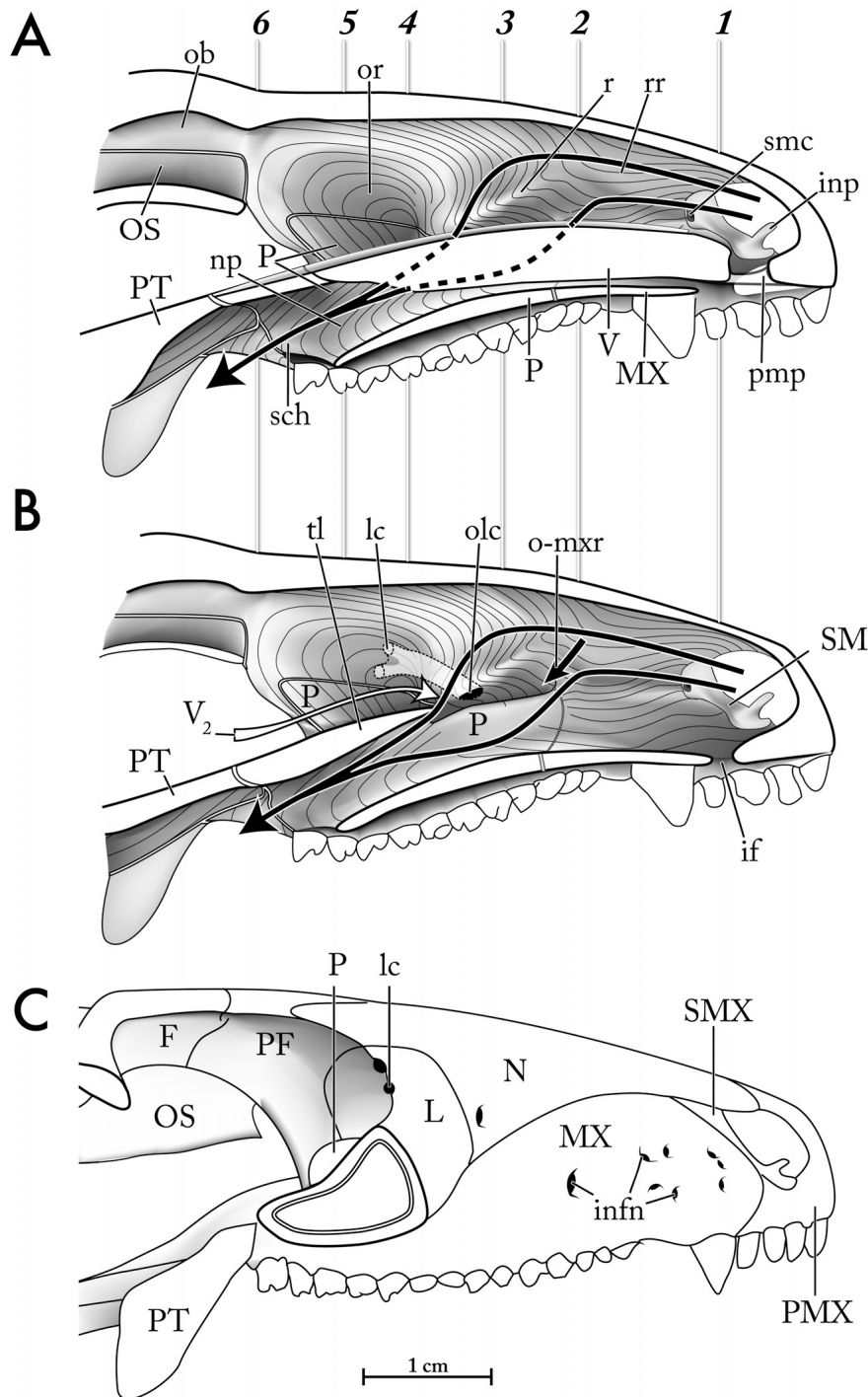
FIGURE 5. *Massetognathus pascuali* (MCZ 3798). **A**, internal view of the nasal region as seen from the mid-sagittal perspective. Reconstruction based on Figure 2A. Long arrows indicate the potential path of inspiratory airflow through the respiratory chamber. **B**, internal view of the nasal region from a parasagittal plane slightly lateral to that of **A**. Short bold arrow points to the large opening into the maxillary recess. **C**, external view of the snout and orbital region. Reconstruction based on Figure 2B.

the posterolateral wall of the olfactory region. A soft palate probably extended the hard palate (Barghusen, 1986) and formed the floor to a wide nasopharynx.

A large foramen connects the nasal cavity with the maxillary recess, or maxillary antrum (Fourie, 1974; Benoit et al., 2016). This is often referred to as a sinus (Kemp, 1980), but because it did not form through secondary pneumatization (Rossie, 2006), the term recess more accurately describes it. The anterior portion of this foramen as seen in a transverse section lies between the palatine and maxilla (Fig. 6). As seen in dorsal view (Fig. 7B, tip of white arrow) the posterior portion lies between the palatine and lacrimal. Figure 7B shows the mediolateral

extent of the maxillary recess in *Massetognathus*, and its extension into the zygoma, as a shaded and dotted outline in the dorsal view of the snout. A branching maxillary canal (mxc) extends forwards from the large maxillary recess and exits to the exterior through several foramina.

The lacrimal canal that opens internally above the maxillary recess and a short ridge (r), best viewed on the left stereographs in Figures 2A and 3B, extends forward beyond the opening. We cannot confirm that this ridge extended further forward onto the nasal bone, as claimed by Hillenius (1994). A nasolacrimal duct may have run forward below this ridge to reach a foramen in the dorsal region of the septomaxilla and continued through the
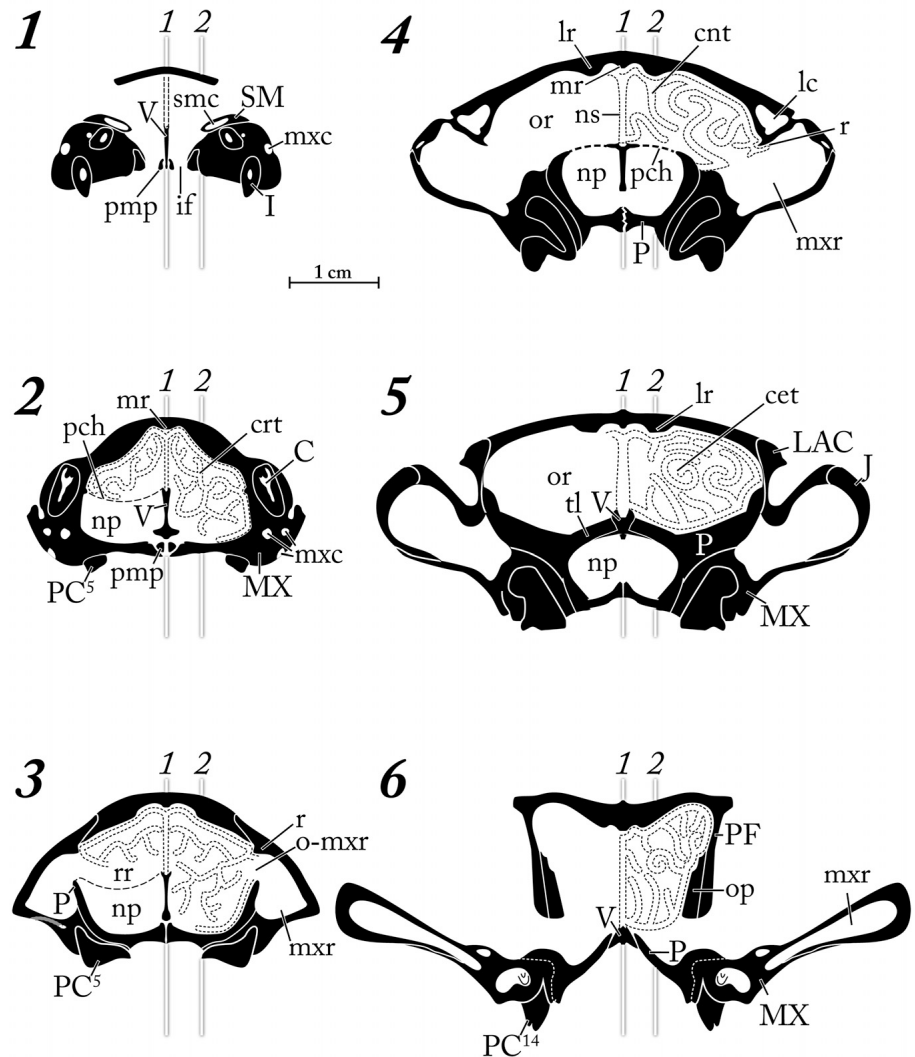
FIGURE 6. *Massetognathus pascuali* (MCZ 3798). A series of transverse sections (1–6) through the nasal region at the positions indicated in Figures 5A and 7A (1–6). Vertical lines labeled 1 and 2 indicate the positions of the sagittal planes shown in Figure 5A and B, respectively. Dotted outlines provide a hypothetical reconstruction of the cartilaginous nasal capsule and olfactory and respiratory turbinals.

septomaxilla to a ventral opening below the intranarial process (Wible et al., 1990; Hillenius, 2000). We cannot identify any suture between the nasal and maxilla on the internal surface of the snout, nor do we find evidence of the ventral edge of the nasal having been pushed over the dorsal edge of the maxilla to produce the ridge described by Hillenius (1994).

The internal surfaces of the membrane bones above the olfactory region in *Massetognathus* contain three ridges: a median and two lateral ridges on the ventral surface of the nasal bones. Such ridges have been reported in the olfactory chamber of several non-mammalian therapsids (Brink, 1955; Fourie, 1974; Kemp, 1980; Hillenius, 1992; Ruf et al., 2014).

A thin bony wall—formed by the lacrimal, the dorsally directed orbital process of the palatine, and the ventrally directed wings of the frontal and prefrontal—partially separates the olfactory chamber from the orbital region. The only foramina penetrating this posterolateral wall are two openings for the lacrimal canal. We deduce that all nerves and blood vessels entered the nasal cavity medial to this wall (Fig. 8A, white arrow). However, in one specimen (MCZ 3790), the wall is penetrated on both sides of the skull by holes with ragged and ill-defined edges in the palatine and lacrimal (Fig. 3D). We interpret these as the result of poor preservation or damage that occurred during preparation rather than the foramina for infraorbital canals. In similar vein, Kemp (1979, 1980) shows a well-defined foramen in *Procynosuchus* that he considered to have served as an infraorbital canal, and a poorly defined opening in the posterior wall of the nasal cavity in *Luangwa*.

The orbitosphenoid is a long trough-shaped bone with a short median keel. Together with the frontal, it forms a space for the olfactory bulb behind the posterodorsal aspect of the olfactory chamber.

Nasal Region of *Probainognathus jenseni*

The structure of the nasal region of the carnivorous non-mammalian cynodont, *Probainognathus*, generally resembles that of its herbivorous contemporary, *Massetognathus*.

A tall, thin plate constitutes the anterior part of the vomer, bifurcating a deep and wide nasopharyngeal passage. The vomer in *Probainognathus* does not extend as far forward as in *Massetognathus*, and only the dorsal border of the posterior two thirds of the vomer has a groove for the reception of a cartilaginous nasal septum. The posterior vomer has short lateral wings wedged posteriorly between the transverse processes of the palatine, together forming the transverse lamina. As in *Massetognathus*, inhaled air could flow either through the respiratory chamber (upper arrow in Fig. 9A), then through the primary
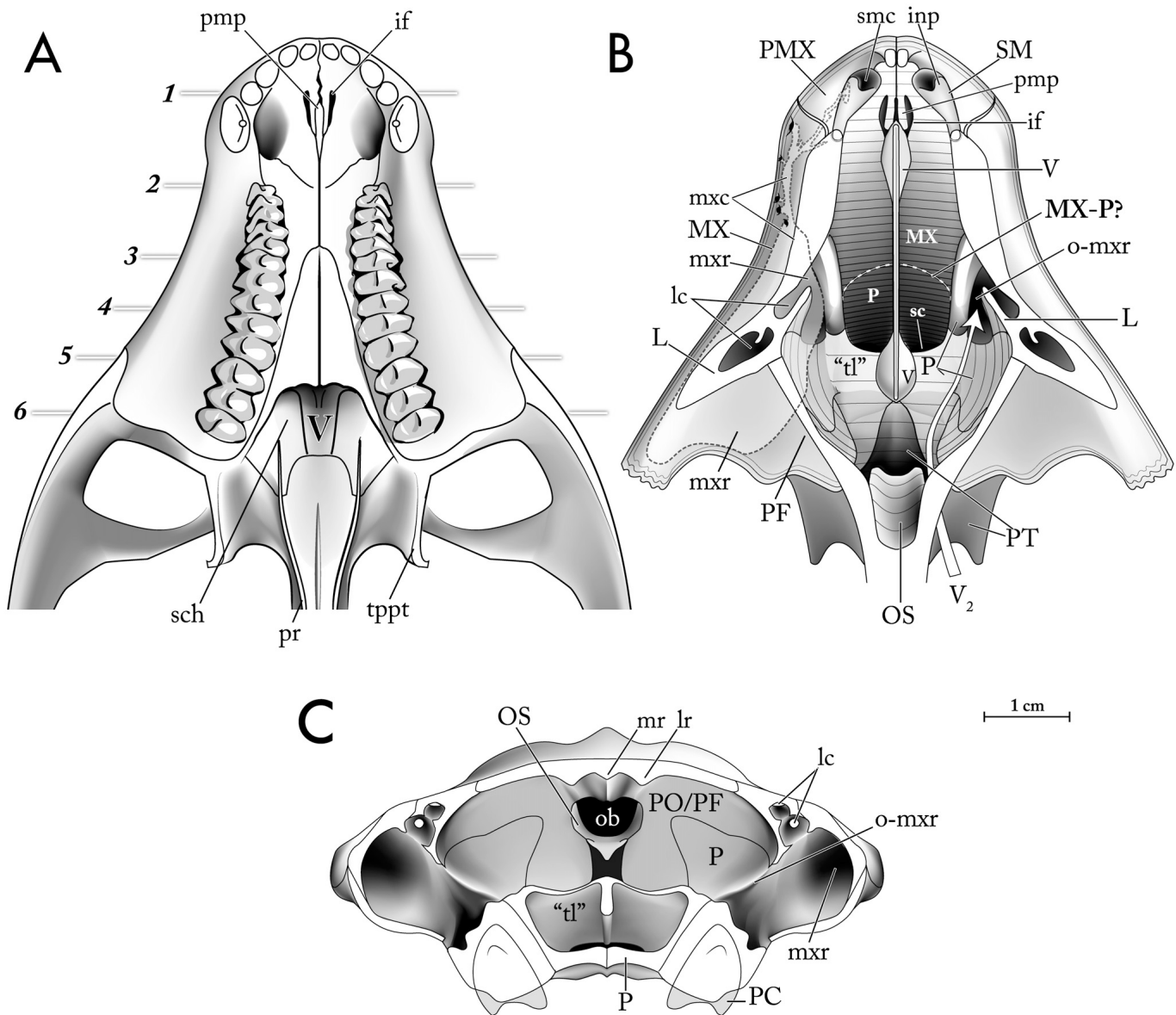
FIGURE 7. *Massetognathus pascuali* (**A**, **B**: MCZ 3798, **C**: MCZ 3790). **A**, ventral view of palate. Lines labeled 1–6 indicate positions of sections in Figure 6; **B**, snout in dorsal aspect, based upon Figure 4A, with the roof removed to expose the internal structure. Dotted line on the left side indicates a dorsal view of the extent of the maxillary recess. Lines labeled 1–6 indicate positions of sections in Figure 6. **C**, anterior view of postnasal region, based upon Figure 3C.

choana into the nasopharyngeal passage, or directly into the nasopharyngeal passage (lower arrow in Fig. 9A).

The maxillary recess is massive and opens into the olfactory chamber through a long aperture (Fig. 9B). It extends posteriorly into the zygoma and forward as far as the second postcanine. It narrows anteriorly to form as a maxillary canal that branches into several smaller canals, each opening to the exterior surface of the maxilla. The lacrimal canal opens onto the internal surface of the lacrimal and a poorly defined short ridge extends forward from this point.

The olfactory bulb of *Probainognathus* lay in a chamber between a deep depression in the frontal above and a trough in the orbitosphenoid below. A low median ridge on the ventral surface of the frontal bisects the chamber. In some specimens of *Probainognathus*, the bones surrounding the nasal capsule are substantially thicker than in others of similar size. For example, MCZ 4275 has a transverse lamina with a maximum thickness of 3.07 mm, whereas that of MCZ 4019 is only 2.07 mm. The orbitosphenoid, positioned high in the skull behind the nasal cavity, has a short median keel. As in *Massetognathus*, no ossifications are found between the orbitosphenoid above and the dorsal edges of the parasphenoid and pterygoid below. Anterior to the recess for the olfactory bulb, the ventral surfaces of the frontal and nasal support a deep median 'V'-shaped ridge of cancellous bone. Some slices show a poorly defined midline suture. In an anterior direction, this ridge decreases in height and expands laterally to form two lateral ridges. In one specimen (MCZ 4280), fragments of bone that seem to have broken off from the membrane bones surrounding the nasal cavity float in matrix above the opening of the nasolacrimal duct.
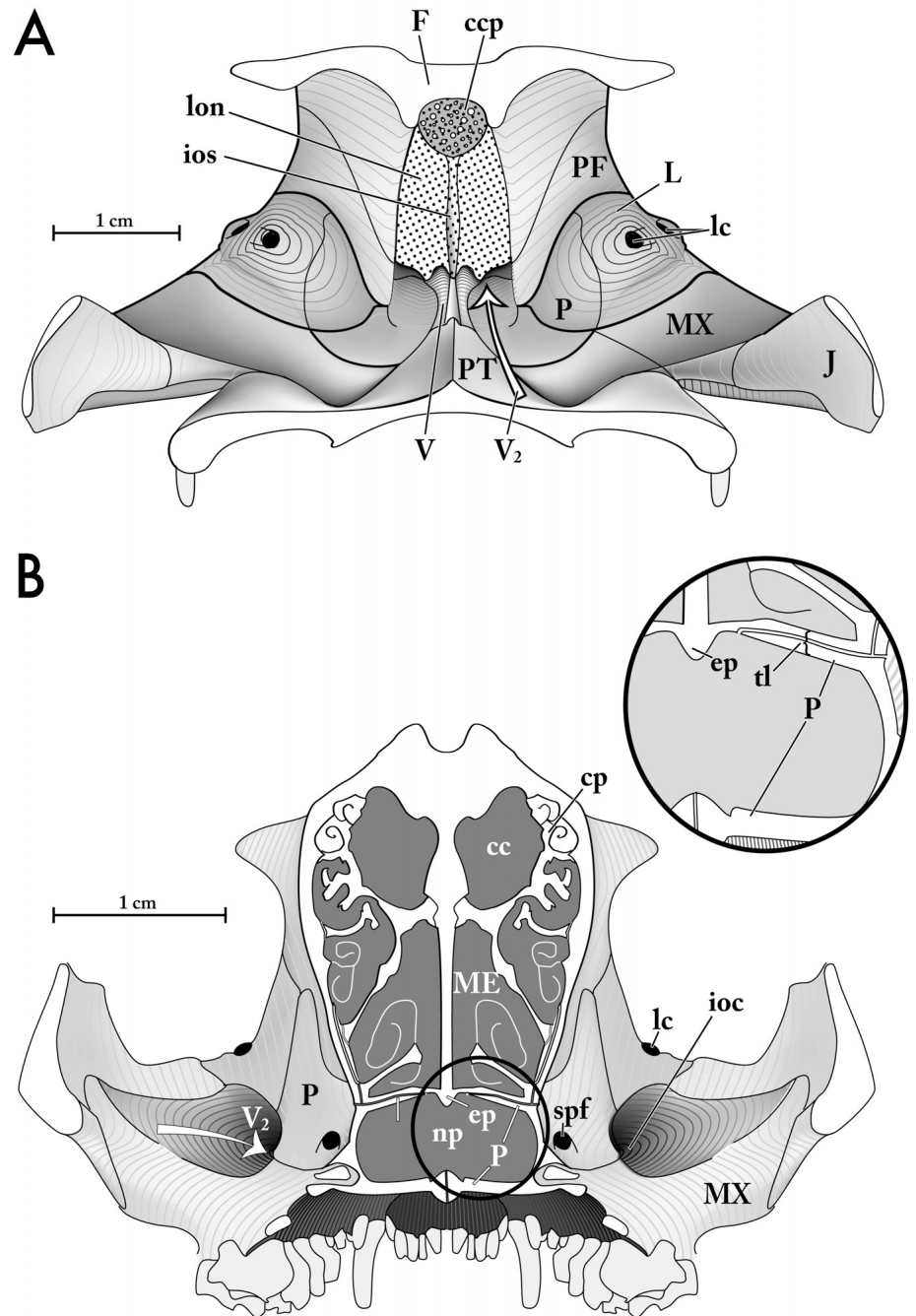
FIGURE 8. **A**, reconstruction of the nasal region of *Massetognathus pascuali* from a posterior view, based partially on MCZ 3798 and 3790 and Figure 3D; **B**, posterior view of the nasal region of *Didelphis virginiana*. The magnified region shows that the ethmoid plate (ossification of the floor of the nasal capsule) constitutes the major portion of the transverse lamina.

A wide notch extends laterally into the medial edge of the posterolateral wall to the nasal cavity. The notch continues into the maxillary recess and has a short extension into the zygoma. Because there are no foramina in the posterolateral wall of the nasal cavity other than the openings for two lacrimal canals, the maxillary branch of the trigeminal nerve (Fig. 9C), with associated blood vessels, probably entered the nasal cavity through this notch.

The maxillary recesses of gomphodont cynodonts such as *Massetognathus* and *Luangwa* (Kemp, 1980) and the tritylodontid *Kayentatherium* (Sues, 1986) are much larger than that of *Thrinaxodon*. The latter retains an exceptionally well-preserved maxillary canal with several branches to the exterior and to the upper dentition (Fourie, 1974). A long slender anterior maxillary recess above the postcanine dentition is present in the therocephalian *Tetracynodon darti* (Sigurdsen et al., 2012).

In therocephalians, from which the non-mammalian cynodonts probably arose (Kemp, 1979; Botha and Smith, 2007), the respiratory chamber opens directly into the oral cavity through the primary choana (Sigurdsen, 2006; Sigurdsen et al., 2012). The vomer of basal therocephalians, such as scylacosaurids, had a deep ventromedial keel (Van Den Heever, 1994). Soft tissue choanal folds may, hypothetically, have pressed against the ventral edge of this keel during mastication to form a transitory secondary palate (Maier et al., 1996) and temporary nasopharyngeal passages on either side of the vomer. In non-mammalian cynodonts such as *Massetognathus*, a bony secondary palate obviates the need for choanal folds. The primary choana of primitive
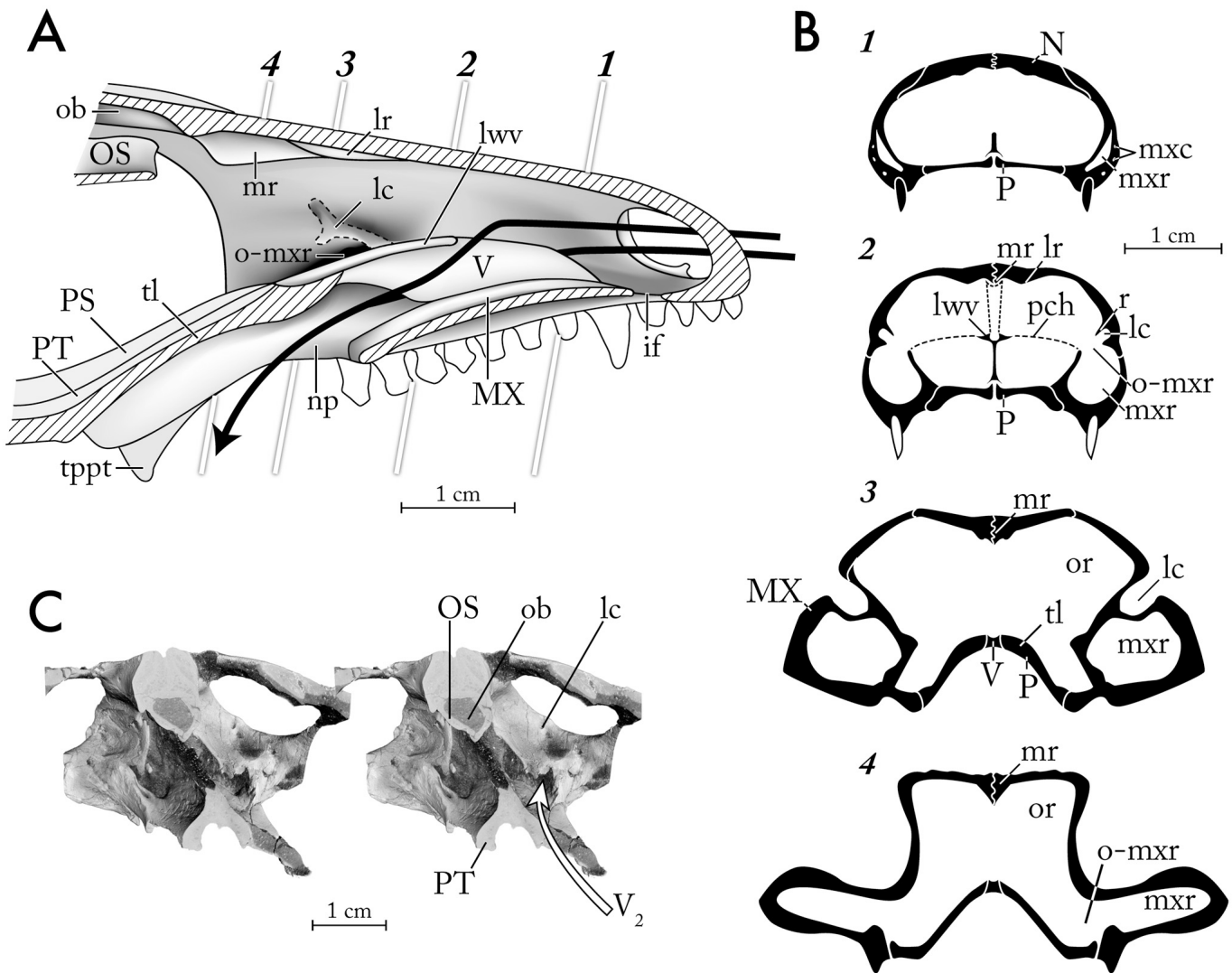
FIGURE 9. *Probainognathus jenseni* (MCZ 4019, 4119). **A**, internal view of the reconstructed nasal region as seen from the parasagittal perspective, slightly lateral of the midline; **B**, transverse slices at positions indicated in **A**, 1–4. **C**, stereo pair of a posterior view of the nasal region.

therocephalians is bordered posteriorly by the junction between the vomer and palatine (i.e., the transverse lamina), laterally by the palatine and maxilla, anteriorly by the premaxilla, and medially by the vomer. The respiratory chamber, smaller than that of non-mammalian cynodonts, lay above the vomer. A marked increase in the volume of the respiratory chamber constitutes a major feature of non-mammalian cynodonts.

Nasal Region of Non-mammaliaform Cynodonts—Non-mammaliaform cynodonts include two separate families: the Tritheledontidae and Brasilodontidae (Sidor and Hancox, 2006; Martinelli and Rougier, 2007; Bonaparte and Migale, 2015). Genera included in the Brasilodontidae are the most closely related to Mammaliaformes (Martinelli and Bento Soares, 2016). Here we describe the nasal region of a tritheledontid, *Elliotherium* sp., and compare it with a published account of the brasilodontid *Brasilitherium riograndensis* (Ruf et al., 2014).

The following description is based upon the snout of a specimen, tentatively identified as *Elliotherium*, from the Late Triassic Lower Elliot Formation of South Africa. We identified the specimen based upon several features also present in *Elliotherium kersteni* (see Sidor and Hancox, 2006), such as the presence of an interpterygoid vacuity, a ventrally depressed secondary

palate, and a row of 13 simple conical postcanine teeth aligned parasagittally. The new specimen of *Elliotherium* appears closely related to *Pachygenelus* and *Diarthrognathus* from the Upper Elliot Formation. All have a deep and slender transverse process of the pterygoid that contacts the lower jaw, and two procumbent lower incisors that occlude between two upper incisors (Allin and Hopson, 1992). The snout of the new specimen is slightly distorted, riddled with small cracks, and some of the bones have separated along suture lines.

The anterior part of the vomer is a tall vertical plate partially dividing the nasopharyngeal passage. Palatine processes of the premaxilla flank the anterior tip of the vomer. The vomer increases in height until it reaches a location above the third postcanine, then shrinks to a slender rod with lateral wings. Transverse processes of the palatine contribute to the transverse lamina and hold in place the posterior portion of the vomer (Fig. 10C:section 5). The dorsal edge of the posterior half of the vomer forms a groove to support a cartilaginous nasal septum. The anterior portion of the vomer lacks a groove, suggesting, as in *Probainognathus*, that any cartilaginous nasal septum stopped short of the most rostral region of the respiratory chamber. There is no clear division of the nasal cavity into olfactory and
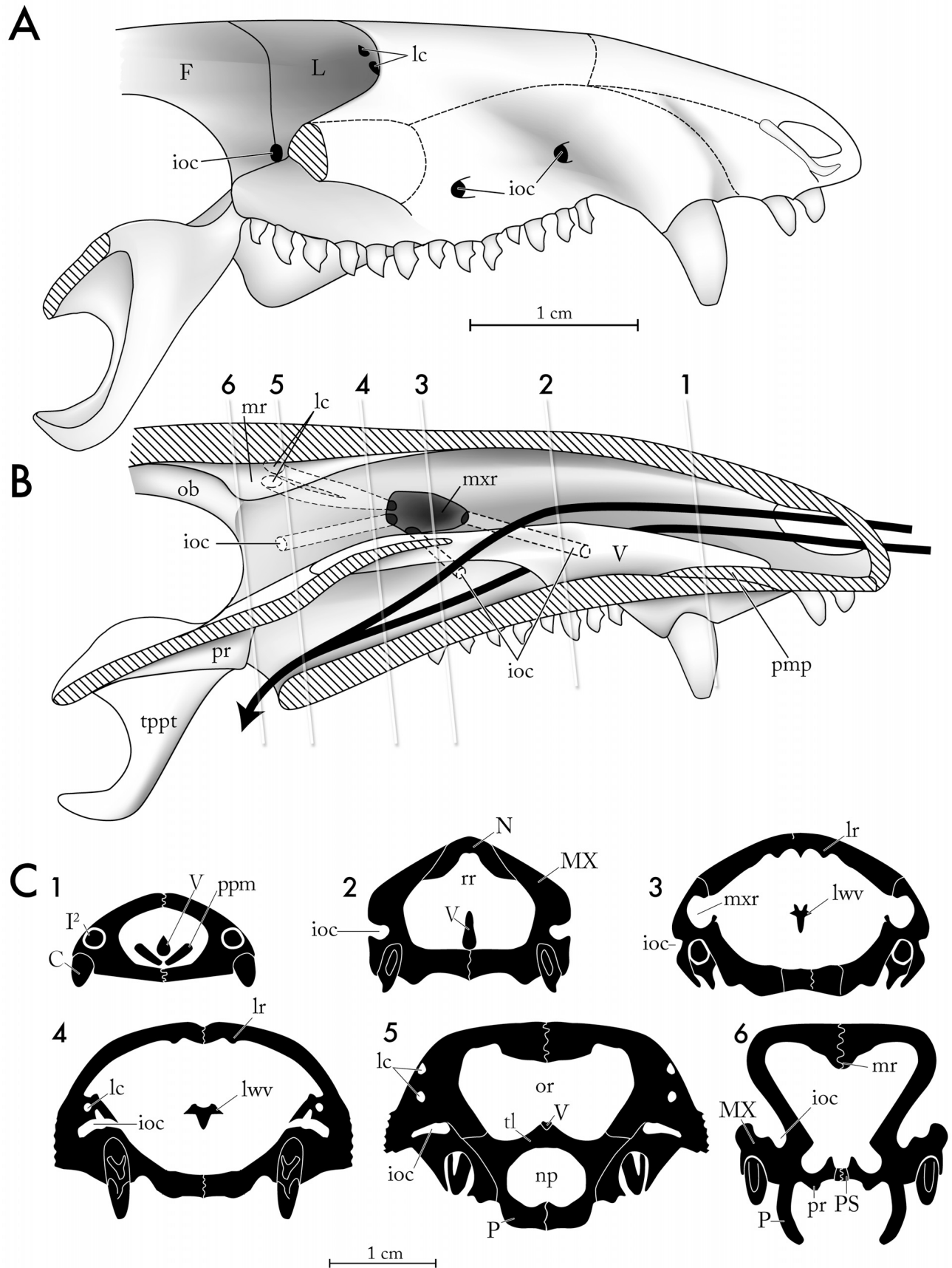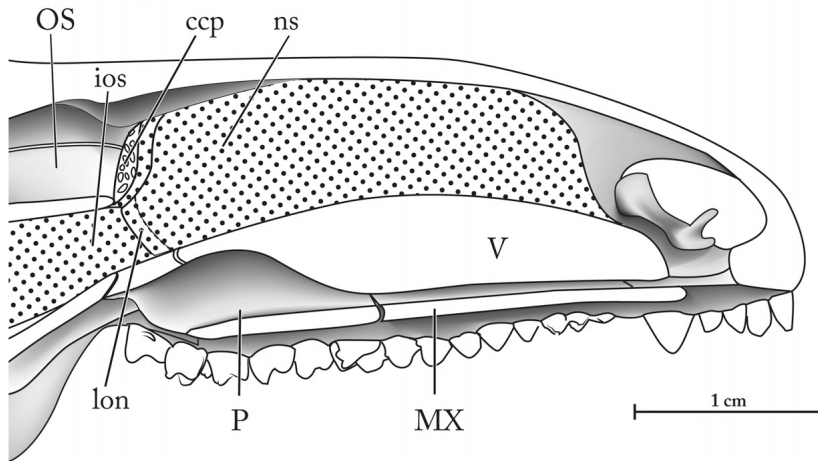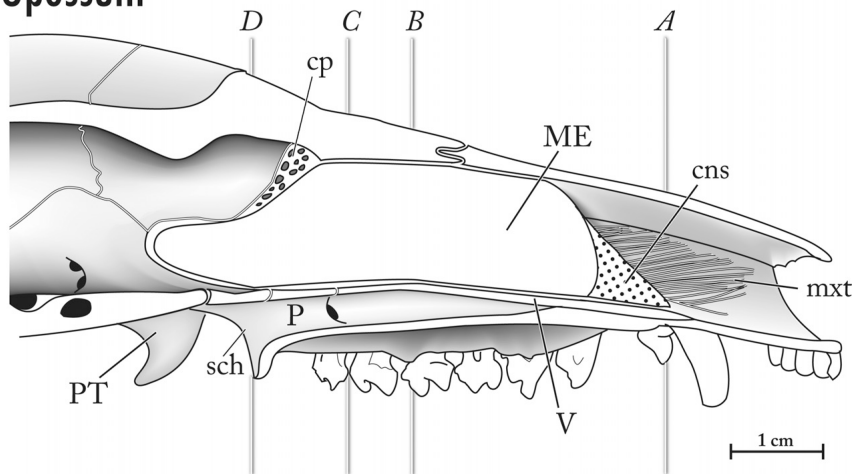
FIGURE 10. *Elliotherium kersteni* (uncataloged specimen). **A**, external view of the reconstructed snout; **B**, internal view of the reconstructed nasal region as seen from the parasagittal perspective, slightly lateral of the midline; **C**, transverse slices corresponding to lines 1–6 in **B**.
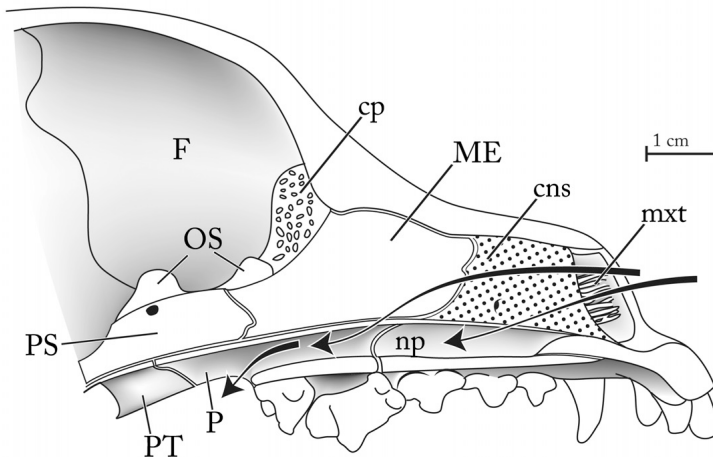
FIGURE 11. Comparison of the mid-sagittal sections of the nasal region of **A**, *Massetognathus pascuali*, **B**, *Didelphis virginiana*, and **C**, *Canis lupus domesticus*. Bone is shown as shaded white, cross sections of bone as white, and cartilage as stippled.

respiratory chambers, but the olfactory chamber occupied the space above the transverse lamina, and the respiratory chamber the space above the vomer, anterior to the transverse lamina. Air flowed through the respiratory chamber (upper arrow, Fig. 10B) or directly into the nasopharyngeal passage (lower arrow, Fig. 10B). Posteriorly, the ventral surface of the secondary palate is convex and its lowest point extends well below the level of the postcanine teeth.

The bones surrounding the nasal cavity are much thicker in this specimen of *Elliotherium* than in *Probainognathus* (Figs. 9B, 10C). The nasal bones have a thick and deep median ridge divided by a midline suture anterior to a depression in the

ventral surface of the frontal that marks the location of the olfactory bulb. Faint lateral ridges extend forward, parallel to the median ridge. We can identify no additional ridges that could have been associated with respiratory turbinals.

In contrast to *Probainognathus*, the *Elliotherium* specimen has a foramen rather than a notch in the posterolateral wall of the nasal cavity. This foramen, bordered by the lacrimal, a descending flange of the frontal, and an orbital flange of the palatine, opens into a canal that projects to the posterior edge of a shallow pocket on the inner surface of the nasal cavity. We suggest that the canal is an infraorbital canal and the pocket a remnant of the large maxillary recess present in earlier non-mammalian cynodonts. Two other canals run from the maxillary recess and open on the external surface of the maxilla: one above the sixth postcanine and the other above the first. They are found in similar positions to such canals in *Morganucodon* (Kermack et al., 1981), opening more posteriorly than the multiple openings for cranial nerve V_2 in earlier non-mammalian cynodonts. This may suggest (Estes, 1961) the presence of a fleshy cheek in *Elliotherium* and *Morganucodon*, with nerves exiting further back to supply muscles not present in earlier forms. Two lacrimal canals run forward from the anterior edge of the orbit to the maxillary recess. The posterior and anterior openings are clear, but it is difficult to identify the canals clearly within the lacrimal bone.

As in *Probainognathus*, fragments of bone are preserved within the nasal cavity. They appear to be parts of the broken inner wall of the nasal cavity, and it is unlikely that they represent remnants of turbinals or other ethmoid bones.

Ruf et al. (2014) suggest that the nasal cavity of *Brasilitherium* has several derived features compared with more basal non-mammaliaform cynodonts, such as (1) a lamina terminalis (ossified floor of the cartilaginous nasal capsule); (2) a transversely wide ridge joined to the ventral surface of the frontal, identified as parts of a mesethmoid; (3) pieces of ossified turbinals; and (4) a nasopharyngeal duct undivided by the vomer as in some therian mammals. The space for an olfactory bulb in *Brasilitherium* (Rodrigues et al., 2014) lacks a floor that in earlier non-mammalian cynodonts is formed by the orbitosphenoid. This suite of characters leads Ruf et al. to conclude, "…*Brasilitherium riograndensis* represents a transitional stage in the evolution of the mammalian nasal pattern not known so far" (Ruf et al., 2014:2028).

In non-mammalian cynodonts, the vomer partially divides the nasopharyngeal passage. The vomer, together with medially directed flanges of the palatine, forms the transverse lamina. In mammals, in contrast, the cartilaginous nasal capsule floor (lamina transversalis posterior, sometimes referred to as the lamina terminalis—see Zeller, 1989; Maier and Ruf, 2014) ossifies and together with a reduced contribution of the palatine and vomer forms most of the transverse lamina above the nasopharyngeal passage. Ruf et al. (2014) claim a similar arrangement existed in *Brasilitherium*. Although it is difficult to judge from the relevant figure in Ruf et al. (2014:fig. 4b), the transverse section through this region in *Brasilitherium* closely resembles that of non-mammalian cynodonts, suggesting that here too only the palatine and vomer formed the transverse lamina.

Ruf et al. (2014) interpret the broad protuberance of cancellous bone, that forms a pronounced median ridge on the ventral surfaces of the frontal and nasal in *Brasilitherium*, as a dorsal part of the *mesethmoid*. However, a similar ridge is found in *Elliotherium, Probainognathus,* and *Massetognathus*, except that in these specimens it is divided by a midline suture and therefore cannot be interpreted as a *mesethmoid*. The same may be true for this structure in *Brasilitherium*.

The position of the olfactory bulb in *Brasilitherium* (Rodrigues et al., 2014) is identical to that of non-mammalian cynodonts. As described above, in *Probainognathus*, a recess or 'roof' in the dorsal part of the frontal and a 'floor' formed by the orbitosphenoid housed the olfactory bulb. The *Brasilitherium* specimen to

which Ruf et al. (2014) referred lacks an orbitosphenoid in this position. Instead, they misidentify an orbitosphenoid in the posterolateral wall of the olfactory chamber. This would be an unusual location for an orbitosphenoid in a non-mammalian cynodont or mammaliaform. In therian mammals (Figs. 11 and 12), the orbitosphenoid lies more ventral in position and in many cases medial to the ethmoid recess (sinus sphenoidalis; Rowe et al., 2005; Maier and Ruf, 2014). In *Massetognathus, Probainognathus*, and *Elliotherium*, the descending flange of the frontal, the lacrimal, and an orbital flange of the palatine form the posterolateral wall of the olfactory chamber. The position and shape of this wall in all three forms resembles that of *Brasilitherium*. Even in *Morganucodon* (see below), the orbitosphenoid forms a floor to the pocket for the olfactory bulb. Therefore, we suggest that in *Brasilitherium*, the orbitosphenoid occupied a similar position but was lost in the referred specimen.

Ruf et al. (2014) describe a ridge on the ventral surface of the nasal bone, which they conclude supported nasoturbinals. They also identify isolated pieces of bone within the nasal cavity of *Brasilitherium* as ossified ethmoturbinals, nasoturbinals, or hyoid. The vertical plate identified as a nasal septum occupies the same position as the vomer does in *Elliotherium*. In the absence of a more complete description of the shape of these pieces, it is difficult to confirm the view that the isolated fragments of bone constituted ossified portions of a cartilaginous nasal capsule. We conclude that the structure of the nasal region in *Brasilitherium* is close to that of *Elliotherium* and that the evidence for ossification of parts of the nasal capsule in *Brasilitherium* is not strong.

Nasal Region of Mammaliaformes

Kermack et al. (1981) describe isolated bones of *Morganucodon* as having median and lateral ridges on the ventral surface of the nasal, as well as a ridge on the maxilla above the nasolacrimal 'groove' that extends forward from the opening of the nasolacrimal canal. These appear to be identical to those present in *Massetognathus*. They claim that the ethmoid and turbinals attached to these ridges and that "the presence of these ridges on the medial surface of the maxilla is the only direct evidence for the existence of maxillo-turbinals in *Morganucodon*, but we believe it to be conclusive" (Kermack et al., 1981:36). Although no part of the ethmoid complex is preserved in *Morganucodon*, Kermack et al. (1981) claim that it possessed ossified maxilloturbinals. The only well-preserved part of the nasal region in the *Morganucodon* specimen available to us (IVPP V8682) is the vomer. Reduced in height, the vomer lacks the tall median plate that divides the nasopharyngeal passage in non-mammalian cynodonts. Also present in this specimen is a partial orbitosphenoid including a segment of an ossified interorbital septum. A vertical ridge on the internal surface of the orbitosphenoid indicates the position of a deep annular fissure between the olfactory bulb and the cortex (Rowe et al., 2011). Anterior to the orbitosphenoid, no parts of the nasal capsule appear to have been ossified. In *Morganucodon*, the space for the olfactory bulb is situated posterodorsal to the olfactory chamber, as it is in *Massetognathus* and *Probainognathus* (Rowe et al., 2011).

Docodontan mammaliaforms diversified and flourished during the Middle Jurassic (Luo et al., 2015; Meng et al., 2015). The only docodont in which the nasal region is known to be preserved is *Haldanodon exspectatus* from the Upper Jurassic (Lillegraven and Krusat, 1991). Despite its poor state of preservation, this specimen of *Haldanodon* exhibits the first signs of ossification of the nasal capsule. According to Lillegraven and Krusat (1991), these ossifications include a mesethmoid, a cribriform plate, and turbinal scrolls (including a maxilloturbinal), but these structures were not figured or described in detail. If verified,
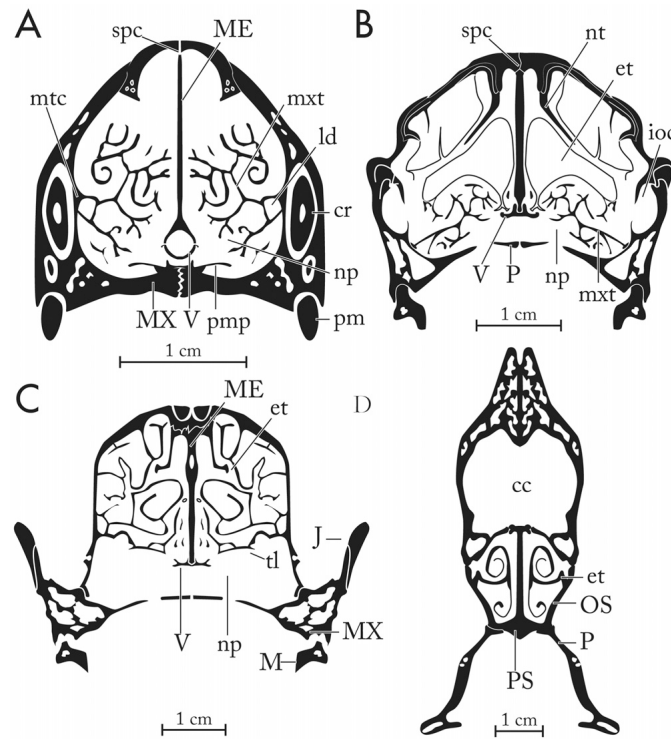
FIGURE 12. Transverse sections through the nasal capsule of an adult *Didelphis virginiana*. Position of sections **A** through **D** are indicated by vertical lines in Figure 11B.

these would further support the phylogenetic proximity of docodonts to crown-clade mammals (Luo et al., 2015).

DISCUSSION AND CONCLUSIONS

Speculations on the Structure of the Nasal Capsule of Non-mammalian Cynodonts

Turbinals—Several features of the mammalian nasal region are also present in non-mammalian cynodonts and mammaliaforms: a large respiratory region anterior to the olfactory region, a transverse lamina, and a nasopharyngeal passage. Given these features and the close relationship between non-mammalian cynodonts and mammals, it is reasonable to assume that both non-mammalian cynodonts and mammaliaforms possessed respiratory and olfactory turbinals. In amphibians, reptiles, and birds, the nasal capsule is cartilaginous, as it is during the early stages of ontogeny in mammals. We conclude that non-mammalian cynodonts and mammaliaforms also possessed a cartilaginous nasal capsule and that no structures comparable to the ossified portions of the nasal capsule in mammals were present. The sequence in which different regions of the mammalian nose develop and ossify during ontogeny forms the basis for our interpretation of the internal structure of the nasal capsule in non-mammalian cynodonts, including the position and support of hypothetical cartilaginous turbinals (Fig. 6).

In mammals, the median or septal crest develops above a cartilaginous nasal septum, which ossifies to form the mesethmoid. Lateral ridges develop above the cartilaginous precursors of ossified nasoturbinals. These ridges either fuse with the mesethmoid and nasoturbinals, or directly abut them, leaving sutures that indicate their separate origins. We therefore surmise that the midline ridge in non-mammalian cynodonts similarly adjoined a cartilaginous nasal septum and the lateral ridges contacted cartilaginous nasoturbinals. However, if the lateral lamina fused with

the adjoining membrane bones and the turbinals were lost or damaged in the preserved specimen, remaining ridges would indicate their previous presence.

Mammalian ethmoturbinals and maxilloturbinals form in different ways (Fig. 13). Early in ontogeny, ethmoturbinals first appear as the result of resorption within the thick posterior cartilaginous wall of the nasal capsule (Fig. 13A). In some mammals such as *Canis* (Miller et al., 1968) and *Didelphis*, parts of the lateral wall of the olfactory region ossify to form a thin lateral lamina that is fused to the lateral edges of some ossified ethmoturbinals (Fig. 13C). The external surface of the lateral lamina abuts the smooth inner surface of the surrounding membrane bones. If the ethmoturbinals are lost in dried skulls, ridges, which would otherwise indicate erstwhile ethmoturbinals, may not remain on the surrounding membrane bones. In non-mammalian cynodonts, a cartilaginous lateral wall of the nasal capsule may have similarly supported cartilaginous ethmoturbinals, which would explain the absence of ridges on the membrane bones surrounding the olfactory region in *Massetognathus*.

In contrast, maxilloturbinals form at the ventral edge of the cartilaginous capsule, growing medially into the respiratory chamber either in the form of simple scrolls or with multiple bifurcations (Fig. 13B). Ossification of the maxilloturbinal begins in the middle of the cartilaginous scroll or in the individual branches. During development, this ossification process spreads laterally until the new bone joins a thin ossified sidewall of the capsule that either abuts against the maxilla or fuses with it (Fig. 13D). Sometimes the maxilla is slightly thickened at the point of contact. In adult *Tachyglossus*, for instance, the maxilloturbinal remains cartilaginous at the base, abutting a ridge on the maxilla, but has ossified distally (Fig. 13D). If the maxilloturbinals are lost in dried skulls, a long scar or ridge remains, indicating where the maxilloturbinals were previously attached. Some advanced
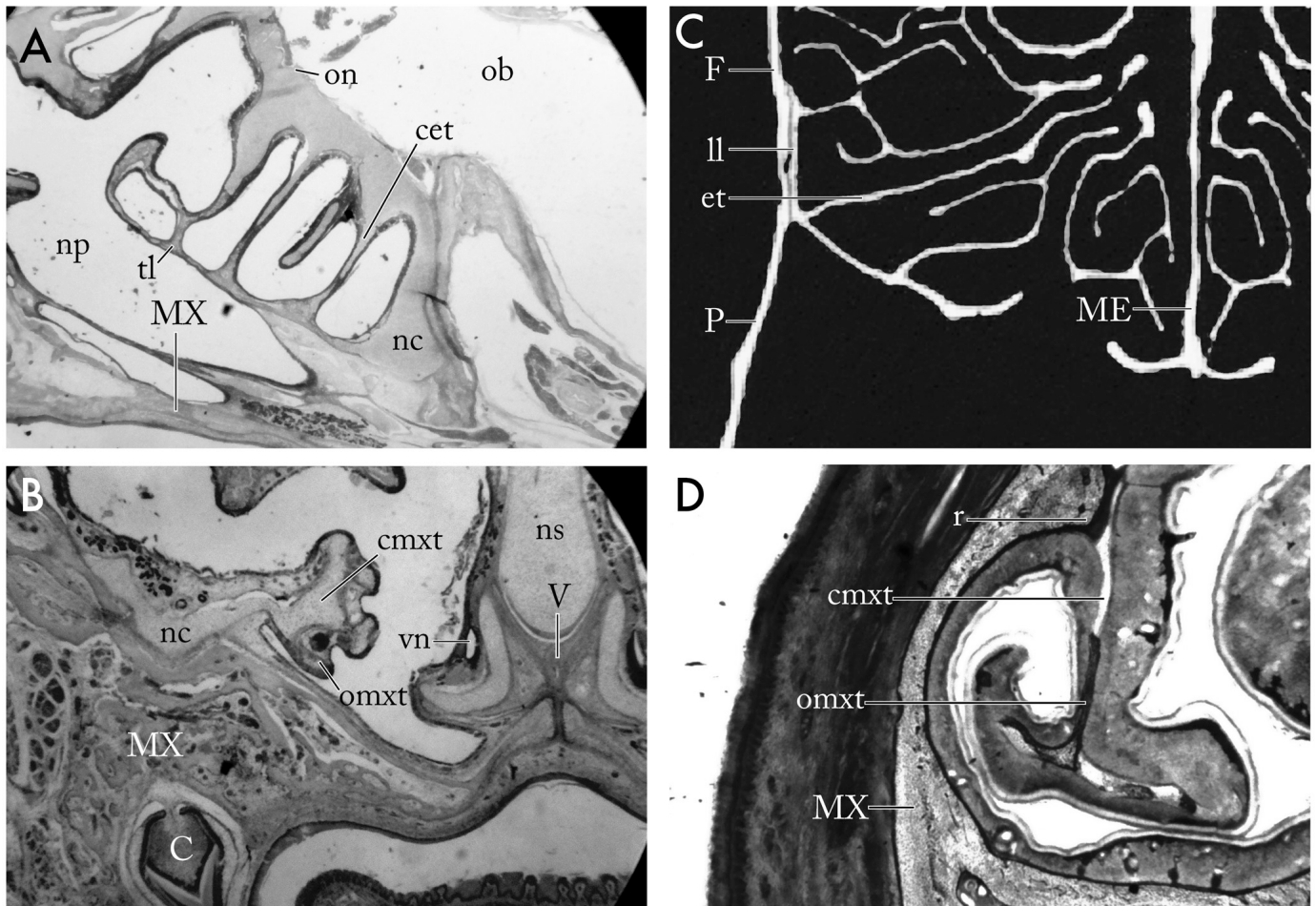
FIGURE 13. **A–C**, *Didelphis virginiana*. **A**, parasagittal section through the nasal region; **B**, transverse section through the anterior nasal region of a neonate at the age or stage when it would still be securely attached to the teat; **C**, transverse section based upon a CT scan through the olfactory region of an adult *Didelphis virginiana* showing the fusion of ethmoturbinals to the lateral lamina (ossified lateral wall of the nasal capsule). **D**, transverse section through the anterior nasal region of an adult *Tachyglossus aculeatus*, showing the separate origins of the maxillary ridge (dermal) and a maxilloturbinal (endochondral).

non-mammalian cynodonts may lack a supporting ridge for respiratory turbinals because, like the conchae in reptiles (Malan, 1946), the maxilloturbinals are supported entirely by the cartilaginous sidewall of the nasal capsule.

Posterior Wall and Nasal Septum—We propose that in non-mammalian cynodonts, a cartilaginous lamina orbitonasalis or antorbital plate (Figs. 8A, 11A) formed a posterior wall to the nasal capsule and abutted the descending flanges of the frontal and prefrontal as well as the orbital process of the palatine. The gap between the recess for the olfactory bulb and the olfactory chamber may have been filled with a cartilaginous cribriform plate that ossifies in mammals. In earlier non-mammalian cynodonts, nerves and blood vessels entered the nasal chamber medial to the orbital process of the palatine, above the transverse lamina (arrow in Fig. 8A). During the transition to mammals, their path shifted laterally; in extant mammals, they enter through either the sphenopalatine foramen or the infraorbital canal (Fig. 8B).

Transverse Lamina—In non-mammalian cynodonts, a solid plate formed by the vomer and the palatine constitutes the transverse lamina. In mammals such as *Didelphis*, the same bones still contribute, but most of the lamina is formed by the ethmoid plate (Fig. 8B), an ossified floor of the nasal capsule (Rowe et al., 2011). We propose that in non-mammalian cynodonts, a

cartilaginous floor of the nasal capsule lay above the vomer and palatine but never ossified, whereas in mammals this floor is ossified and the contributions of the palatine and the vomer to the transverse lamina are reduced.

Role of Respiratory Turbinals in Non-mammalian Cynodonts

The conclusion reached by Hillenius (1994) and Ruben et al. (2012) that early non-mammalian cynodonts possessed elevated resting ventilation and metabolic rates is in part based upon the evidence that they possessed respiratory turbinals whose primary function was to prevent the loss of heat and water in expired air. Indeed, a strong positive correlation is found between the respiratory turbinal surface area and field metabolic rates in extant mammals (Owerkowicz et al., 2015). This functional relationship, however, depends on bidirectional airflow through the nasal cavity, because only then do respiratory turbinals function as temporal countercurrent exchange sites and permit heat and water conservation. This occurs in extant mammals, when the larynx is held in an intranarial position by the palatopharyngeus muscle. However, in non-mammalian cynodonts, the structure of the bony palate behind the hard secondary palate differs fundamentally from that of extant mammals. In early non-mammalian

cynodonts such as in *Procynosuchus* (Kemp, 1979) and *Thrinaxodon* (Fourie, 1974), the nasopharynx was wide and shallow, pterygoid hamuli were not present, and there is no evidence that a tensor veli palatine muscle had differentiated from the reptilian pterygoideus muscle (Barghusen, 1986). On the assumption that in non-mammalian cynodonts the postdentary bones were involved in the transmission of vibrations from a tympanic membrane supported by the reflected lamina of the angular bone, then a wide opening between the pharynx and middle ear must have been present (Allin, 1975; Allin and Hopson, 1992). This is in contrast to mammals, where communication between the pharynx and middle ear is via a narrow Eustachian tube and suggests that early non-mammalian cynodonts probably lacked palatopharyngeus and tensor veli palatini muscles. They could not, therefore, place the larynx in an intranarial position.

It is worth noting that lack of an intranarial larynx does not necessarily preclude respiratory turbinals acting as efficient countercurrent exchange sites. As long as inspiratory and expiratory airflows occur across the nasal cavity, the respiratory epithelium will conserve a fraction of heat and water in exhaled air. It is therefore possible that in an arid environment, with water conservation at a premium, cartilaginous respiratory turbinates could have enabled the operation of the countercurrent exchange mechanism, even in the absence of an intranarial larynx. This would have been possible provided the mouth was tightly closed and breathing took place exclusively through the nose, as has been observed in extant lizards at rest (Schultz et al., 1999). With the mouth partially open (as seen in exercising lizards; Schultz et al., 1999), however, most of the exhaled air would escape through the mouth, thus promoting heat dissipation via respiratory evaporative water loss.

Given the hot and humid environment of the Late Permian and Early Triassic (Sun et al., 2012; Holz, 2015; Rey et al., 2015), respiratory turbinals were ideally suited to reduce body temperature as they do in mammals during panting, when air passes in through the nose and out through the mouth. The efficiency of heat exchange between the air stream and the nasal epithelium would have depended on the area of the maxilloturbinals, the amount of blood flow to the respiratory epithelium, and the amount of secretions from nasal gland. The latter two factors would have been under autonomic control, much as it is in extant mammals (Negus, 1958; Bamford and Eccles, 1983). A similar mechanism is present in some extant reptiles. For example, a well-vascularized preconcha of crocodiles and portions of the nasal concha of some squamates lie in the path of respiratory airflow (Bourke et al., 2014; Owerkowicz et al., 2015), suggesting that they participate in heat exchange.

In the Early Triassic, temperatures were exceptionally high, limiting vertebrates to high latitudes (Sun et al., 2012). Cynodonts, anomodonts, labyrinthodont amphibians, early archosaurs, and other small diapsids shared similar habitats: warm, humid lowland floodplains traversed by meandering streams, subjected to seasonal rainfall interspersed with periods of increasing aridity (Tucker and Benton, 1982; Retallack et al., 2003; Botha and Smith, 2007). Under these conditions, when subjected to increased heat loads, the need to reduce body and brain temperature would have ranked higher in importance than the need to conserve water and heat. This may also have been true for the anomodont *Lystrosaurus*, which shared the environment with non-mammalian cynodonts. Laaß et al. (2011) claim that in this form, cartilaginous maxilloturbinals lay directly in the airflow and thus that "*Lystrosaurus* was already endothermic" (Laaß et al., 2011:363). We doubt that this factor alone proves endothermy, but it does suggest that, if present, cartilaginous maxilloturbinals may have provided a mechanism for decreasing body temperature during activity.

Beginning in the Late Permian and lasting through the Triassic, a global bout of hypoxia has been posited as a potential driving force behind the origin of respiratory turbinates (Huey and Ward, 2005). Hypoxia is known to increase respiratory rates in extant air-breathers, primarily via higher breathing frequencies. Hypoxia-induced hyperventilation, therefore, increases the risk of heat and water loss from the respiratory tract. Any elaboration of the internal surface of the nasal cavity (such as cartilaginous turbinals) could be expected to be heavily favored by selection forces, if heat or water conservation was of utmost importance to the animal's survival. Interestingly, extant rodent species (*Peromyscus maniculatus*) from lowland and highland populations show no apparent differences in the internal morphology of their nasal cavities (T.O., pers. observ.). Further, with the prevalent hot and humid conditions of the Triassic, heat dissipation via water loss was presumably more important to contemporary amniotes than either heat or water conservation (see above). We conclude that heat loss was the original function of cartilaginous respiratory turbinals.

Role of Respiratory Turbinals in Non-mammalian Mammaliaforms

A shift in priority from dropping body heat to conserving heat and water probably occurred during the increasingly arid conditions of the Late Triassic (Retallack et al., 2003; Holz, 2015). In a number of Late Triassic or Early Jurassic non-mammalian cynodonts such as *Diarthrognathus* (Crompton, 1958, 1963), *Pachygenelus* (Allin and Hopson, 1992), *Elliotherium* (A.W.C., pers. observ.), *Brasilitherium* (Bonaparte et al., 2005), and *Kayentatherium* (A.W.C., pers. observ.), and mammaliaforms such as *Morganucodon* (A.W.C., pers. observ.), the pterygopalatine ridges align parasagittally, rather than converging posteriorly as in earlier non-mammalian cynodonts, and they extend ventrally to form the lateral walls of a relatively narrow nasopharynx, much as the pterygoid hamuli do in mammals. This new architecture approached that of extant mammals and provided an origin site for the palatopharyngeus muscle, which could maintain the larynx in an intranarial position. Other pharyngeal muscles, such as the tensor veli palatini and palatoglossus, could now invade the soft palate supported between the ventral edges of the hamuli. These modifications of the palate improved the ability of cartilaginous respiratory turbinals to conserve heat and water in resting animals, while retaining the ability to dissipate heat during periods of sustained activity. Non-mammalian cynodonts and early mammaliaforms may have been similar to extant heterothermic echidnas, which rely on shivering thermogenesis and conspicuous heat input from locomotor activity to maintain an elevated body temperature most of the time (Grigg et al., 2004) and must avoid overheating because they lack functional sweat glands (Brice, 2009). Thus, depending on ambient conditions, the function of their cartilaginous respiratory turbinals may have switched between heat conservation (at low ambient temperatures and at rest) and heat dissipation (at high ambient temperatures and during activity).

Practically nothing is known about the nasal structure in the earliest mammals or late surviving mammaliaforms. Ossified turbinals may have been present in docodonts such as *Haldanodon* (Lillegraven and Krusat, 1991), and because ossified respiratory turbinals are present in the two major groups of mammals (monotremes and therians), parsimony dictates that the earliest mammals must also have possessed them. The shift from cartilaginous respiratory turbinals of mammaliaforms to the ossified turbinals of mammals provided a greatly enlarged surface area for respiratory epithelium (Rowe et al., 2011). This would have been accompanied by increased ventilation and higher metabolic rates, supporting the view that early mammals were endotherms.

SUMMARY AND CONCLUSIONS

Changes in the Structure and Function of Respiratory Turbinals in the Evolution of Mammals

Cooling—In the extremely warm temperatures of the Early Triassic, the ability to reduce body temperature during activity was a priority. Early non-mammalian cynodonts are characterized by a greatly enlarged respiratory chamber filled with cartilaginous respiratory turbinals. Evaporative cooling of the surface of the turbinals cooled cranial blood flowing through their surface layers and oral and pharyngeal surfaces and warmed the inspired air. Body heat was transferred to the environment in air expired through the mouth.

Conservation—Changes in the structure of the hard palate above the nasopharynx in late Triassic non-mammalian mammaliaformes and mammaliaforms suggests the development of mammalian pharyngeal muscles, including a palatopharyngeus muscle that could hold the larynx in an intranarial position. This resulted in a single path for both inspired and expired air (in and out through the nose) during both rest and mild activity. The respiratory turbinals could then act efficiently as temporal countercurrent exchange sites to conserve heat and water in dry and cold environments.

Ossified Respiratory Turbinals—In Early to Middle Jurassic mammals and docodonts, respiratory turbinals ossified, allowing for greater surface area of respiratory epithelium in the nasal cavity. Ossified turbinals improved the ability to respond to changes in the environment or behavior that called for either conservation of heat and water or a reduction of body temperature.

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