



# Turbinal bones are still one of the last frontiers of the tetrapod skull: hypotheses, challenges and perspectives

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## ABSTRACT

Turbinals are bony or cartilaginous structures that are present in the nasal cavity of most tetrapods. They are involved in key functions such as olfaction, heat, and moisture conservation, as well as protection of the respiratory tract. Despite recent studies that challenged long-standing hypotheses about their physiological and genomic correlation, turbinals remain largely unexplored, particularly for non-mammalian species. Herein, we review and synthesise the current knowledge of turbinals using an integrative approach that includes comparative anatomy, physiology, histology and genomics. In addition, we provide synonyms and correspondences of tetrapod turbinals from about 80 publications. This work represents a first step towards drawing hypotheses of homology for the whole clade, and provides a strong basis to develop new research avenues.

*Key words:* turbinate, olfaction, heat conservation, moisture conservation, respiratory tract.

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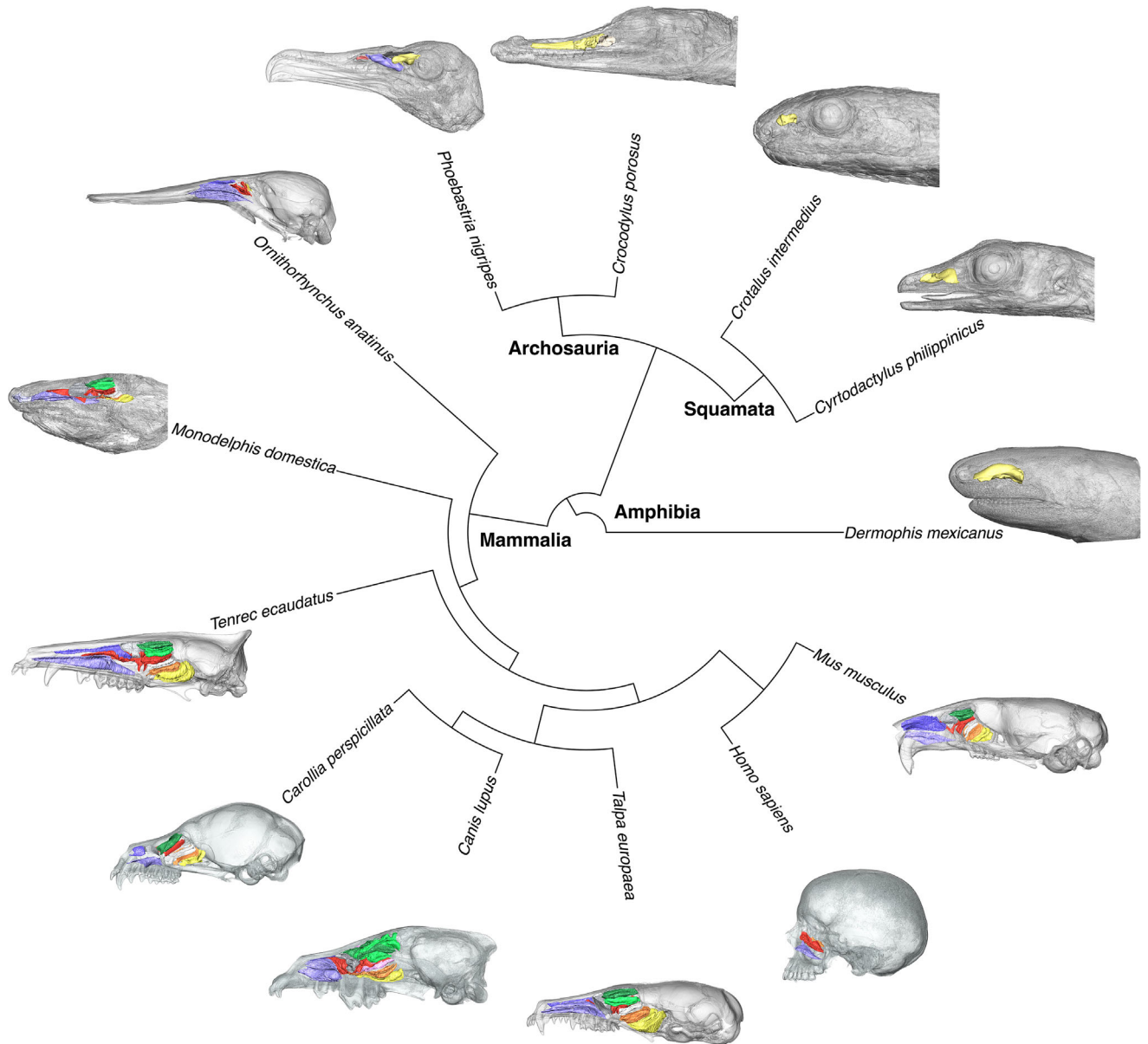
## I. INTRODUCTION

Turbinals (also named turbinates, conchae, turbinares, turbines, turbinaux, tubercles, ethmoidal labyrinth, cornets, scroll bones, and lateral mass) (e.g. Negus, 1958; Portmann, 1961; Bang, 1965; Roper, 1999) are bony or cartilaginous structures involved in olfaction, heat, and moisture conservation, as well as protection of the respiratory tract (Figs 1–3; Negus, 1958; Morgan & Monticello, 1990; Harkema, Carey & Wagner, 2006). The earliest studies on turbinal anatomy are most likely anatomical contributions for humans (*Homo sapiens*), in which turbinals were named conchae (e.g. Bourguery & Jacob, 1831). During recent decades, turbinals have been rather neglected in comparison to studies of other parts of the skull (Rowe *et al.*, 2005). Turbinals are thin, perforated and scrolled bony or cartilaginous plates (Figs 4–8) that are fragile and difficult to extract from the skull. Early anatomists visualised these structures using tedious protocols such as cross-sectioning skulls, elaborate transparency projections, cardboard models, wax plate reconstructions and different types of casts (Born, 1883; Voit, 1909; Watson, 1913; Dawes, 1952; Negus, 1958; Folkow, Blix & Eide, 1988; Morgan & Monticello, 1990). In this context, the works of Simon Paulli, Sir Victor Negus,

Betsy G. Bang, and Thomas S. Parsons (Paulli, 1900*a,b,c*; Negus, 1958; Parsons, 1967; Bang, 1971) became landmark studies in this field.

Invented in the early 1980s, high-resolution X-ray micro-computed tomography (micro-CT,  $\mu$ CT) was at first extremely expensive and limited to exceptional projects. Improvements and popularisation of this tool subsequently resulted in a significant cost reduction. Micro-CT completely revolutionised the sensory ecology field in general, and that of turbinal anatomy in particular. In a context where biodiversity is drastically decreasing, museum specimens are becoming extremely valuable. Micro-CT, which is non-destructive, enables acquiring data from rare specimens, holotypes or specimens from extinct or endangered species. One of the first studies on turbinals that used CT was Ruben *et al.* (1996) who investigated respiratory turbinals in birds, crocodylians, and non-avian theropods. Since then, the number of CT studies related to turbinals has significantly increased.

The nasal cavity (and therefore turbinals) is probably still one of the least studied regions of the tetrapod skull despite its key functional role (Rowe *et al.*, 2005; Smith, Eiting & Rossie, 2011). Van Valkenburgh and her team developed quantitative analyses based on turbinal data, acquired

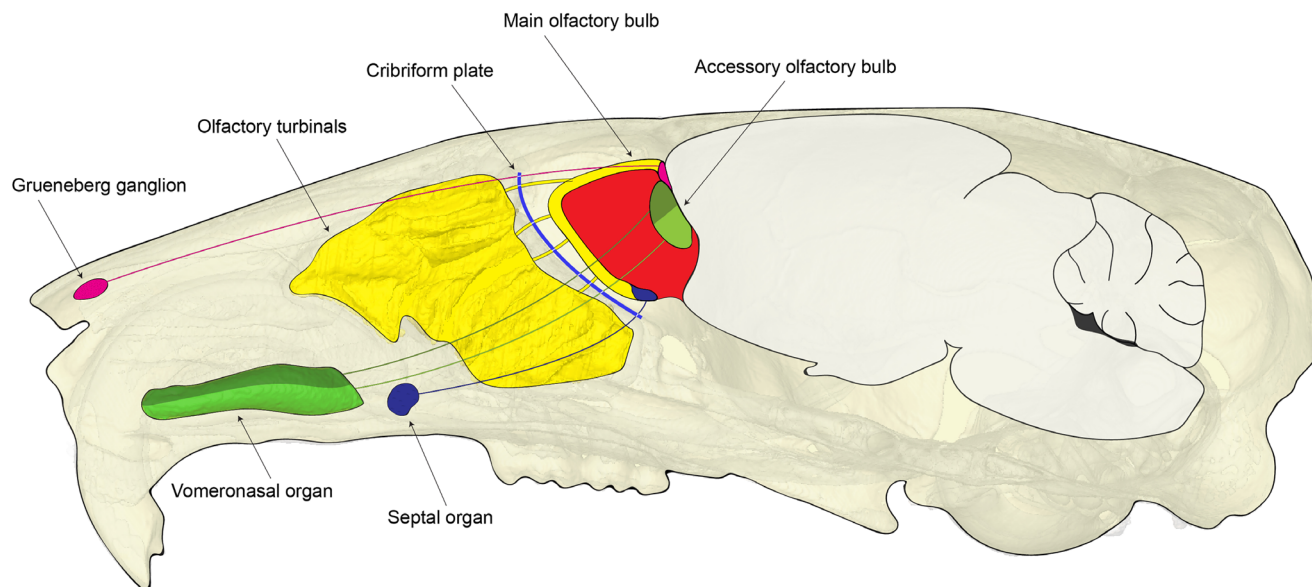


**Fig. 1.** Variation in turbinals across tetrapods. Sagittal views of the skull or the head of the 13 tetrapod species discussed in this review with three-dimensional segmentation of the left turbinals. Colour coding represents turbinal homology, see later figures for detailed illustrations.

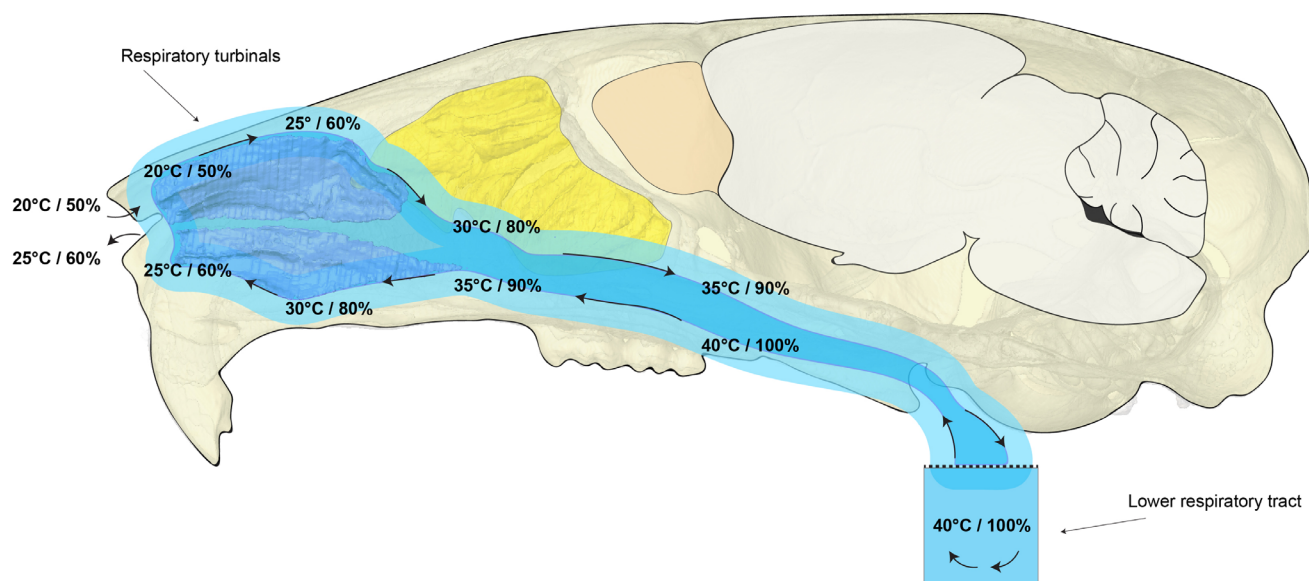
through micro-CT (e.g. Van Valkenburgh *et al.*, 2004, 2011, 2014; Green *et al.*, 2012). One of the biggest challenges is now the time required to process the data, particularly for segmentation (= isolation of an area or structures of interest). In mammals, segmentation time to extract all turbinals from one side can range from half a day to several days. This process is longer for micro-CT images with background noise (= an artifactual grainy texture), fossils, or for species with highly complex turbinals (e.g. amphibious mammals) as semi-automatic segmentation tools may not be applicable. In the next few years, semi-automated segmentation as well as deep-learning technology may considerably reduce segmentation time (e.g. Cardona *et al.*, 2010; Lösel *et al.*, 2020, 2023; Herbst *et al.*, 2021).

The number of studies related to mammalian turbinals is growing rapidly. However, studies on other tetrapods (e.g. birds or lizards), where most of their turbinals are cartilaginous and therefore not visible with micro-CT, remain rare. The recent development of staining methods [e.g. Lugol's iodine, phosphotungstic acid (PTA), and phosphomolybdic acid (PMA)] provide methodological avenues to explore this field further by enabling the contrast enhancement of soft tissue and therefore making them visible in micro-CT (Metscher, 2009; Pauwels *et al.*, 2013; Gignac *et al.*, 2016; Gabner *et al.*, 2020).

Here we review the current knowledge on turbinals from various fields and with new, standardised anatomical plates, in order to provide a strong morphological, functional, evolutionary and developmental basis for future studies. Because



**Fig. 2.** Mouse (*Mus musculus domesticus*) olfactory system, showing position of the olfactory turbinals. Modified after Kaluza *et al.* (2004), Storan & Key (2006), Roppolo *et al.* (2006), Ekberg *et al.* (2011) and Salazar & Sánchez-Quinteiro (2011).



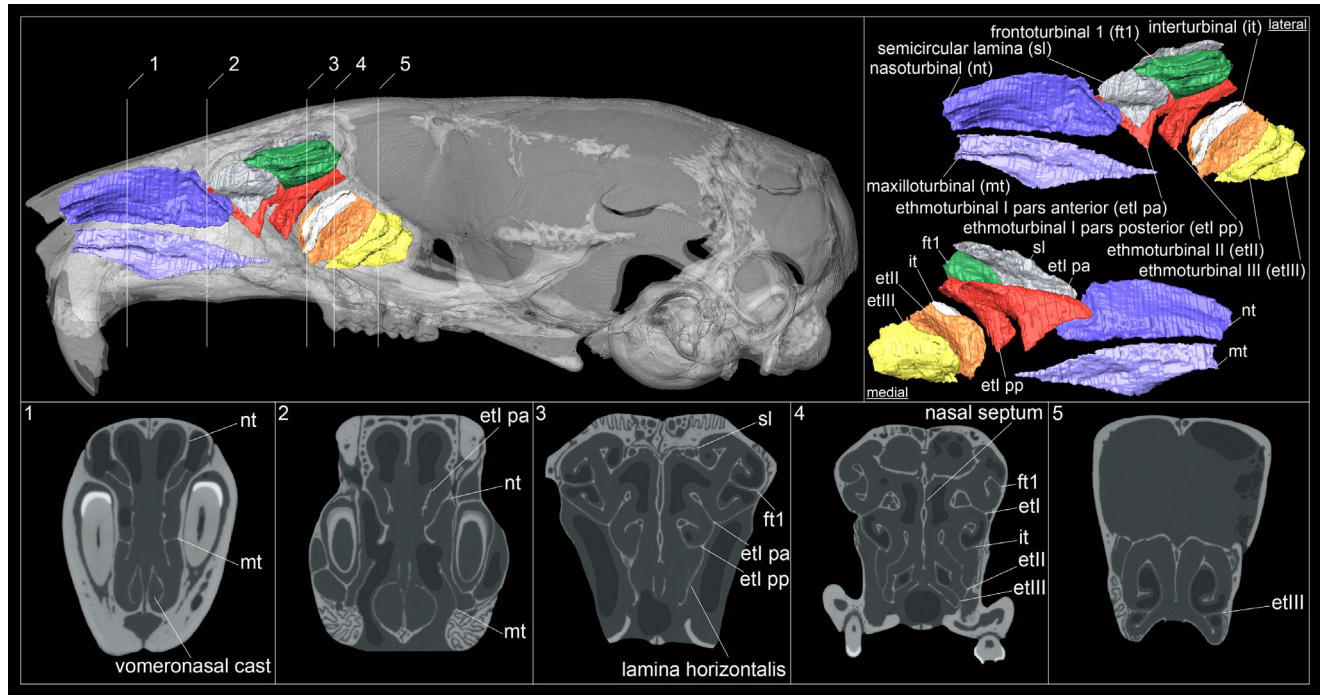
**Fig. 3.** Mouse (*Mus musculus domesticus*) respiratory turbinals, with blue shading showing the principle of heat and moisture conservation along the upper respiratory tract. Heat transfer is the result of convection, whereas water transfer is driven by evaporation and condensation. In this example, the performance of the respiratory tract allows conservation of 15 °C and 40% of humidity at expiration. Modified after Walker & Wells (1961), Jackson & Schmidt-Nielsen (1964) and Collins *et al.* (1971).

most turbinal-related works have been performed in mammals, we focus the first part of this review on this clade as a reference, and then consider other tetrapods.

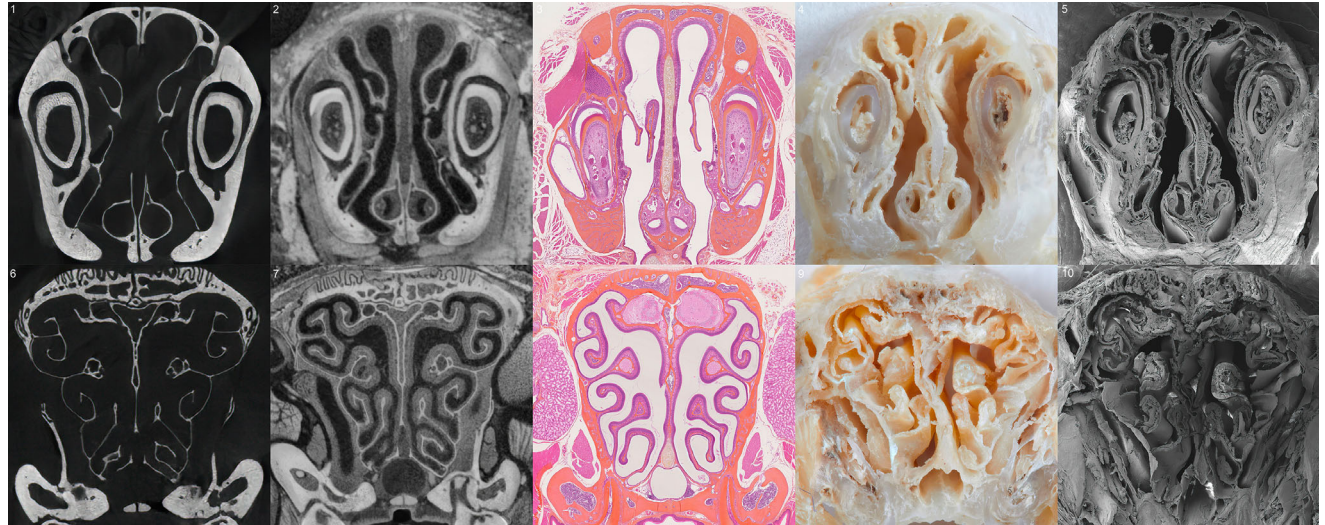
## II. MAMMALS

Among extant tetrapods, mammals have relatively the largest and most complex turbinals (e.g. Negus, 1958; Parsons, 1971a). Despite a great number of morphological studies on prenatal

stages of almost all mammalian orders (e.g. Fischer, 1901; Voit, 1909; Fawcett, 1921; Starck, 1960), postnatal and especially adult stages are significantly underrepresented. This is due to several reasons, such as a focus on the so-called 'stadium optimum', in placentals corresponding to fetal stages with a fully developed chondrocranium, but also to technical limitations as histological techniques are limited by ossification in older stages or simply by size (Maier & Ruf, 2014). These barriers now can be mostly overcome by CT technologies (e.g. Van Valkenburgh *et al.*, 2011, 2014; Macrini, 2012;



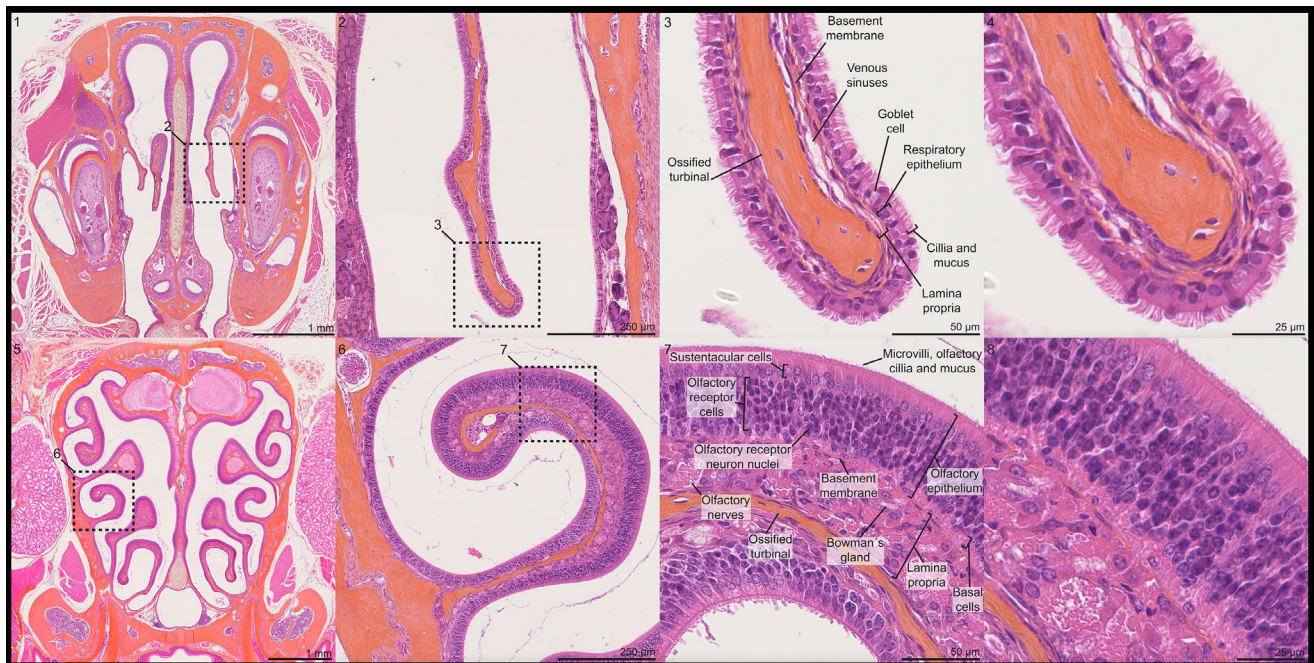
**Fig. 4.** (Top) Sagittal view of the skull of a mouse [*Mus musculus domesticus*, wild individual from Monastir, Tunisia, Institut des Sciences de l'Évolution de Montpellier (ISEM) K7503] with three-dimensional illustration of the segmented turbinal shown in lateral and medial views. (Bottom) Five coronal sections along the nasal cavity at positions identified by numbers in the top left image. Raw micro-computed tomography (micro-CT) data from Quentin Martinez (MorphoSource ID number 000523925).



**Fig. 5.** Coronal sections of the turbinals of a mouse (*Mus musculus domesticus*) along the nasal cavity visualised using different approaches: classical micro-computed tomography (micro-CT) scan (1, 6), iodine-stained micro-CT scan (diceCT; 2, 7), haematoxylin-eosin-saffron (HES) stained histology (3, 8), photograph of fresh sections (4, 9), and scanning electron microscope (SEM) image with 5 nm gold-palladium coating (5, 10). The top and bottom views approximately correspond to sections (1) and (4) in Fig. 4, respectively.

Ruf, Janßen & Zeller, 2015; Smith *et al.*, 2016; Martinez *et al.*, 2018, 2020, 2023a,b; Wagner & Ruf, 2019; Ruf, 2020; Ito *et al.*, 2021, 2022; Smith & Bonar, 2022), although large species of Afrotheria, Carnivora, Artiodactyla or Perissodactyla have still not been the focus of detailed morphological analyses

of the turbinal complex. Thus, the homology of turbinals remains unclear in several species and groundplan reconstructions of specific clades are still pending. Issues with turbinal homology are mainly associated with the olfactory turbinals (= fronto-, ethmo-, and interturbinals; e.g. Fig. 4), where an



**Fig. 6.** Details of histological sections [haematoxylin-eosin-saffron (HES) stain] of the nasoturbinal (respiratory turbinal) and interturbinal (olfactory turbinal) of a mouse (*Mus musculus domesticus*, WLA Toulouse inbred line derived from wild population) showing the differences between respiratory and olfactory epithelium. 1 and 5 approximately correspond to sections (1) and (4) in Fig. 4, respectively.

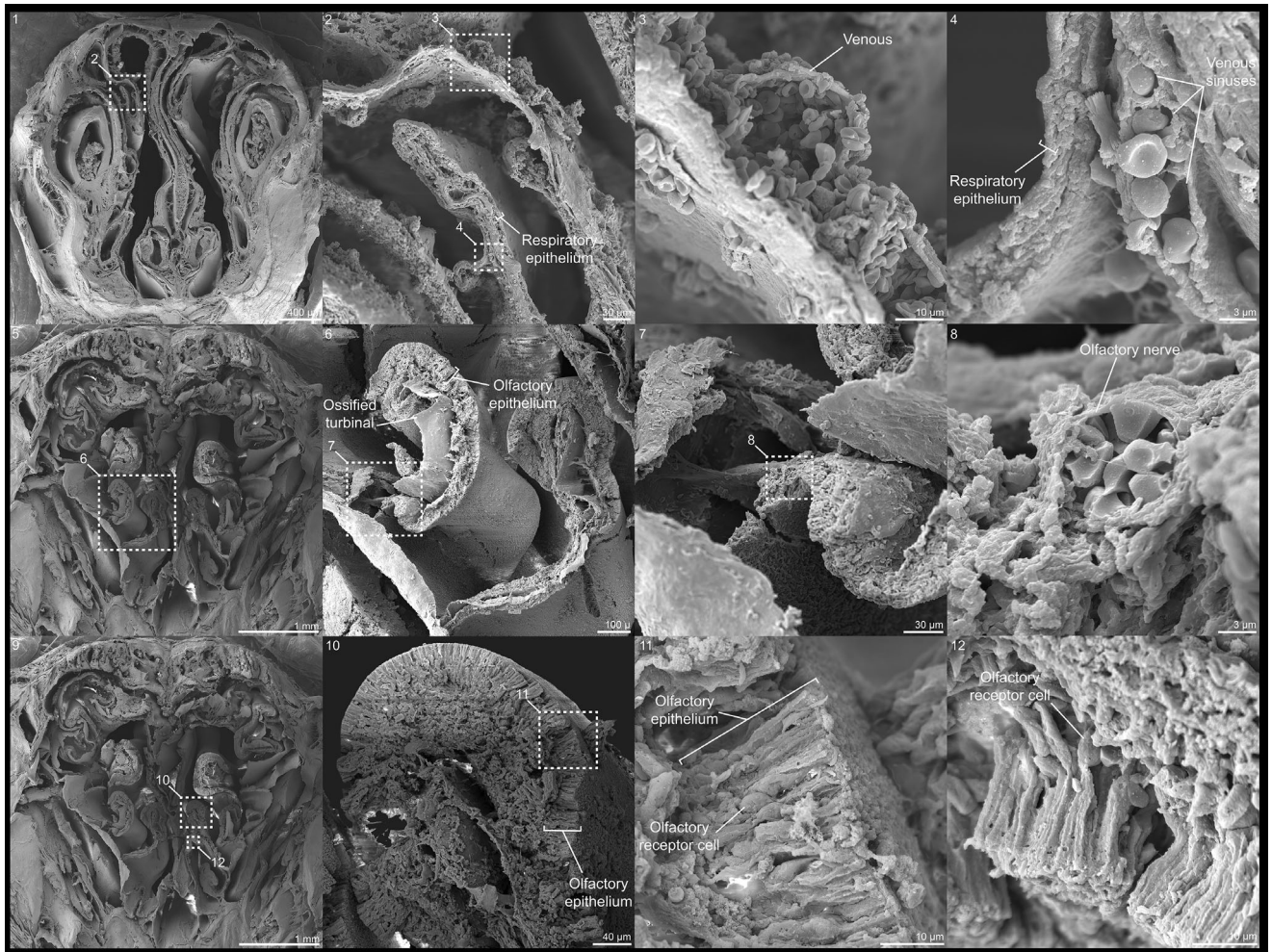
increase in turbinal complexity may involve a greater number of small and potentially independently developing lamellae. Even in rodents, homology of olfactory turbinals is sometimes unclear, with the number of some frontoturbinals ranging from 0 to 3 (Fig. 4; Martinez *et al.*, 2020; Ruf, 2020; Smith & Bonar, 2022). In light of variations in the shape, location, and number of these frontoturbinals, developmental studies must be carried out to derive hypotheses of homology that can be used within a phylogenetic framework (Ruf, 2020; Macrini *et al.*, 2023). Similarly, it is difficult to distinguish between interturbinals, which are sometimes present, and the lamellae of the other olfactory turbinals (Rowe *et al.*, 2005). This is especially true for species with highly complex olfactory turbinal bones such as armadillos, elephants or tapirs (e.g. Paulli, 1900b; Hautier *et al.*, 2019; Martinez *et al.*, 2024b). In some cases, examination of young individuals is sufficient because the complexity and number of turbinals does not change during postnatal ontogeny (Ruf, 2020; Ito *et al.*, 2021, 2022). However, precise developmental studies remain necessary in most cases. To date, comprehensive and comparative developmental studies are rare and limited to certain species and families (Smith & Rossie, 2008; Smith *et al.*, 2016, 2021c; Ruf, 2014, 2020; Ito *et al.*, 2021, 2022; Wagner & Ruf, 2021), and additional developmental studies will be necessary to test hypotheses of turbinal homology (Maier & Ruf, 2014).

### (1) Development of nasal structures in mammals

A thorough discussion of nasal capsule development is beyond the scope of this review, but certain developmental

relationships are critical to understanding homology. During development in mammals, turbinals emerge from the cartilaginous nasal capsule, the most rostral element of the chondrocranium (Maier, 1980, 1993; Zeller, 1987; Rowe *et al.*, 2005). The nasal capsule is the source of the ethmoid bone, a shared skeletal element of the basicranium and facial skeleton, and a number of cartilages (e.g. septal, alar). During the early developmental stages, the nasal capsule has three initially independent mesenchymal condensations, which become centres of chondrification (Fig. 9; Reinbach, 1952b; Maier, 1993; Smith & Rossie, 2008; Maier & Ruf, 2014; Van Valkenburgh, Smith & Craven, 2014; Ruf, 2020). These chondrification centres, also referred to as pars, are specifically designated here as centres of chondrification (Fig. 9) to prevent potential confusion with the distinct lamellae of the ethmoturbinal I (see Section II.4.c). The anterior centre gives rise to cartilages that extend the furthest rostrally, such as the marginoturbinal and atrioturbinal if present (Maier, 2020), and two lamellae that project posteriorly, the maxilloturbinal and the semicircular lamina. Most olfactory turbinals develop from the middle (= intermedia) and posterior chondrifications centres. The middle centre houses the frontoturbinals, and the posterior centre gives rise to the ethmoturbinals. Each of these may have smaller turbinals called interturbinals and which are nested between larger turbinals. These form later than the larger turbinals, and do not extend as far medially.

The three parts of the nasal capsule eventually fuse into a tent-like housing for the developing nasal cavity, with openings rostrally and caudally (anterior and posterior nares), and openings for olfactory nerves caudally and dorsally;



**Fig. 7.** Scanning electron micrographs showing details of the nasoturbinal and interturbinal of a mouse (*Mus musculus domesticus*, WLA Toulouse inbred line derived from wild population) showing venous sinuses, olfactory nerves and olfactory receptor cells. Images 1 approximately corresponds to section (1), and images 5 and 9 to section (4) in Fig. 4, respectively.

ventrally the capsule has an incomplete floor (Fawcett, 1918, 1919, 1921; De Beer, 1937). Once the nasal capsule is fully formed, the degree to which the three parts overlap creates complex recesses that eventually convey airflow at different velocities. The posterior part of the capsule ends in a *cul-de-sac*, the ethmoturbinal (= olfactory) recess, which is spatially separated from nasopharyngeal passageways, and is dedicated to olfaction in most mammals, as are the ethmoturbinals and interturbinals within it. The posterior transversal lamina (= lamina transversalis posterior) of the nasal capsule forms the floor of the ethmoturbinal recess, the paries nasi form the sidewalls, the lamina cribrosa and lamina infracribrosa form the roof and the cupula nasi posterior is the blind end of the nasal cavity (Maier & Ruf, 2014; Ruf, 2020).

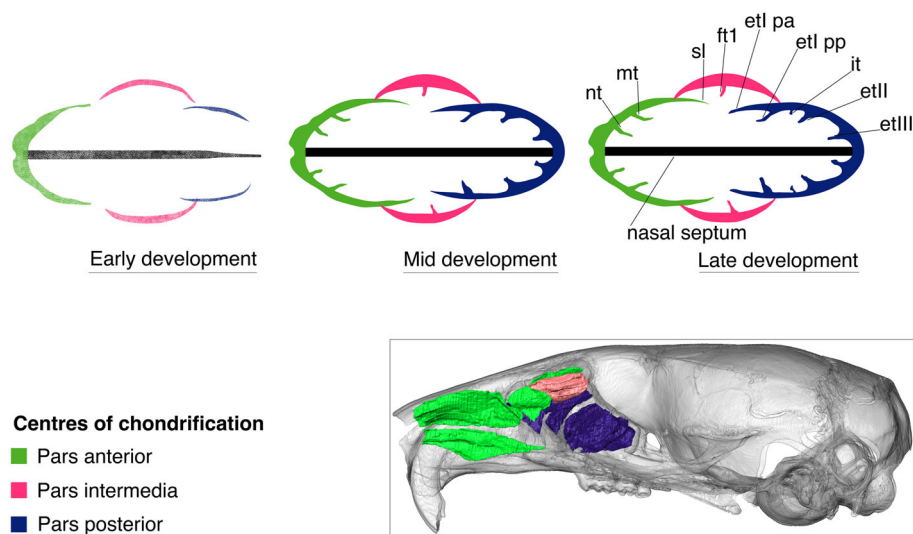
During ontogeny, the anterior chondrification centre become mostly resorbed, although some parts remain cartilaginous (e.g. external nasal cartilages, atrioturbinal), whereas the inferior part separates in mammals and becomes the ossified maxilloturbinal. Large parts of the middle and posterior chondrification centres ossify. The posterior

transversal lamina fuses with the vomer in many species (= lamina terminalis); the lamina cribrosa ossifies as well and becomes part of the ethmoid bone (Ruf, 2020; Smith, Ruf & DeLeon, 2023). Individual turbinals ossify in mammals (e.g. frontoturbinals, ethmoturbinals). Parts of the sidewall (paries nasi) may ossify into parts of the orbital wall.

Overlap of the tripartite nasal capsule occurs where the first ethmoturbinal of the posterior chondrification centre juts forward medial to the middle chondrification centre; this turbinal can project so far into the anterior chondrification centre that it overlaps the maxilloturbinal (Smith, Rossie & Bhatnagar, 2007b). Similarly, the semicircular lamina of the anterior chondrification centre projects posteriorly; in some species it becomes so large that the middle chondrification centre is not visible from the medial perspective (De Beer, 1937; Maier, 1993; Smith & Rossie, 2008). The entire space that is lateral to the semicircular lamina and ethmoturbinal I is termed the lateral recess. The lateral recess is subdivided by the horizontal lamina into a superior frontoturbinal recess (housing the frontoturbinals and interturbinals, if present)



**Fig. 8.** Details of the nasoturbinal and interturbinal of a mouse [*Mus musculus domesticus*, WLA Toulouse inbred line derived from wild population, Institut des Sciences de l'Évolution de Montpellier – Quentin Martinez (ISEM-QM)1796] imaged with iodine-stained micro-computed tomography (diceCT) showing the difference in epithelial thickness between the respiratory and olfactory areas. The bracketed tissue from the panel 4 can also be called olfactory mucosa, as it includes olfactory epithelium as well as glandular tissue just deep to it. Panels 1 and 2 approximately correspond to sections (1) and (4) in Fig. 4, respectively. Raw micro-CT data from Quentin Martinez (Morphosource ID number 000524240).



**Fig. 9.** Development of the mammalian nasal capsule, organised into three regions named pars (adapted from Smith & Rossie, 2008). Turbinals are derived from these specific parts and are coloured accordingly. Bottom right image is a sagittal view of the skull of an adult mouse with three-dimensional illustration of positions of segmented turbinals similarly colour coded. etI pa, ethmoturbinal I pars anterior; etI pp, ethmoturbinal I pars posterior; etII, ethmoturbinal II; etIII, ethmoturbinal III; ft1, frontoturbinal I; it, interturbinal; mt, maxilloturbinal; nt, nasoturbinal; sl, semicircular lamina.

and inferior maxillary recess (which may pneumatise further into the maxillary bone to form the maxillary sinus); in many mammals, there is a more anterior extension of the lateral recess that is not subdivided, but communicates posteriorly with the frontoturbinal and maxillary recesses. The frontoturbinal recess is an olfactory space, which contains the frontoturbinals and interturbinals, if present. The midline nasal septum divides the nasal cavity into two halves (= fossae; Fig. 4). This structure arises early in ontogeny (from neural crest cells) and remains mostly cartilaginous throughout life (Rowe *et al.*, 2005; Ruf, 2020). The posterior part, which will be ossified in adult stages, is named the mesethmoid (Rowe *et al.*, 2005). Mediolaterally, turbinals are symmetric and with occasional exceptions, intra-individual variation is rare (Rowe

*et al.*, 2005; Macrini, 2012; Martinez *et al.*, 2018, 2020; Ruf, 2020).

These developmental relationships of turbinals with primordial parts of the nasal capsule form the basis for discussion of homology (e.g. Maier, 1993; Smith & Rossie, 2008), as well as an understanding of variations by which turbinal numbers are increased or decreased in various taxa. Indeed, some mammals have far more turbinals than most, and others have apparently lost turbinals that were ancestrally present. Supernumerary or lost turbinals create confusion for several reasons. Turbinals develop as serial homologues, and also in a temporal sequence. For example, the maxilloturbinal and first ethmoturbinal undergo mesenchymal condensation prior to more caudal ethmoturbinals and frontoturbinals, and chondrify



before the most posterior ethmoturbinal even forms a mesenchymal condensation (Zeller, 1987; Smith & Rossie, 2008; Smith *et al.*, 2021c). Interturbinals undergo mesenchymal condensation after the ethmoturbinals and the lateral wall have chondrified. In light of this, a question arises about taxa with the most turbinals (e.g. carnivorans): do new ethmoturbinals arise in an iterative caudal direction, or do they form between existing turbinals? Related to this, Macrini (2014, p. 2008) wrote that ‘with the current state of knowledge it is not possible to homologise individual endoturbinals or ectoturbinals’ (his term for ethmoturbinals and frontoturbinals, respectively). However, Macrini (2014) was able to identify a fascinating developmental history of the third ethmoturbinal (he used ‘endoturbinal’) of some adult marsupials. In a series of pouchlings (broadly equivalent to fetal stages of placental mammals), this turbinal first appears as an interturbinal between two ethmoturbinals, and subsequently grows to a position adjacent to the septum (i.e. as is the case for the other ethmoturbinals). Macrini (2014) advocated that this turbinal should bear the name ‘interturbinal’ in the adult, to denote its developmental distinction (see also Macrini *et al.*, 2023). However, a different implication of his finding is that interturbinals are a pool of potential ethmoturbinals. Some mammals have multiple interturbinals (e.g. Paulli, 1900a,b,c); hypothetically, accelerated growth of any interturbinal could explain supernumerary ethmoturbinals. But an alternative hypothesis could be that additional mesenchymal condensations form, perhaps through accelerated or prolonged nasal capsular development, perhaps caudal to the last ethmoturbinal in ancestral forms. Along these lines, Smith & Rossie (2008) suggested that the posterior transversal lamina of eutherian mammals (which forms the cartilaginous floor of the caudal nasal capsule) may be homologous with the last ethmoturbinal of metatherians. Unfortunately, we still lack sufficient information to homologise all ethmoturbinals. To resolve this, we require detailed study of embryonic placental mammals with the most numerous ethmoturbinals (e.g. Carnivora or Perissodactyla).

Existing collections of serially sectioned mammals or contrast-enhanced CT volumes may already hold the key to understanding which turbinals have been lost evolutionarily in taxa such as some bats or primates. Smith & DeLeon (2021) suggested that the position of the eyes in embryonic and early fetal haplorhine primates (humans, apes, monkeys and tarsiers) may place constraints on the posterior part of the nasal capsule during the phase of mesenchymal condensation, reducing the overall mesenchymal pool. Bats lacking ethmoturbinals may also have a reduced mesenchymal pool; Frick’s (1954) description of the nasal capsule in *Myotis* (which has a reduced ethmoturbinal count) implies a lack of tripartite organisation. Regardless of the basis for loss, we do not yet know whether placental mammals with three or fewer ethmoturbinals have lost the second, third or fourth ethmoturbinal. Even in humans and other anthropoids, for which we have the most data, it remains unclear whether the second ethmoturbinal (etII, or superior nasal concha) is homologous with the pars

posterior of ethmoturbinal I (etI pp, see Section II.4.c), or ethmoturbinal II (etII) in ancestral forms.

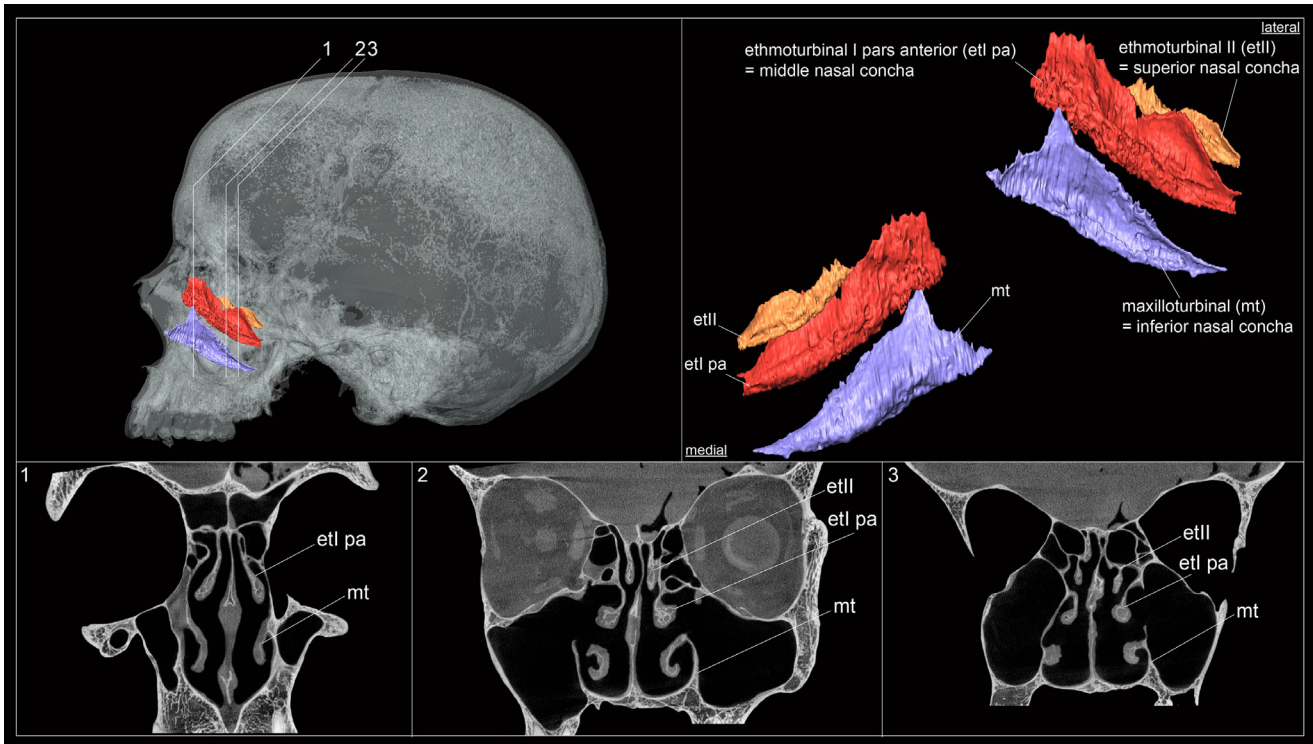
## (2) Two functional categories

Turbinal bones are generally divided into two functional categories: (i) heat and moisture conservation, and (ii) olfaction (Negus, 1958; Parsons, 1959b, 1971a; Hillenius, 1992). These categories often fit with an antero-posterior position with turbinals functionally named as respiratory and olfactory turbinals (Figs 2 and 3). These bony structures increase the surface area of the nasal cavity and are covered by a vascular system, mucus glands or olfactory epithelium (Rowe *et al.*, 2005). However, epithelial composition varies between species. Extensive histological studies in rabbits, rats and mice (e.g. Le Gros Clark, 1951; Ressler, Sullivan & Buck, 1993; Harkema & Morgan, 1996; Harkema, Carey & Wagner, 2006; Barrios *et al.*, 2014; Herbert *et al.*, 2018) and in some non-model species (e.g. Negus, 1958; Maier, 1980; Smith *et al.*, 2004; Smith, Eiting & Bhatnagar, 2012; Smith & Rossie, 2008; Eiting, Smith & Dumont, 2014a; Yee *et al.*, 2016; Martinez *et al.*, 2020) have enabled us to characterise the distinct functions of turbinals (some have a dual function). The number of respiratory turbinals in terrestrial mammals varies from one per side in some naked mole rat (*Heterocephalus glaber*) individuals (Martinez *et al.*, 2023b) to three or four in some other rodent species (Martinez *et al.*, 2020; Q. Martinez, personal observations). The number of olfactory turbinals in terrestrial mammals varies from one or two per side in humans to about 55 in the African bush elephant (*Loxodonta africana*) (Martinez *et al.*, 2024b). Turbinals are also present in semi-aquatic and even fully aquatic mammals whereas toothed whales (odontocetes) may be the only mammals to lack turbinals (Godfrey, Geisler & Fitzgerald, 2013; Berta, Ekdale & Cranford, 2014; Ichishima, 2016) but further investigations are still needed (see Section II.6.b). In addition to the number of turbinals, their relative size and complexity vary greatly between mammalian species (Figs 4, 10–16) (e.g. Parsons, 1971a; Hillenius, 1994; Van Valkenburgh *et al.*, 2004, 2011, 2014; Green *et al.*, 2012; Ruf *et al.*, 2014; Martinez *et al.*, 2018, 2020, 2023b).

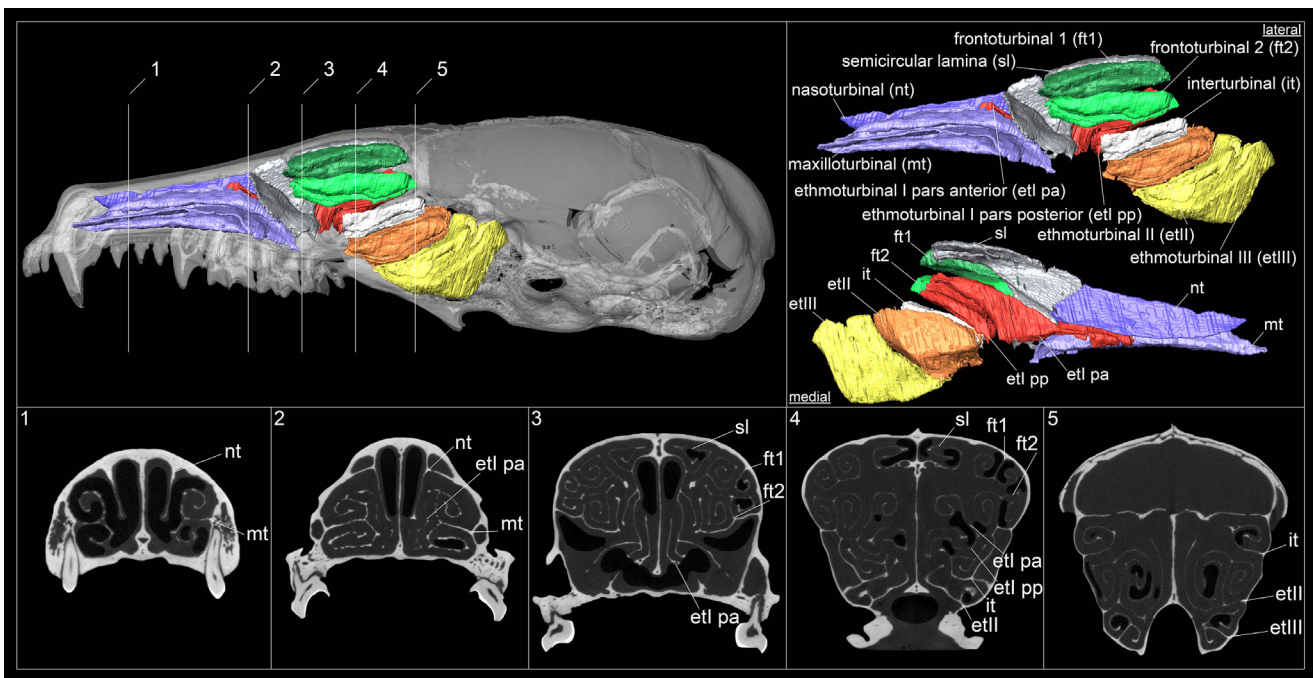
In the two following sections, we discuss turbinal anatomy from the anterior part of the nasal cavity where the respiratory turbinals are located (Fig. 3) to the posterior part where the olfactory turbinals are located (Fig. 2). For the respiratory turbinals, we discuss three different sections: (i) margino- and atrio-, (ii) maxillo-, and (iii) nasoturbinal. For the olfactory turbinals, we discuss four different sections: (i) semicircular lamina, (ii) fronto-, (iii) ethmo-, and (iv) interturbinals.

## (3) Respiratory turbinals

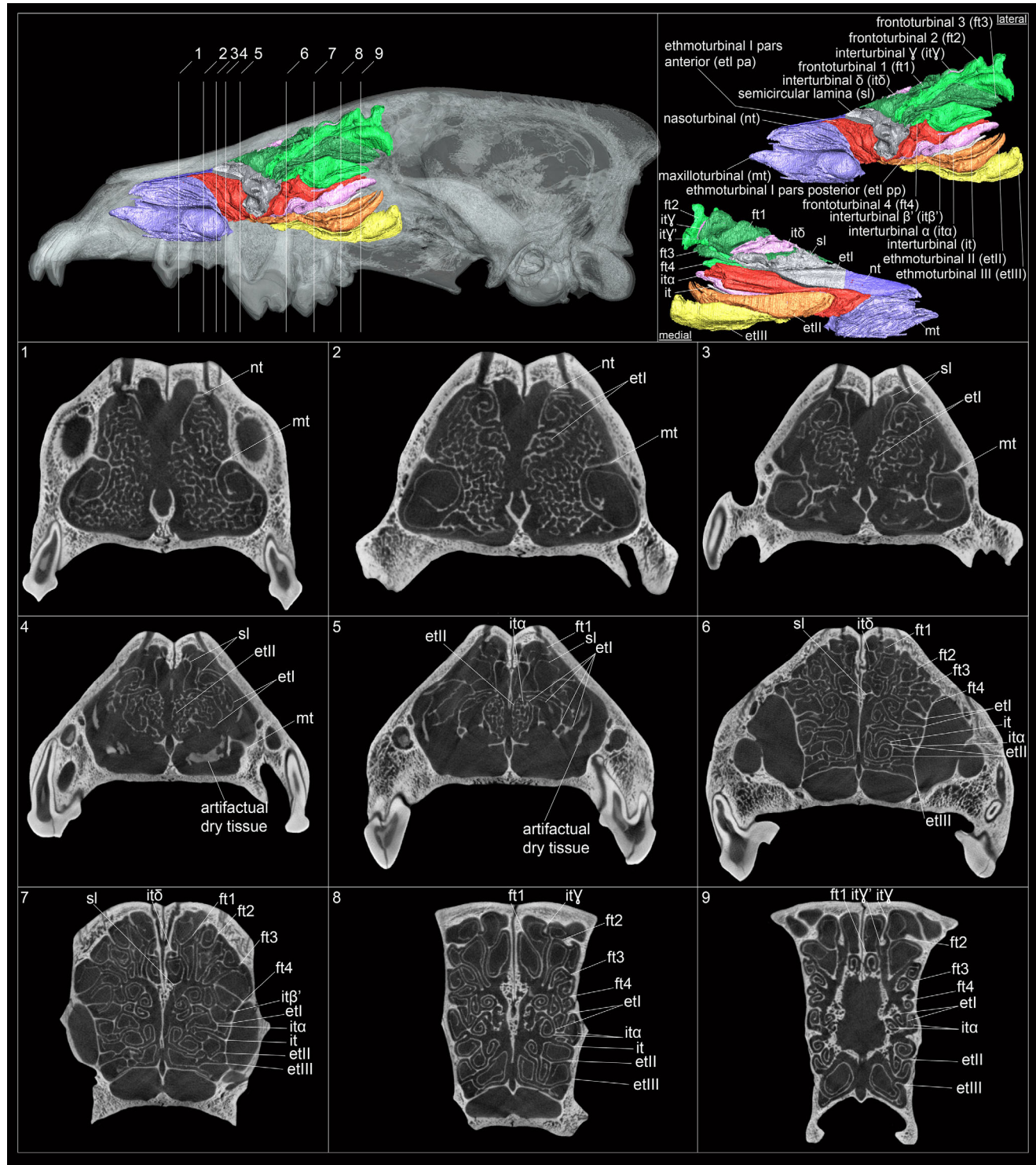
Respiratory turbinals are involved in heat and moisture conservation. During inhalation, the air is warmed up to body temperature due to contact with the vascularised anterior part of the respiratory turbinals. Simultaneously, the air in contact with nasal mucus is moistened (Fig. 3). During



**Fig. 10.** (Top) Sagittal views of the skull of a human (*Homo sapiens sapiens*) with three-dimensional illustration of the segmented turbinial shown in lateral and medial views. (Bottom) Three coronal sections along the nasal cavity at positions identified by numbers in the top left image. Raw micro-computed tomography (micro-CT) data from Renaud Lebrun (MorphoMuseuM ID:<https://doi.org/10.18563/journal.m3.195>).



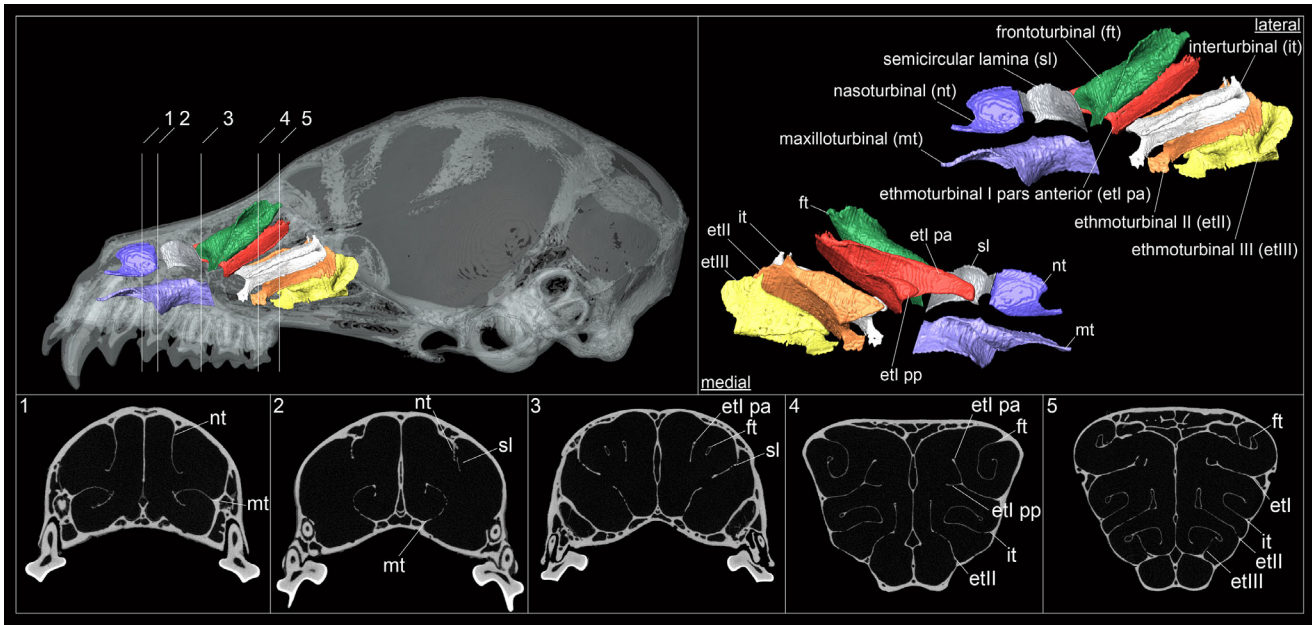
**Fig. 11.** (Top) Sagittal views of the skull of an Aquitanian mole [*Talpa aquitania*, Institut des Sciences de l'Évolution de Montpellier – Quentin Martinez (ISEM-QM)] with three-dimensional illustration of the segmented turbinial shown in lateral and medial views. (Bottom) Five coronal sections along the nasal cavity at positions identified by numbers in the top left image. Raw micro-computed tomography (micro-CT) data from Quentin Martinez (MorphoSource ID number 000524233).



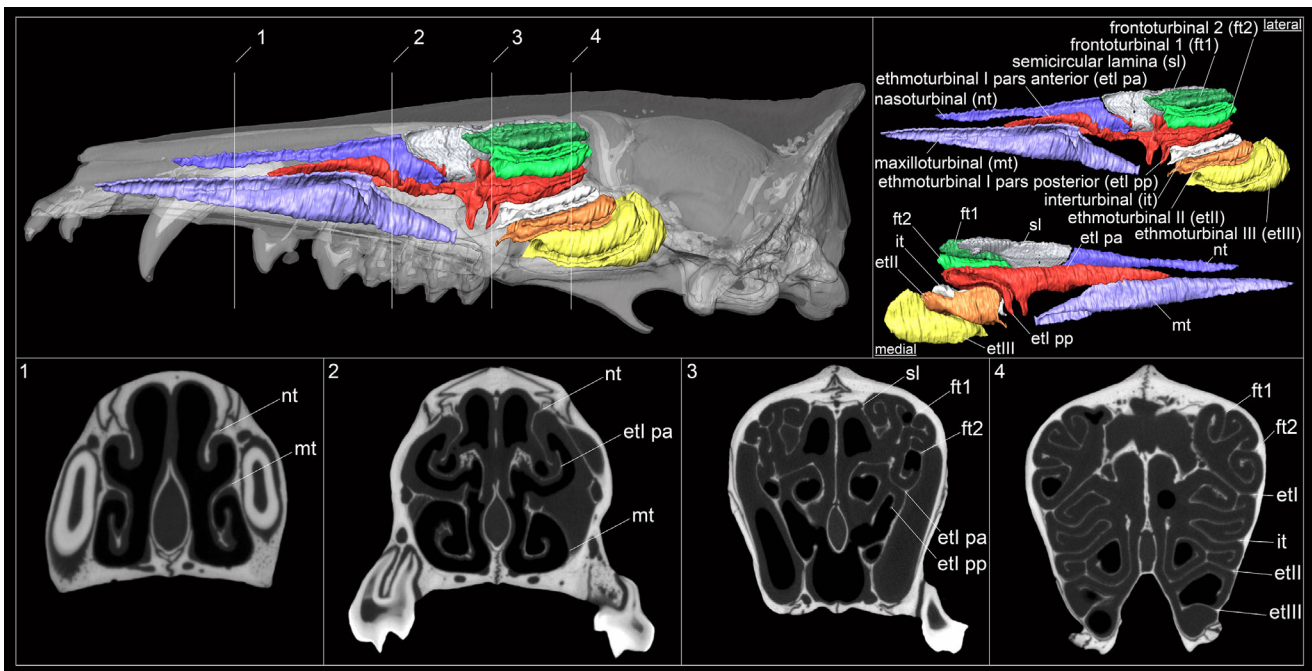
**Fig. 12.** (Top) Sagittal views of the skull of a grey wolf [*Canis lupus*, University of Alaska Museum (UAM) 115907] with three-dimensional illustration of the segmented turbinal shown in lateral and medial views. (Bottom) Nine coronal sections along the nasal cavity at positions identified by numbers in the top left image. Raw micro-computed tomography (micro-CT) data from Axel Newton (MorphoSource ID number 000165185).

subsequent exhalation, this warmed air is cooled down by the anterior portion of the respiratory turbinals that were previously cooled down by inspired air (Fig. 3). This heat

reduction will condense water within the nasal cavity and allow the expiration of drier air, conserving on average 66% of the humidity of the exhaled air (Negus, 1958; Walker &



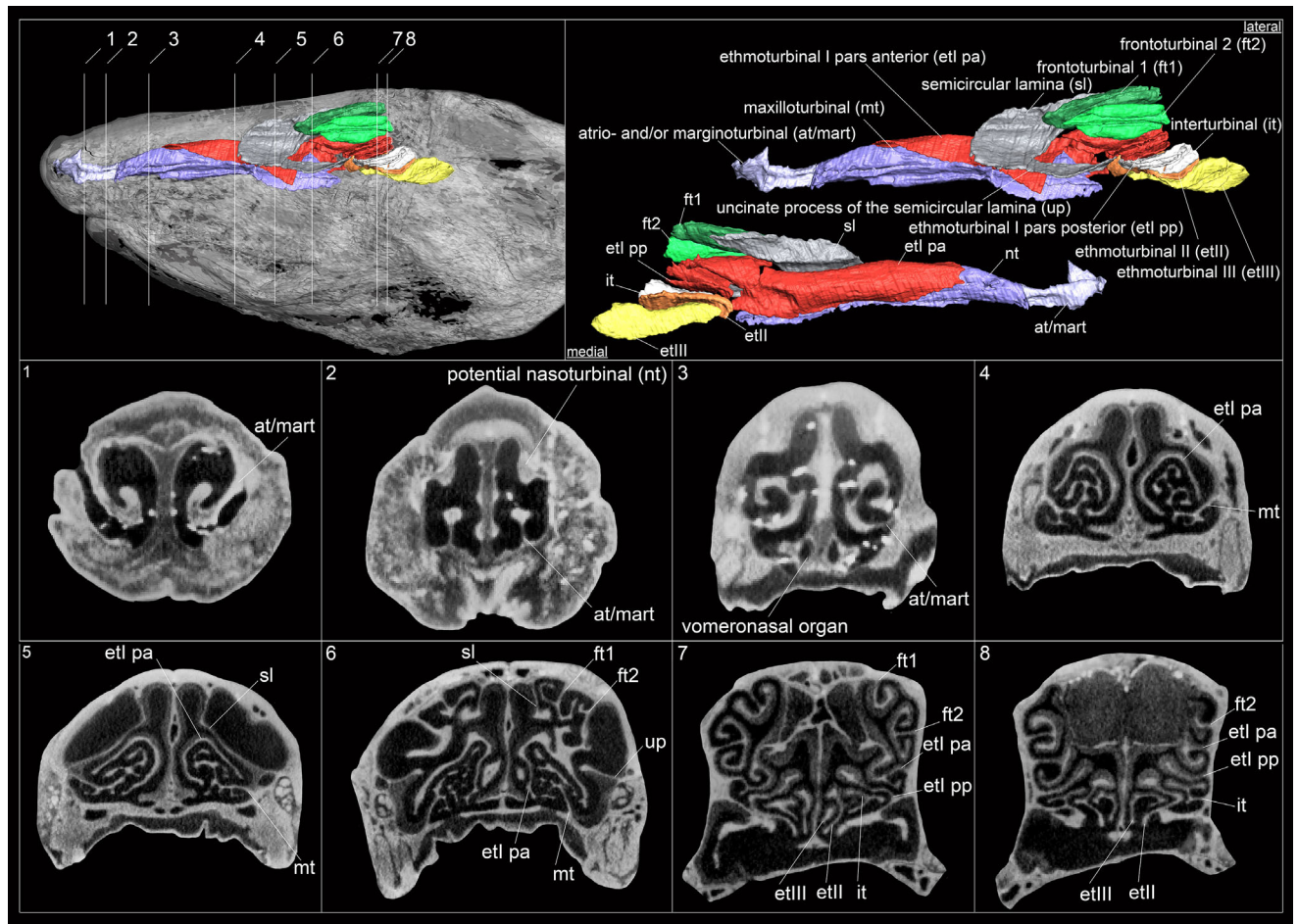
**Fig. 13.** (Top) Sagittal views of the skull of a Seba's short-tailed bat [*Carollia perspicillata*, Natural History Museum of London (NHMUK) 66 3432] with three-dimensional illustration of the segmented turbinale shown in lateral and medial views. (Bottom) Five coronal sections along the nasal cavity at positions identified by numbers in the top left image. Raw micro-computed tomography (micro-CT) data from Quentin Martinez (MorphoSource ID number 000524234).



**Fig. 14.** (Top) Sagittal views of the skull of tailless tenrec [*Tenrec ecaudatus*, Institut des Sciences de l'Évolution de Montpellier – Quentin Martinez (ISEM-QM-201)] with three-dimensional illustration of the segmented turbinale shown in lateral and medial views. (Bottom) Four coronal sections along the nasal cavity at positions identified by numbers in the top left image. Raw micro-computed tomography (micro-CT) data from Quentin Martinez (MorphoSource ID number 000523932).

Wells, 1961; Jackson & Schmidt-Nielsen, 1964; Schmidt-Nielsen, Hainsworth & Murrish, 1970; Collins, Pilkington & Schmidt-Nielsen, 1971; Schroter & Watkins, 1989; Hillenius, 1992; Ruben

*et al.*, 1996; Hillenius & Ruben, 2004). This countercurrent heat exchange is a widespread physiological process (Jackson & Schmidt-Nielsen, 1964). In rabbits and in some rodent species,



**Fig. 15.** (Top) Sagittal views of the head and the soft tissues of a gray short-tailed opossum [*Monodelphis domestica*, Laboratory of Vera Weisbecker (l-vw:umelns-md11)] with three-dimensional illustration of the segmented turbinal shown in lateral and medial views. (Bottom) Eight coronal sections along the nasal cavity at positions identified by numbers in the top left image. Raw micro-computed tomography (micro-CT) data from Vera Weisbecker and Alison Carlisle (MorphoSource ID number 000021415).

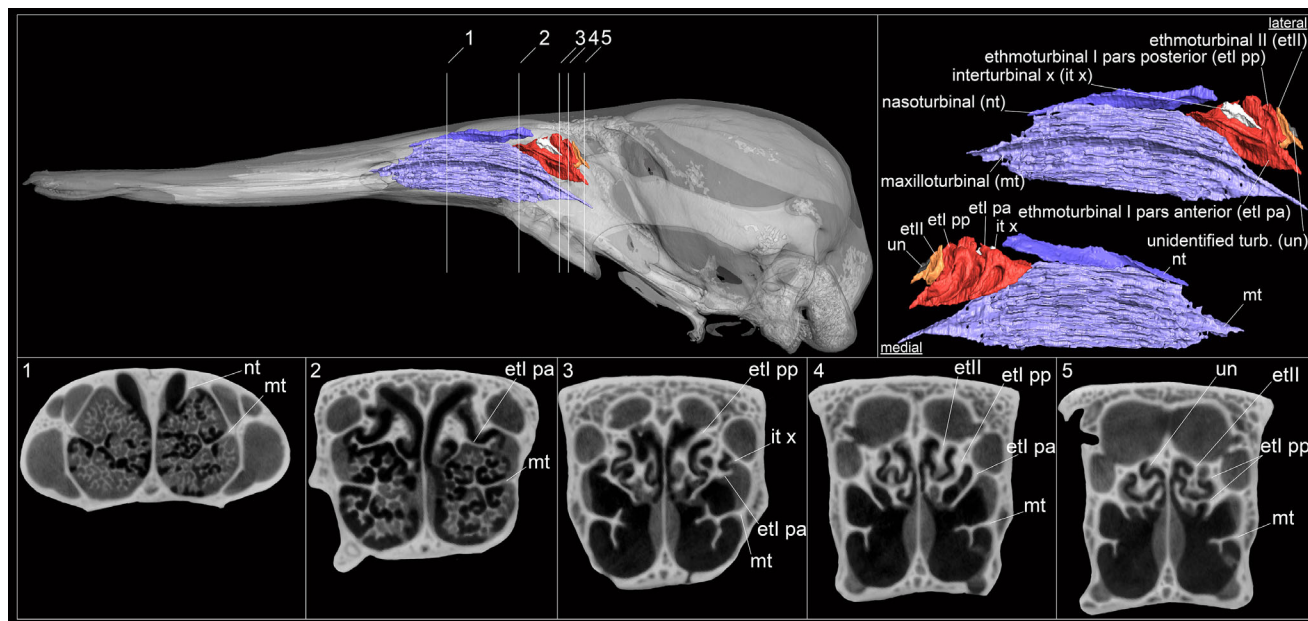
it has been demonstrated that during inhalation, the maxilloturbinal participates in the temperature increase of air inspired through the nasal cavity to reach body temperature (Jackson & Schmidt-Nielsen, 1964; Schmidt-Nielsen, 1969; Schmidt-Nielsen *et al.*, 1970; Caputa, 1979). Heat and water saving during exhalation varies widely among species (Schmidt-Nielsen, Schroter & Shkolnik, 1981). Interestingly, heat dissipation by the respiratory turbinas has been argued to have a role in brain cooling (Baker & Hayward, 1968; Langman *et al.*, 1978; Schmidt-Nielsen *et al.*, 1981; Bourke *et al.*, 2014; Owerkowicz *et al.*, 2015). However, despite their previously demonstrated physiological role, Martinez *et al.* (2023b) failed to identify a significant relation between the relative surface area of one of the respiratory turbinas (the maxilloturbinal) and mammalian physiological proxies such as the corrected basal metabolic rate and body temperature.

Respiratory turbinas are involved in the protection of the lower respiratory tract and of the posterior neuroepithelium. Respiratory turbinas filter, absorb, and dispose of both macro- and microscopic particles but also volatile substances

that could cause injuries (e.g. Morgan & Monticello, 1990; Harkema *et al.*, 2006). These processes are carried out by the cilia of the respiratory epithelium (see Fig. 6) and through its absorption and regeneration properties.

Finally, respiratory turbinas are involved in airflow dynamics, maintaining and redirecting the inspired airflow to specific areas such as the olfactory turbinas (e.g. Craven, Paterson & Settles, 2010; Bourke & Witmer, 2016; Pang *et al.*, 2016).

Respiratory turbinas are mostly covered by transitional and respiratory epithelium (Fig. 6). For simplification, and to differentiate from the olfactory epithelium, several authors have merged transitional with respiratory epithelium, only referring to the latter type to describe the epithelium that lines respiratory turbinas. Respiratory epithelium is composed of six cell types: ciliated columnar, non-ciliated columnar, mucous, brush, cuboidal, and basal. The relative composition of these cell types will change the properties of the respiratory epithelium in terms of mucus production, capacity to retain macro- and microscopic particles as well



**Fig. 16.** (Top) Sagittal views of the skull of a platypus [*Ornithorhynchus anatinus*, Museum of Vertebrate Zoology (MVZ) 32885] with three-dimensional illustration of the segmented turbinial shown in lateral and medial views. (Bottom) Five coronal sections along the nasal cavity at positions identified by numbers in the top left image. Note the absence of ossified turbinals on the anterior part of the nasal cavity. Turbinial homology modified after Zeller (1989) but see Fig. S1 for alternative interpretations. Raw micro-computed tomography (micro-CT) data from Carol Spencer and Edward Stanley (MorphoSource ID number 000059596).

as enzyme activities (Herbert *et al.*, 2018). The lamina propria (= most ventral part of the epithelium) of the respiratory epithelium is highly vascularised and contains many mucous glands (Figs 6 and 7). The transitional epithelium is a thin layer composed of cuboidal or low columnar cells that vary in their degree of ciliation.

#### (a) Margino- and atrioturbinal

In mammals, the most anterior portion of the nasal cavity houses a cartilaginous structure named the outer nasal cartilage (Maier, 2020; Ruf, 2020). This structure makes up the junction between the external nares and the nasal bones. Species with elongated rhinariums or trunks [e.g. shrews (Lipotyphla) or elephant shrews (Macroscelidea)] have a long outer nasal cartilage (Maier, 2020).

Anteriorly, two single turbinals, margino- and atrioturbinal, are fully cartilaginous at the adult stage (Fig. 15). These turbinals are formed by the anterior nasal cupula and/or the paries nasi (Voit, 1909; Reinbach, 1952a,b; Ruf *et al.*, 2015; Ruf, 2020). Due to their cartilaginous composition, these two turbinals are difficult to identify without precise histological investigation or dissection (Fig. 15). Therefore, in mammals, mentions of margino- and atrioturbinals are rare (De Beer, 1929; Reinbach, 1952a,b; Maier, 1980, 2000, 2020; Rossie & Smith, 2007; Macrini, 2012, 2014; Maier & Ruf, 2014; Ruf, 2014, 2020; Ito *et al.*, 2021), even in groups like rodents (e.g. Fawcett, 1917; Parsons, 1971a; Ruf, 2020). Because they are directly in contact with the exterior environment, margino- and atrioturbinals are composed of lightly

keratinised and squamous epithelium that may protect the posterior epithelium (Ruf, 2014, 2020; Herbert *et al.*, 2018). Margino- and atrioturbinals are extremely complicated to discriminate and some authors refer to the former or latter without clear homology (Ruf, 2020). Rare studies with very precise histology can differentiate between margino-, atri-, and maxilloturbinal [e.g. Reinbach (1952a,b) in the nine-banded armadillo *Dasyurus novemcinctus* and Ruf (2020) in rodents] in some species by the presence of an incisura while in other species there is no distinct incisura. Maier (2000) noted an absence of an atrioturbinal in cercopithecoids and therefore a gap between the margino- and maxilloturbinal. In addition to their role in heat and moisture conservation, the margino- and atrioturbinal, in concert with the cartilages of the anterior nasal cupula, may also play a role in the shape of the nostril. Finally, some links with facial muscles may imply a role in airflow direction into upper and lower components and even in the sniffing process (Hofer, 1980; Göbbel, 2000; Maier & Ruf, 2014). Given the difficulty involved in identifying these two cartilaginous turbinals even with diceCT scans (diffusible iodine-based contrast-enhanced computed tomography; Fig. 15; e.g. Ito *et al.*, 2022), they remain widely understudied.

#### (b) Maxilloturbinal

The maxilloturbinal is a product of the anterior chondrification centre of the nasal capsule (Fig. 9) and is located at the posterior end of the atrioturbinal if present (Maier, 2000; Ruf, 2020). The maxilloturbinal ossifies from the ventral

rim of the paries nasi and is considered a separate bone in mammals (Ruf, 2020). It is thought to be the largest respiratory turbinal; however there is significant variation across mammals (Figs 4, 10–16; Martinez *et al.*, 2023b). Its shape can vary from a simple lamella to a single or double scroll or even a highly dendritic structure.

In some bats, recent findings suggest that the morphology and the development of a potential maxilloturbinal may be constrained by skull adaptations linked to nasophonation (= nasal echolocation) or may even participate in such emission (Curtis & Simmons, 2017; Curtis *et al.*, 2020). However, its homology to the maxilloturbinal is debated (Ito *et al.*, 2021).

#### (c) Nasoturbinal

The nasoturbinal is located dorsally to the maxilloturbinal and also originates from the anterior chondrification centre. In rodents, it is a distinct turbinal with no connection to other turbinals (Fig. 4). In some mammals, the nasoturbinal is connected to the lamina semicircularis that reaches into the posterior part of the olfactory recess (Fig. 14; e.g. Ruf, 2014) and in these cases some authors do not discriminate between the nasoturbinal and the lamina semicircularis [e.g. Le Gros Clark (1951) in the rabbit]. The posteromedial part of the nasoturbinal is often covered by olfactory epithelium, suggesting a dual function in respiratory and olfactory processes. However, the epithelial cover of the nasoturbinals varies greatly among species (Smith *et al.*, 2004, 2012; Smith & Rossie, 2008; Yee *et al.*, 2016; Herbert *et al.*, 2018).

Finally, the nasoturbinal has a key function in directing the anterior airflow to the posterior olfactory recess and the olfactory turbinals. In placentals, the passage of the air along the nasoturbinal results in a decreasing airflow velocity in the olfactory recess that may increase absorption and therefore the detection of volatile odorant molecules (e.g. Craven *et al.*, 2010). However, in some blind recesses shaped by turbinals, both the volatility and the sorption strength of the odorant molecules may also play a role (Mozell, Kent & Murphy, 1991).

#### (4) Olfactory turbinals

Olfactory turbinals are responsible for olfaction and support olfactory epithelium and neurons (Ressler *et al.*, 1993; Ressler, Sullivan & Beck, 1994; Harkema *et al.*, 2006; Barrios *et al.*, 2014; Herbert *et al.*, 2018). Olfactory turbinals chondrify and ossify antero-posteriorly, although larger turbinals in the olfactory region form prior to smaller turbinals [e.g. interturbinals (Smith & Rossie, 2008; Ruf, 2020; Smith *et al.*, 2021c)]. Olfactory turbinals are generally fully ossified in adult stages and contribute to the ethmoid bone (e.g. Van Valkenburgh, Smith & Craven, 2014; Ruf, 2020). The ethmoid bone comprises several sub-structures: beside all olfactory turbinals, the ossified part of the nasal septum (lamina perpendicularis), the cribriform plate, the crista galli, and to a specific extent ossified parts of the former cartilaginous nasal capsule (e.g. in muroid rodents; Ruf, 2020). It is well

known that the relative size and complexity of olfactory turbinals varies significantly among species (Figs 4, 10–16; e.g. Van Valkenburgh *et al.*, 2011; Martinez *et al.*, 2018, 2020); in dog breeds, the complexity but not the number (except for the interturbinals) of olfactory turbinals is related to rostrum length (Wagner & Ruf, 2019, 2021). Developmentally, extreme reduction is generally attributed to the merging of embryonic structures, whereas multiple turbinals may result from repetitive mesenchymal growth (Smith & Rossie, 2008; Van Valkenburgh, Smith & Craven, 2014; Smith *et al.*, 2021c). However, recent findings in anthropoid primates indicate that some turbinals fail to differentiate due to deficient space and mesenchyme (Smith & DeLeon, 2021).

In most mammals, these turbinals are almost completely covered by olfactory epithelium (Figs 6–8). The olfactory epithelium is pseudostratified and composed of olfactory sensory neurons, supporting cells, and basal cells (Herbert *et al.*, 2018). At the dorsal surface of the olfactory epithelium, the olfactory vesicles of the olfactory neurons participate in increasing the surface area for the reception of odorant molecules. Olfactory neurons are ventrally extended by an axon that joins other axons and nerve fascicles (panel 8 in Fig. 7). These nerve fascicles run through the perforated cribriform plate to join glomeruli from the olfactory bulb (Fig. 2). The olfactory neurons are constantly regenerated with an estimated turnover rate of 30 days in the laboratory rat (Graziadei & Monti Graziadei, 1978). The lamina propria (= most ventral part of the epithelium) of the olfactory epithelium includes Bowman's glands (= submucosal glands; Fig. 6) which participate in moistening the olfactory epithelium and which secrete a solvent that bonds the volatile odorant molecules to the olfactory receptors. Some parts of the nasal roof, the nasal septum and the lateral wall of the olfactory recess are also covered by olfactory epithelium (Figs 6, 8; Smith *et al.*, 2004, 2014; Rowe *et al.*, 2005; Eiting *et al.*, 2014a; Herbert *et al.*, 2018; Ruf, 2020). Some 'olfactory' turbinals have a dual function of respiratory air-conditioning and olfactory sensing. These exceptions are noted below.

#### (a) Semicircular lamina

Because the semicircular lamina (= lamina semicircularis, sometimes called crista semicircularis in prenatal stages) is mostly covered by olfactory epithelium (Fig. 8), it is often considered functionally as an olfactory turbinal (e.g. Martinez *et al.*, 2018, 2020, 2023a; Wagner & Ruf, 2019, 2021). However, since at least some mammals lack olfactory mucosa on the semicircular lamina (Smith & Bonar, 2022), we currently may not fully appreciate functional variation. The semicircular lamina is part of the anterior chondrification centre and forms the anterior border of the hiatus semilunaris, the entrance into the lateral recess; its dorsal part can reach far posteriorly under the lamina cribrosa (Ruf, 2014, 2020). Here, we also include the ventral projection named the uncinate process (Fig. 15). The presence of this process and its size varies significantly among species without any particular

phylogenetic or ecological pattern identified so far (Macrini, 2012, 2014; Ruf, 2014, 2020).

#### (b) Frontoturbinals

Frontoturbinals are defined as turbinals located in the frontal recess and therefore do not meet the posterior transversal lamina (= lamina terminalis in fully ossified stages; Rowe *et al.*, 2005; Ruf, 2020). The frontoturbinals originate from the middle chondrification centre and/or the horizontal lamina that separates the frontoturbinal recess from the maxillary recess; frontoturbinals are often fused to the lamina cribrosa posteriorly (Van Valkenburgh, Smith & Craven, 2014; Ruf, 2020); frontoturbinals are the first turbinals to ossify in *Tupaia* (Scandentia) (Ruf, 2020, citing Spatz, 1964), however this may not be a common pattern. They are also described as turbinals that do not develop medially and remain far from the nasal septum (Rowe *et al.*, 2005, citing Allen, 1882). This character has been used by some authors to distinguish between ectoturbinals (= frontoturbinals and interturbinals) and endoturbinals (= ethmoturbinals and semicircular lamina) (Paulli, 1900a,b,c); the latter reach closer to the nasal septum.

#### (c) Ethmoturbinals

Ethmoturbinals originate from the posterior chondrification centre and are fully ossified in adult stages (Van Valkenburgh, Smith & Craven, 2014; Ruf, 2020). Like the frontoturbinals, the ethmoturbinals are connected posteriorly to the cribriform plate and therefore to the olfactory bulb *via* olfactory nerves (Fig. 2; Herbert *et al.*, 2018; Ruf, 2020). In many mammals, ethmoturbinals are more complex and numerous than frontoturbinals and therefore considered as the structures that are the most involved in olfactory processes.

Among ethmoturbinals, ethmoturbinal I (etI) has received much more attention than the others (e.g. Smith *et al.*, 2007a, 2021b; Deleon & Smith, 2014). Indeed, through its anterior projection and its division into two distinct lamellae (pars anterior and posterior; Figs 4, 10–16), it is easy to identify. The etI is generally the largest ethmoturbinal and the first ethmoturbinal to develop during ontogeny (Rowe *et al.*, 2005; Ruf, 2020). The etI is the olfactory turbinal that reaches the most anterior part of the nasal cavity (Figs 4, 10–16). In lagomorphs and some rodents, the etI projects anteriorly to the limit or with a small overlap to the respiratory turbinals (Fig. 4; Ruf, 2014, 2020; Martinez *et al.*, 2018). In some species among Lipotyphla (Fig. 11), Tenrecoidea (Fig. 14; elongated in *Tenrec ecaudatus* but not in *Potamogale velox*), Scandentia (e.g. the treeshrew *Ptilocercus loui*), Carnivora and Marsupialia, the pars anterior of the etI projects furthest rostrally and may have great overlap with the respiratory turbinals (Fig 12, Ruf *et al.*, 2015; Ruf, Behrens & Zeller, 2020; Wagner & Ruf, 2019; Martinez *et al.*, 2020; Ito *et al.*, 2022). In these species, and similarly to the nasoturbinal of some other species, the etI may have

a dual function as a respiratory and olfactory turbinal (see also Smith *et al.*, 2007a, 2016; Pang *et al.*, 2016; Yee *et al.*, 2016). Indeed, part of the pars anterior is covered by respiratory epithelium and the rest is covered by olfactory epithelium (Smith *et al.*, 2007a; Martinez *et al.*, 2020; Ruf, 2020). Using histology and micro-CT images, Martinez *et al.* (2020) identified a small incisura in some Lipotyphla and Tenrecoidea that may be used to estimate precisely the antero-posterior functional subdivision. In rodents, these two lamellae may be assigned to the etI since they fused proximally (e.g. Ruf, 2020). Smith & Rossie (2008), investigating primate nasal development, asserted that the etI pars posterior (etI pp) is distinct (with its own root lamella) from the etI pars anterior in its earliest phase of ontogeny. For that reason, these authors refer to etI pp as etII. Additional work will need to clarify whether etI pp is developmentally distinct in other mammals as well (see also Smith & Bonar, 2022). Readers should be alert to such terminological differences (see online Supporting Information, Table S1).

#### (d) Interturbinals

Interturbinals are olfactory turbinals that can develop between both fronto- and ethmoturbinals. In rodents, lagomorphs, primates, bats, and carnivorans, interturbinals develop later than fronto- and ethmoturbinals (Smith & Rossie, 2008; Ruf, 2014, 2020; Wagner & Ruf, 2019; Smith *et al.*, 2021c). Typically, interturbinals do not extend as far medially as the fronto- and ethmoturbinals (Ruf, 2020) but some exceptions may occur (Macrini, 2012; Q. Martinez, personal observations). In mammals, the number of interturbinals varies greatly across species (Paulli, 1900a,b,c; Ruf, 2014; Martinez *et al.*, 2018, 2020). Their homology is also unclear in some orders with highly complex olfactory turbinals [e.g. Cingulata or Proboscidea (Paulli, 1900a,b,c; Hautier *et al.*, 2019; Martinez *et al.*, 2024b)]. However, one particular interturbinal located between ethmoturbinal I (etI) and II (etII) has received more attention and may be homologous in mammals. In the common fronto-/ethmoturbinal terminology, this interturbinal is simply named interturbinal (it) (Figs 4, 10–15; e.g. Ruf, 2014, 2020, 2022; Ruf *et al.*, 2015; Martinez *et al.*, 2018). However, the presence of additional interturbinals between etI and II as well as anteriorly and posteriorly to this homologous interturbinal, complicates the anatomical nomenclature (Fig. 12; e.g. Wagner & Ruf, 2019, 2021). These additional interturbinals are probably the most variable turbinals in the mammalian clade and do not seem to follow a particular pattern. For example, in rodents, intra-individual (on left and right sides) and intra- and inter-specific variations were observed in these additional interturbinals (Martinez *et al.*, 2018; Q. Martinez, personal observations). Finally, it is noteworthy that in some rodents, new turbinals have been identified between the naso- and maxilloturbinal and also may be considered as interturbinals (Martinez *et al.*, 2020).



## (5) Other terminologies

Among the numerous homologous terms referring to the turbinals, ‘turbinals’, ‘turbinate’ and ‘conchae’ are the most widespread. The first two are mostly used for mammals while the latter is mostly used for other tetrapods. Some use ‘turbinals’ for the cartilaginous or bony structure, and ‘conchae’ for the combination of this structure and the epithelium that covers it (Bourke *et al.*, 2014; Bourke & Witmer, 2016; Hogan *et al.*, 2020). Because these terms have been used interchangeably and to avoid confusion, in this review, we simply refer to ‘turbinals’ for all tetrapods. We provide a non-exhaustive list of synonyms and correspondences of turbinal terminologies among numerous species and studies in Tables S1 and S2.

In mammals, the two most widespread terminologies are: (i) fronto-/ethmoturbinal terminology and (ii) endo-/ectoturbinal (Macrini, 2012; Maier & Ruf, 2014). Fronto-/ethmoturbinal is mostly based on homology determined by developmental studies, which is the most widespread approach in comparative and systematic studies. Endo-/ectoturbinal terminology is based on observations of adult specimens and by the medial extension of the turbinals. It presents an advantage in that it is easy to understand and illustrative, but has rather poor significance in systematics and evolutionary biology. In particular, it makes the comparison and discussion of homology of turbinals across species difficult. In most cases, ectoturbinals correspond to the turbinals found in the frontoturbinal recess (fronto- and interturbinals) but also interturbinals in the olfactory recess, while endoturbinals correspond to the remaining olfactory turbinals (semicircular lamina and ethmoturbinals) with the exception for some authors of the interturbinal located between ethmoturbinal I (etI) and II (etII) (Macrini, 2012 but see Paulli, 1900*a,b,c*). We also note that some authors mix these terminologies (e.g. Rossie, 2006) or use both together to be didactic (Macrini, 2014; Smith & Bonar, 2022).

Herein we retain the fronto-/ethmoturbinal terminology which is meaningful from an evolutionary perspective (Tables S1 and S2). We mostly consider groups for which developmental studies exist and which do not have complex olfactory turbinals that will require extensive embryological studies to produce a proper terminology. Furthermore, our results are then easily comparable to recent studies (e.g. Smith *et al.*, 2012, 2021*c*; Martinez *et al.*, 2018, 2020; Lundeen & Kirk, 2019; Wagner & Ruf, 2019, 2021; Ruf, 2020, 2022; Ito *et al.*, 2021, 2022; Smith & Bonar, 2022) employing the fronto-/ethmoturbinal terminology adapted from Paulli (1900*a,b,c*). However, these studies do not include mammals with complex olfactory turbinals or with a large number of inter- and ethmoturbinals. Homology of olfactory turbinals is not yet clear for species with highly complex olfactory turbinals such as Carnivora, Perissodactyla or some myrmecophagous placental mammals (e.g. Paulli, 1900*b*; Reinbach, 1952*a,b*; Van Valkenburgh *et al.*, 2014; Hautier *et al.*, 2019). For these species, it may be

unwise to name olfactory turbinals using the fronto-/ethmoturbinal terminology. Clarification awaits developmental studies of mammals with the most complex arrays of olfactory turbinals.

In this review, we follow the fronto-/ethmoturbinal terminology for mammals and have replaced the term concha with turbinals in the terminology proposed by Witmer (1995) for non mammalian species.

## (6) Selective pressures affecting turbinals

It has been hypothesised that the number and the shape of turbinal bones are conserved across orders while their relative size and complexity are more labile, with variation related to species ecology (e.g. Van Valkenburgh *et al.*, 2011, 2014; Van Valkenburgh, Smith & Craven, 2014; Green *et al.*, 2012; Macrini, 2012; Ruf, 2014, 2020; Yee *et al.*, 2016; Curtis & Simmons, 2017; Martinez *et al.*, 2018, 2020; Lundeen & Kirk, 2019; Wagner & Ruf, 2019). However, few studies have investigated this hypothesis using statistics, geometric morphometrics, evolutionary models or developmental approaches.

### (a) Phylogeny

At higher taxonomic levels, turbinals are thought to carry a phylogenetic signal and several studies identified potential characters linked to phylogenetic relationships (Paulli, 1900*a,b,c*; Negus, 1958; Ruf, 2014, 2020). Within mammalian orders or families, gross turbinal anatomy generally does not vary significantly. For example, Ruf (2020) identified a rodent groundplan for olfactory turbinals that comprises two frontoturbinals, three ethmoturbinals, and one interturbinal between ethmoturbinals I and II [for dog, ochotonid and leporid groundplans, see Ruf (2014) and Wagner & Ruf (2019)]. Maier (2000) also suggested that the marginoturbinal is typical of therian mammals but some exceptions exist. Other studies attempted to score turbinal characters from adult specimens (e.g. Voss & Jansa, 2003; Macrini, 2012; Ruf, 2014, 2020; Lundeen & Kirk, 2019). The shape, complexity and relative size of maxilloturbinals varies greatly across the mammalian phylogeny (Rowe *et al.*, 2005; Martinez *et al.*, 2020, 2023*b*). For example, in Carnivora, Van Valkenburgh *et al.* (2014) demonstrated that the complexity of the maxilloturbinal differs between caniforms and feliforms with apparently similar ecologies (e.g. terrestrial, semi-aquatic). Not surprisingly, in mammals, the maxilloturbinal has a strong and significant phylogenetic signal (Martinez *et al.*, 2023*b*).

Developmental constraints are also hypothesised to impact turbinal evolution (e.g. Rowe *et al.*, 2005), which might be in conflict for space with other structures in the nasal cavity. This hypothesis was widely discussed for eye proportions and some evidence has been found in Primates (Smith *et al.*, 2014), Scandentia (Ruf *et al.*, 2015) and Carnivora (Van Valkenburgh, Smith & Craven, 2014; Wagner & Ruf, 2019, 2021; Ruf, 2020). For instance, in the dog snout,

length (and thus space limitation) does not constrain the number of turbinals (except additional interturbinals) but rather their complexity and shape (additional lamella, scrolls and branching). The observed increase in turbinal complexity from prenatal stages *via* brachycephalic breeds (e.g. pug), mesaticephalic breeds (e.g. German shepherd) to dolichocephalic breeds (e.g. borzoi) may correspond to an ontogenetic continuum (Wagner & Ruf, 2021). Rodents have large jaw muscles sometimes attaching on the rostrum as well as continuously growing incisors with roots occupying a significant part of the nasal cavity. Therefore, it is possible that muscle proportions and shape variations of their incisors constrained the shape and development of turbinals in rodents. The geometric organisation of the masticatory apparatus, which starts earlier in development than does ossification of the ethmoid complex, supports this hypothesis (e.g. Rowe *et al.*, 2005). In the naked mole rat (*Heterocephalus glaber*), loss of the maxilloturbinal in some individuals results in a partially empty nasal cavity (Martinez *et al.*, 2023b). The absence of replacement of this empty space by other structures suggests that conflict for space between different structures in the nasal cavity of the naked mole rat is unlikely. An alternative hypothesis is that the loss of this structure is ongoing (as suggested by the intra-individual and intra-specific variation) and that there is a delay between maxilloturbinal loss and the replacement of its space by other structures in the naked mole rat (Martinez *et al.*, 2023b). This question will need to be addressed by using covariation and/or landmark-based geometric morphometric approaches that remain extremely rare in the field (e.g. Curtis *et al.*, 2020). Finally, loss of the maxilloturbinal in the naked mole rat suggests that this turbinal may be energetically costly to maintain in mammals. Structures or functions that are not costly to maintain may be conserved even if they are no longer under strong selective pressures (Jeffery, 2005; Lahti *et al.*, 2009; Charles *et al.*, 2013).

Turbinals are rarely preserved in the fossil record either due to their delicate nature or to the fact that they are cartilaginous. As turbinals are hidden inside the nasal cavity, access is limited and, in the past, was based on prepared or broken specimens (e.g. Hürzeler, 1936). In mammals turbinals have been described in fossil species of several groups, including Apatemyidae (Koenigswald, Ruf & Gingerich, 2009), Lagomorpha (Ruf, Meng & Fostowicz-Frelik, 2021), Primates (Lundeen & Kirk, 2019), terrestrial Artiodactyla (Hürzeler, 1936; Czubak, 2013; O'Brien *et al.*, 2016; Keppeler *et al.*, 2023), Cetacea (e.g. Tsai & Fordyce, 2018), and Xenarthra (Fericola *et al.*, 2012; Amson, Billet & Muizon, 2018). The anatomy of turbinals was recently used to discuss the phylogenetic position of some extinct primates, including the early Eocene *Shoshonius cooperi*, the late middle Eocene *Rooneyia viejaensis*, and the early Miocene *Homunculus patagonicus* (Lundeen & Kirk, 2019; Kirk & Lundeen, 2020; Lundeen & Kay, 2022). Recently, the first description of turbinal remnants in a fossil lagomorph (*Palaeolagus haydeni* from the early Oligocene of North America) helped to elucidate the polarisation of certain characters in the turbinal

skeleton of extant rabbits, hares and pikas (Ruf *et al.*, 2021). Turbinal structures or their remnants (respiratory as well as olfactory) are also known from the basal mammaliaforms *Haldanodon expectatus* (Lillegraven & Krusat, 1991) and *Morganucodon* (Kermack, Mussett & Rigney, 1981), the non-mammaliaform cynodont *Brasiltherium riograndensis* [Ruf *et al.* (2014) but see Crompton *et al.* (2017)] and the dicynodonts *Lystrosaurus declivis* and *Kawingasaurus fossilis* (Laaß *et al.*, 2011; Laaß & Kaestner, 2023). However, as turbinals were likely cartilaginous in mammalian ancestors, evidence from other non-mammalian therapsids is scarce and mostly restricted to bony ridges or scars (attachment sites of turbinals) inside the nasal cavity (e.g. Hillenius, 1994; Sigurdson, 2005; Crompton *et al.*, 2017; Franco *et al.*, 2021). Such bony scars are interpreted as potential attachment sites of respiratory turbinals in the late Permian therocephalian *Glanosuchus* [~ 261 million years ago (Mya); Hillenius, 1992, 1994]. Respiratory ridges are also found in later cynodonts such as *Masselognathus* (Crompton *et al.*, 2017) and in the dicynodont *Pristerodon mackayi*; in the latter two, these ridges are associated with potential maxillo- or nasoturbinals (Laaß *et al.*, 2011; Laaß & Kaestner, 2023). Similarly, some bony scars in the dicynodont *Lystrosaurus* were interpreted as indicating the attachment of potential maxillo- or nasoturbinals (Laaß *et al.*, 2011). These bony scars have been proposed to indicate endothermy. However, recent work on semicircular canal biomechanics demonstrated that therocephalians as well as *Lystrosaurus* were probably ectothermic (Araújo *et al.*, 2022). Olfactory turbinal ridges have also been described in some non-mammalian cynodonts [e.g. *Diademodon* and *Thrinaxodon* (Watson, 1913; Brink, 1956; Parsons, 1971a; Hillenius, 1994)] and dicynodonts (Laaß *et al.*, 2011; Laaß & Kaestner, 2023).

Phylogenetic relationships and developmental constraints cannot explain all the differences in turbinals observed across mammals. Indeed, it is now known that the relative surface area and complexity of turbinals greatly varies with species ecology. In the following two sections, we discuss the evolution of olfaction and heat and moisture conservation in the context of species ecology.

#### (b) Ecology and olfactory turbinals

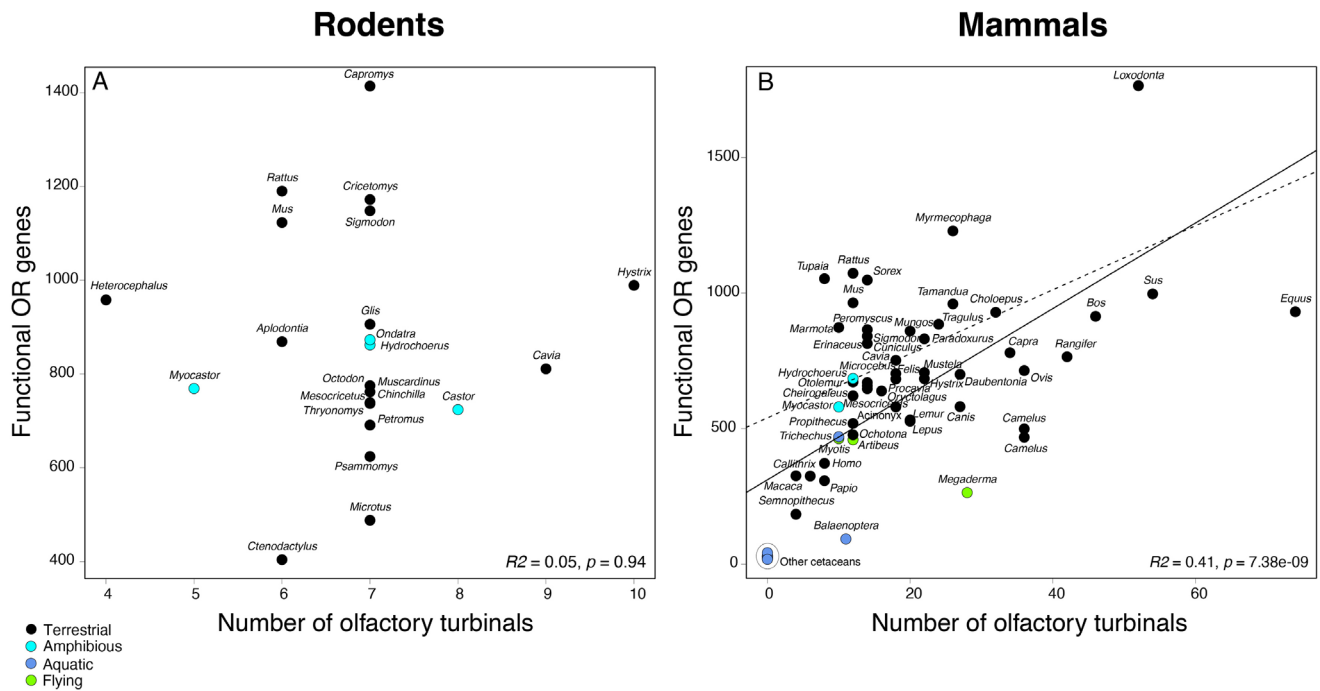
Some comparative work has demonstrated a relation between the relative surface area of turbinals and aspects of species ecology such as diet (e.g. earthworm consumption, scavengers) or lifestyle (Van Valkenburgh *et al.*, 2004, 2011, 2014; Green *et al.*, 2012; Martinez *et al.*, 2018, 2020, 2023a). However, in three species of primates, the absolute surface area bearing olfactory epithelium was negatively correlated to the percentage of frugivory as well as sniffing behaviour (Melin *et al.*, 2022). This absence of a positive relation with frugivory is a striking contrast with the main olfactory bulb volume in these species or with the olfactory receptor (OR) gene composition in frugivorous bats (Hayden *et al.*, 2014; Melin *et al.*, 2022). Using a

comprehensive data set of phyllostomid bats, Yohe *et al.* (2022) found a potential link between diet and the olfactory epithelium surface area of the olfactory turbinals. However, they demonstrated that there was no relation between the diet and the evolutionary rates of OR genes extracted from transcriptomes of the olfactory turbinal epithelium. From data in Laska (2005) and Kowalewsky *et al.* (2006), Van Valkenburgh *et al.* (2011) hypothesised that the relative surface area of turbinals is neither correlated with olfactory sensitivity nor with olfactory discrimination. Instead, they hypothesised that it may characterise the diversity of odorants that can be perceived. By contrast, Martinez *et al.* (2018) demonstrated that highly specialised worm-eating rodents have significantly higher relative surface area and complexity of olfactory turbinals compared to their close omnivorous and carnivorous relatives. This suggests that the relative size of olfactory turbinals may be linked to olfactory sensitivity, at least in these murids. However, the very small number of studies linking olfactory performance to the relative size of olfactory organs leaves many open questions. In rodents (23 species from 15 families, comprising Ctenohytrica, mouse-, and squirrel-related clades), the relative and absolute surface area as well as the number of olfactory turbinals are not significantly correlated with the number of functional OR genes (Fig. 17A; Martinez *et al.*, 2023a). By contrast, comprehensive study of 64 placental mammal species representing most of the living orders found a significant positive correlation between the total number of OR genes (i.e. both functional and non-functional genes) and the number of olfactory turbinals (including the semicircular lamina; Christmas *et al.*, 2023). To investigate the functional significance of this further, we used their data to plot the relation between the number of functional OR genes and the number of olfactory turbinals in the same 64 species. This correlation is also significant and positive (Fig. 17B). This is a striking contrast with the results of Martinez *et al.* (2023a), which perhaps may be explained by the fact that the sampling of the two studies is at different phylogenetic scales (rodents *versus* placental mammals). In addition, within an order, the absolute number of olfactory turbinals may have little functional significance since species with a similar number of olfactory turbinals may have different absolute or relative surface areas of the olfactory turbinals (Fig. 17A; Martinez *et al.*, 2023a).

In mammals, the number of functional OR genes is significantly correlated with the results of performance tests for olfactory sensitivity and discrimination that approximate the olfactory capabilities of the species (Martinez, Amson & Laska, 2024a). Therefore, the number of functional OR genes may be linked to a species' olfactory capabilities. However, when monomolecular odorants are independently considered for olfactory sensitivity performance, the relationships turn out to be non-significant. There was also a lack of significance when considering the discrimination tests independently (Martinez, Amson & Laska, 2024a). These differences may reflect the insufficient statistical power of the tests when considered individually. The functional interpretation of various olfactory proxies must also account for

potential confounding effects such as (i) variation in olfactory epithelium cover (Smith *et al.*, 2004, 2014; Yee *et al.*, 2016; Ruf, 2020), (ii) receptor density (Smith & Bhatnagar, 2004; Smith *et al.*, 2004), (iii) degree of receptive range of the ORs (Kaupp, 2010), (iv) variations in degree of neural connectivity among organs and species (Hildebrand & Shepherd, 1997) and (v) variation in the link between the number of functional OR genes and their expression levels (Young *et al.*, 2003; see also discussion in Martinez *et al.*, 2023b, 2024a). New evidence will probably emerge from medical studies. Pathologies of the sense of smell are numerous and include a reduction or loss of the sense of smell (hyposmia, microsmia, anosmia), an increase in olfactory sensitivity (hyperosmia), the inability to identify a smell correctly (parosmia), or smelling odours that are not actually there (phantosmia; Hernandez *et al.*, 2023). By comparing information on these pathologies with neuronal pathways, causes, and organ differences, it could be possible to fine tune our knowledge on these olfactory components of olfactory capabilities.

A reduction in the relative surface area of the olfactory turbinals has taken place convergently in several amphibious and aquatic mammalian lineages (Van Valkenburgh *et al.*, 2011; Martinez *et al.*, 2020). More generally, olfactory epithelium reduction may be a feature of aquatic tetrapods (Saint Girons, 1976). Among fully aquatic mammals, baleen whales (mysticetes) have ethmoturbinals with some olfactory epithelium (e.g. *Balaena mysticetus*; Farnkopf *et al.*, 2022). An integrative approach suggested that although reduced, *Balaena mysticetus* has a functional sense of smell used to detect airborne odorants during breathing (Farnkopf *et al.*, 2022). Ethmoturbinals are also known in other mysticetes such as *Balaenoptera acutorostrata* and *Eubalaena australis* (Godfrey *et al.*, 2013; Berta *et al.*, 2014; Buono *et al.*, 2015; Ichishima, 2016). Apparently, extant toothed whales (odontocetes) lack ethmoturbinals (Godfrey *et al.*, 2013; Berta *et al.*, 2014; Ichishima, 2016) but more comprehensive and integrative works are still needed. This pattern in cetaceans is also confirmed by the number of OR genes, with mysticetes having more than odontocetes. The latter exhibit the lowest number among all placentals (Christmas *et al.*, 2023). During the evolution of cetaceans, a reduction in the relative size of their olfactory organs has been hypothesised to mirror their land-to-water transition (Farnkopf, 2022). Olfactory turbinals as well as a potential maxilloturbinal and nasoturbinal have been identified in several extinct cetaceans (e.g. Stromer, 1903; Uhen, 2004; Geisler, Sanders & Luo, 2005; Nummela, Hussain & Thewissen, 2006; Pihlström, 2008; Fahlke *et al.*, 2011; Godfrey *et al.*, 2013; Berta *et al.*, 2014; Peri *et al.*, 2020). Berta *et al.* (2014) hypothesised that a reduction in turbinal bones among cetaceans probably occurred during the Eocene or early Oligocene. Available data on cetacean olfactory turbinals are too incomplete to test properly their potential reduction but Peri *et al.* (2020) did document a potential reduction of olfactory turbinals in the middle Eocene protocetid *Aegyptocetus tarfa* as compared to terrestrial Artiodactyla.



**Fig. 17.** Comparison of published results showing the relation between the number of functional olfactory receptor (OR) genes and the number of turbinals in (A) 23 species of rodents (from Martinez *et al.*, 2023a) and (B) 64 species of mammal (from Christmas *et al.*, 2023). In B, the solid line is an ordinary linear regression and the dashed line a phylogenetic generalised least squares (PGLS) regression.

Some shallow-diving tetrapods have acquired a suite of adaptations referred to as bone mass increase, which is thought to assist in underwater trim and buoyancy control (Domning & de Buffr enil, 1991). Interestingly, pachyostosis (additional deposition of periosteal bone), usually restricted to the ribs, has been identified in the turbinals of some extinct aquatic sloths (especially *Thalassocnus carolomartini*; Amson *et al.*, 2018) as well as in some extant and extinct sirenians (Genschow, 1934; Gingerich *et al.*, 1994; Martinez *et al.*, 2024b). Because this pattern seems to affect respiratory and olfactory turbinals equally, it is unlikely that it involves functional adaptations to heat and moisture conservation and/or olfactory capabilities. The exact reason for pachyostotic turbinals remains unclear and is currently only associated with a potentially systemic increase in bone mass (see discussion in Amson *et al.*, 2018).

### (c) Ecology and respiratory turbinals

Most studies investigating the role of nasal morphology in heat and moisture conservation capabilities do not focus specifically on respiratory turbinals, but rather on the whole nasal cavity. As an example, kangaroo rats (*Dipodomys spectabilis*) live in hot environments where water resources are limited, and rely on food to meet their water requirements (Jackson & Schmidt-Nielsen, 1964). In the absence of intense activity, sweating evaporation is relatively low, and therefore the most important source of water loss is breathing. Several

studies demonstrated that this species has more efficient heat and moisture conservation capabilities than other rodents (e.g. *Rattus norvegicus*); kangaroo rats can recover between 54 and 75% of the exhaled water (Schmidt-Nielsen *et al.*, 1970, 1981; Collins *et al.*, 1971). Surprisingly, they are also able to exhale air 14 °C below their body temperature and even below the ambient temperature (Jackson & Schmidt-Nielsen, 1964; Schmidt-Nielsen, 1969). These heat- and moisture-conservation features are assumed to result from their respiratory turbinals. Experiments performed in a dry environment on highly dehydrated camels (*Camelus dromedarius*) with presumed dry nasal cavities showed that the water-saving process works similarly compared to that in non-dehydrated conditions (Schmidt-Nielsen *et al.*, 1981). However, in hot environments, variations were observed in the efficiency of respiratory turbinals between day and night: camels recovered 70% of water loss during night exhalation whereas this fell to 25% during the day. Similar variations were observed for heat-cooling efficiency, and were explained by variations in blood pressure and air-flow current (Schmidt-Nielsen *et al.*, 1981; Langman, 1985). Cold deserts such as in arctic regions generally have drier air than hot deserts (Langman, 1985). Experimental studies on reindeer (*Rangifer tarandus*) demonstrated that this species also exhales relatively cold and dry air, requiring them to drink only 73 ml of water per day (resting at -5 °C; Langman, 1985). In comparison, if a reindeer exhaled saturated and warm air (like humans), it would require 17 times

more water (1.24 l per day; Langman, 1985). Langman (1985) also estimated that during expiration, reindeers recovered 75% of heat that was previously added to the inspired air. Therefore, this species, which experiences extreme climatic conditions, has evolved energy- and water-saving adaptations. Interestingly, reindeers have the second highest relative surface area of the maxilloturbinal of any investigated mammal, at 463% of the predicted value for its skull length (Martinez *et al.*, 2023b).

In small non-flying mammals, there also might be a potential relation between the relative surface area of respiratory turbinals and temperature or elevation (see supplementary information in Martinez *et al.*, 2020). Comparisons can be made with humans (*Homo sapiens*) for example, who expire fully saturated air at a temperature close to the body temperature (Walker & Wells, 1961; Schmidt-Nielsen, 1969) and who have a medium-sized maxilloturbinal relative surface area compared to other mammalian orders (Martinez *et al.*, 2023b). In experimental conditions, the naked mole rat (*Heterocephalus glaber*) has among the highest evaporative water loss recorded in mammals (Buffenstein & Yahav, 1991; but see also Buffenstein & Jarvis, 1985). It is also a poorly thermoregulating endotherm with low basal metabolic rate (McNab, 1966; Withers & Jarvis, 1980; Buffenstein & Yahav, 1991; Hislop & Buffenstein, 1994; Buffenstein *et al.*, 2021; Araújo *et al.*, 2022; but see Braude *et al.*, 2021). This species has a unique pattern of reduction of the maxilloturbinal (Martinez *et al.*, 2023b). At present, these examples remain isolated cases and larger scale analyses are needed to provide functional evidence. However, direct investigations between respiratory turbinals and heat and moisture conservation or physiological proxies are rare. Across 310 mammalian species, differences in the relative surface area of the maxilloturbinal have been linked with ecology (Martinez *et al.*, 2023b). However, they were not significantly explained by heterothermy (such as torpor, hibernation and aestivation), although this could only be tested with a reduced data set of one or two species per thermal condition; (Martinez *et al.*, 2023b). Contrary to previous hypotheses and tests across mammals (reviewed in Owerkowicz *et al.*, 2015), at the mammalian scale, the corrected basal metabolic rate and body temperature are not correlated with the relative surface area of the maxilloturbinal (Martinez *et al.*, 2023b). The same holds true for ventilation rate (but only based on six species; Martinez *et al.*, 2023b).

The best illustration of a correlation between lifestyle and the respiratory turbinals is found for amphibious and aquatic species. Many amphibious and aquatic mammals show greater respiratory turbinal surface area and/or complexity (Van Valkenburgh *et al.*, 2011; Martinez *et al.*, 2020, 2023b; Mason *et al.*, 2020). This has been interpreted as an adaptation to limit heat loss due to the high thermal inertia of water. Pinnipeds (seals and walrus) are also known for efficient moisture conservation, which has been interpreted as an adaptation to salty environments (Lester & Costa, 2006; Van Valkenburgh *et al.*, 2011). To our knowledge, among aquatic species, only cetaceans exhibit a reduction or

an absence of respiratory turbinals and an Eocene protocetid may feature a reduction of the respiratory and olfactory turbinals compared to terrestrial Artiodactyla (Peri *et al.*, 2020). In some mysticetes, a maxilloturbinal has been documented, and there is known variation including some vestigial forms in some odontocetes (reviewed in Berta *et al.*, 2014). However, Farnkopf *et al.* (2022) did not find a maxilloturbinal in the specimens of *Balaena mysticetus* they investigated.

An increase in respiratory turbinal surface area in amphibious and aquatic mammals is in striking contrast to the reduction of their olfactory turbinals (Van Valkenburgh *et al.*, 2011; Martinez *et al.*, 2020). This provides an example of a potential trade-off: when olfactory turbinals are reduced, respiratory turbinals are increased and *vice versa* (Martinez *et al.*, 2020). This implies that there is a strong selective pressure for space in the nasal cavity. Trade-offs have been observed in worm-eating rodents that show a greater allocation of space to olfactory turbinals and a reduction in size of respiratory turbinals (Martinez *et al.*, 2018).

In addition to a protective role against abrasive and toxic substances (Negus, 1958; Morgan & Monticello, 1990; Harkema *et al.*, 2006; Moshkin *et al.*, 2014), respiratory turbinals are also assumed to participate in cooling of the brain *via* the carotid rete (Baker & Hayward, 1968; Langman *et al.*, 1978; Schmidt-Nielsen *et al.*, 1981; Bourke *et al.*, 2014; Owerkowicz *et al.*, 2015). As with olfaction, heat- and moisture-conservation capabilities are multifactorial processes involving other structures in addition to the turbinals, for example in ventilation rate (Martinez *et al.*, 2023b), efficiency of oxygen extraction (Schmidt-Nielsen, 1969), body surface evaporation (Burch & Winsor, 1944), renal mechanisms involved in water conservation (Schmidt-Nielsen & Haines, 1964), lung structure (e.g. alveoli and exchange surface; Lester & Costa, 2006), sweat glands or the fur and keratinous cover of the skin. Finally, as the gap width in the nasal tract may be an important variable (Collins *et al.*, 1971; Schroter & Watkins, 1989; Zwicker *et al.*, 2018), further studies should also consider the epithelium and soft tissues of the nasal cavity including for example those of the marginoturbinal and atrioturbinal.

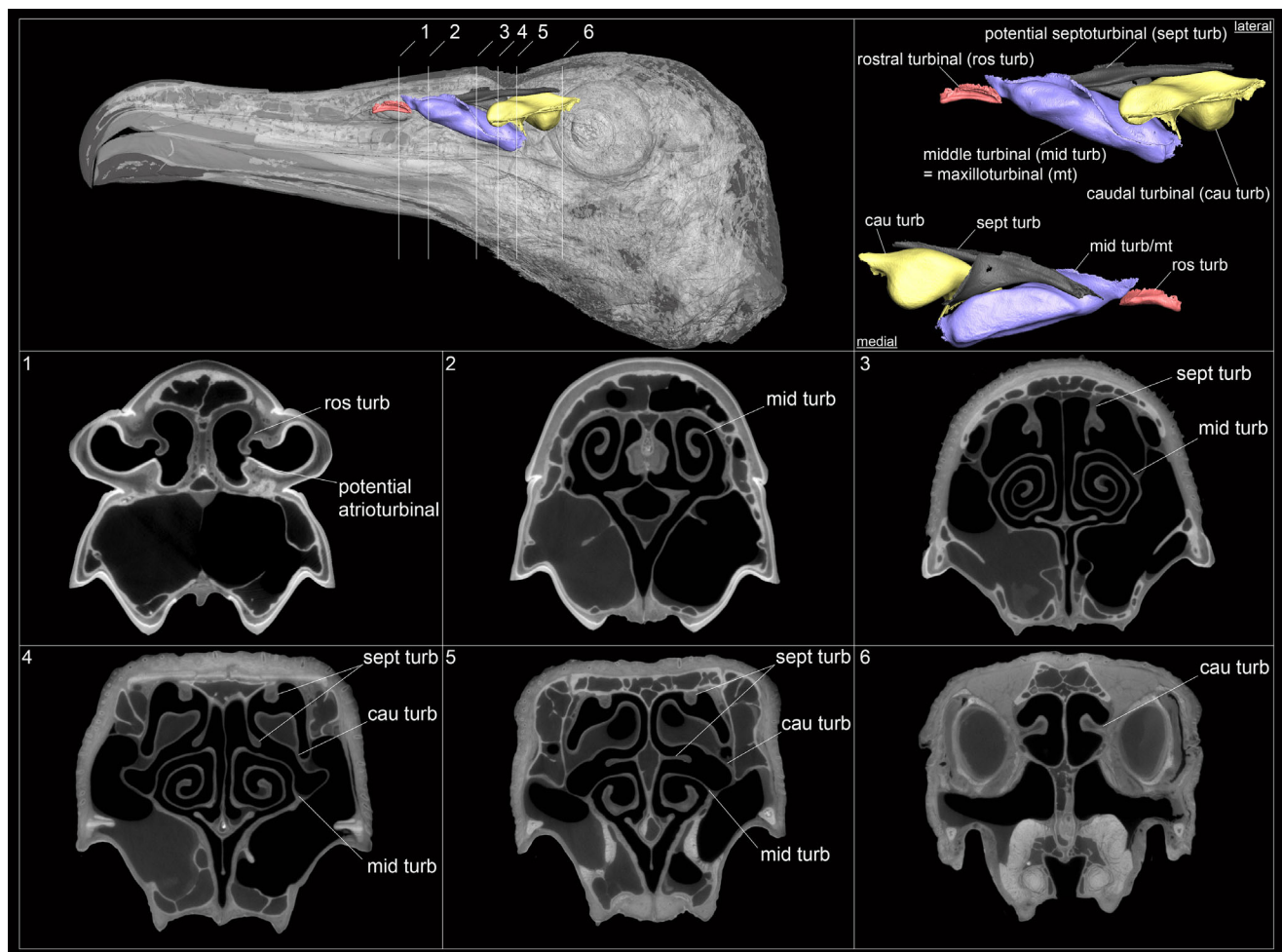
### III. NON-AVIAN DINOSAURS AND BIRDS

Since turbinals are mostly cartilaginous in sauropsids, fossil evidence is still unclear and highly debated. Concerning respiratory turbinals, palaeontologists have discussed the shape and cross section of the nasal cavity of sauropsids (Ruben *et al.*, 1996; Ruben & Jones, 2000). For example, the late Cretaceous ornithurine *Hesperornis* (~ 80 Mya) had a nasal cavity similar to that of extant birds (Witmer, 1997). Hillenius & Ruben (2004) therefore hypothesised that this genus had similar respiratory turbinals to extant birds. Based on the absence of respiratory turbinals in even derived non-avian theropod dinosaurs (e.g. *Archaeopteryx*), Ruben & Jones

(2000) hypothesised that early birds may have been ectotherms. Some scars found in *Tyrannosaurus* (~ 75 Mya) may be potential olfactory turbinals (Ruben *et al.*, 1996), hadrosaur dinosaurs may have had large olfactory turbinals (Parsons, 1971a) and some pachycephalosaurids had extensive olfactory turbinals as well as scars for respiratory turbinals (Bourke *et al.*, 2014).

Turbinals may have evolved convergently in mammals and birds, with similar functions, but this remains an open question (Gauthier, Kluge & Rowe, 1988; Witmer, 1995; Geist, 2000; Owerkowicz *et al.*, 2015). A single turbinal-like structure could have equally parsimoniously been convergently acquired in synapsids and sauropsids, or lost in turtles (see Gauthier *et al.*, 1988; Witmer, 1995). To date, very few comparative studies of turbinal histology in birds have been published (Bang, 1971). Therefore, for many species, the functional distinction between respiratory and olfactory turbinals is based only on their morphology and location. During bird

development, the nasal septum is the first to form followed by the caudal turbinal, then the middle and finally the rostral turbinals (reviewed in Witmer, 1995). It is generally accepted that turbinals in birds are composed of cartilage or poorly ossified bone (Zaher & Abu-Taira, 2013; Owerkowicz *et al.*, 2015), which explains why they have been difficult to study using CT technologies. However, some birds have well-ossified turbinals that are visible using CT scans [e.g. woodpeckers (Owerkowicz *et al.*, 2015); *Apteryx haastii* (Q. Martinez, personal observations from MorphoSource)]. Adult birds generally possess two respiratory and one olfactory turbinal (Negus, 1958; Parsons, 1959b; Portmann, 1961; Wenzel, 1971; Hogan *et al.*, 2020) often named rostral, middle, and caudal turbinal, respectively (Fig. 18). As for mammals, turbinal names have several synonyms (Tables S1 and S2). Here, we use rostral/middle/caudal turbinal terminology, simplifying by replacing the term ‘concha’ with ‘turbinal’. The rostral turbinal is covered by stratified squamous epithelium. The middle turbinal



**Fig. 18.** (Top) Sagittal views of the skull and the soft tissues of a black-footed albatross [*Phoebastria nigripes*, Ohio University Vertebrate Collection (OUVC) 10905] with three-dimensional illustration of the segmented turbinal shown in lateral and medial views. (Bottom) Six coronal sections along the nasal cavity at positions identified by numbers in the top left image. Raw micro-computed tomography (micro-CT) data from Lawrence Witmer and Emily Addams (MorphoSource ID number 000078946).

is mostly covered by ciliated respiratory epithelium and the caudal turbinal by olfactory epithelium (Bang, 1971). Despite this apparent avian bauplan of three turbinals, some variation has been documented in the number of turbinals (Bang, 1966, 1971). As an example, some species have an atrioturbinal located anteriorly or laterally to the rostral turbinal (Fig. 18, Table S2; Bang, 1971; Bourke & Witmer, 2016; Hogan *et al.*, 2020). Like the rostral turbinal, the atrioturbinal is covered by stratified squamous epithelium (Bang, 1971). Interestingly, the atrio- and rostral turbinals play a role in directing and maintaining airflow of the inspired air. They direct airflow towards the olfactory recess as well as humidifying the air that passes along the nasal gland (at the base of the crista nasalis) before it enters the deeper respiratory tract (Bourke & Witmer, 2016). We suspect that the presence of the atrioturbinal may be overlooked in studies that are not based on CT data (e.g. Bang, 1971). Indeed, in the black-footed albatross (*Phoebastria nigripes*) (Fig. 18), we identified a potential atrioturbinal that is weakly differentiated from the nasal floor (Fig. 18). As another example of turbinal variation in birds, the white-rumped vulture (*Gyps bengalensis*) may lack both rostral and caudal turbinals (Bang, 1971). The caudal turbinal also varies from highly complex in the kiwi (*Apteryx* sp.) or highly developed in the turkey vulture (*Cathartes aura*) to strongly reduced or completely absent in swifts, pigeons, wood hoopoes and the white-rumped vulture (Bang, 1971; Parsons, 1971a). When present, the caudal turbinal of birds often contains a pneumatic cavity (= *cavum conchae*; Witmer, 1995; Hogan *et al.*, 2020). Most studies on turbinals in birds assume that only the caudal turbinal is covered by olfactory epithelium and therefore that the other turbinals are respiratory. However very few histological works exist (Bang, 1971; Jin *et al.*, 2008). As in most mammals, in some birds the olfactory epithelium lines other parts of the nasal cavity such as parts of the floor, roof and nasal septum (Bang, 1971). In some species, olfactory epithelium may even line some part of the middle turbinal (Bang, 1971). Interestingly, swifts, which lack a caudal turbinal, have an expansion of their olfactory chamber where olfactory epithelium is present (Bang, 1971). The respiratory turbinal surface area may be on average three times smaller in birds than in mammals (Owerkowicz *et al.*, 2015). It has been demonstrated that the respiratory tract (including the respiratory turbinals) of the cactus wren (*Campylorhynchus brunneicapillus*) helps to limit water loss over a range from 49% (at 30 °C) to 74% (at 15 °C; Schmidt-Nielsen *et al.*, 1970). This effective countercurrent heat-exchange mechanism was also demonstrated in other bird species (Geist, 2000; Michaeli & Pinshow, 2001). In emus (*Dromaius novaehollandiae*), respiratory turbinals have a key role in heat conservation (Owerkowicz *et al.*, 2015). However, field metabolic rates were not significantly correlated with the surface area of respiratory turbinals (estimated using two-dimensional slices) and their respiratory turbinals may not be critical for bird endothermy (Owerkowicz *et al.*, 2015). Indeed, when absent, respiratory turbinals may be compensated by the well-developed avian trachea (Owerkowicz *et al.*, 2015).

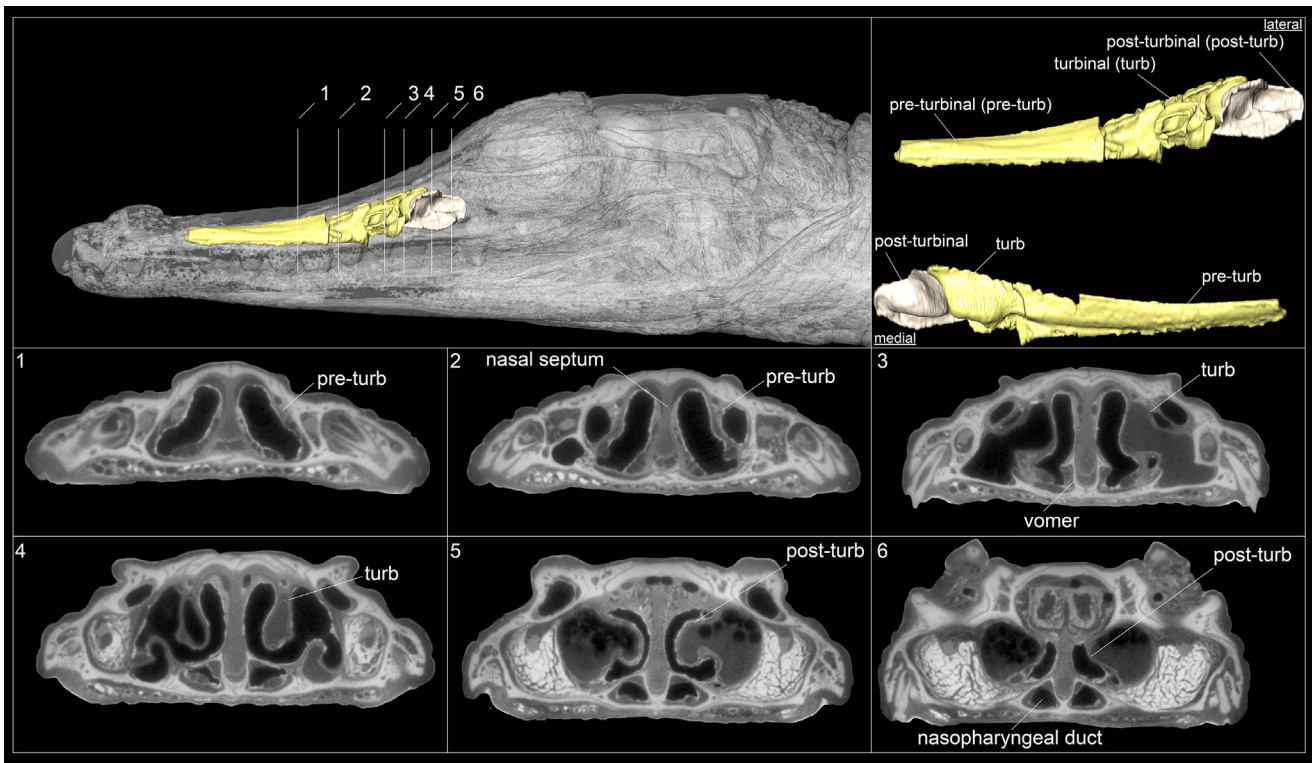
#### IV. CROCODYLIANS

Crocodylians have a very complex nasal chamber in comparison to other non-mammalian tetrapods, which integrates several recesses and sinuses (Parsons, 1967; Witmer, 1995). Crocodylians have three turbinals (Parsons, 1959a; Saint Girons, 1976; Witmer, 1995) referred to here as pre-turbinal, turbinal, and post-turbinal (Fig. 19, Table S2). In Fig. 19, the colour used for the turbinals of the saltwater crocodile indicates homology as proposed by Witmer (1995) in comparison to avian turbinals (Fig. 18). However, from a general perspective homology remains subject to debate. (e.g. Saint Girons, 1976).

Histology, immuno-histology, and electron microscopy studies have demonstrated that most of the nasal cavity (comprising the nasal roof, walls, and turbinals) is lined with olfactory epithelium (Saint Girons, 1976; Hansen, 2007). There is an antero-posterior gradient of olfactory neuron density (Hansen, 2007). Interestingly, some olfactory neurons are also present on the thin epithelial surface (Hansen, 2007). Because of their high density of olfactory neurons, an olfactory function of the turbinal and the post-turbinal is not debated (Saint Girons, 1976; Hansen, 2007; Bourke *et al.*, 2014). Bourke *et al.* (2014) classified the pre-turbinal as a respiratory turbinal because of its position and vascularisation. However, in addition to some respiratory epithelium (composed of mucous and ciliated cells), the pre-turbinal is also covered in part by olfactory epithelium (Saint Girons, 1976; Hansen, 2007). Therefore it is likely that the pre-turbinal of crocodylians has a dual function. The anterior part of the pre-turbinal is not differentiated from the roof and walls of the nasal cavity (Fig. 19) which complicates its identification using classical two-dimensional histology (Table S2). Future precise mapping of the epithelium of the pre-turbinal will be required to identify its exact function. In any case, the presence of a respiratory or partially respiratory turbinal in crocodylians suggests that the respiratory turbinals are not necessarily associated with endothermy (Bourke *et al.*, 2014; Owerkowicz *et al.*, 2015; Martinez *et al.*, 2023b). However, we should note that the ancestors of modern crocodylians may have been endotherms (Seymour *et al.*, 2004). Interestingly, the olfactory epithelium of crocodylians contains two types of olfactory sensory neurons as well as some solitary chemosensory cells (Hansen, 2007). Their function remains unknown but may be linked to the ability of some crocodylians to detect both air-borne and water-soluble odours (Weldon *et al.*, 1990). Among semi-aquatic vertebrates, the crocodylian pattern of large olfactory regions (including olfactory turbinals) and loss of the vomeronasal organ (another olfactory organ) appears rare but has only been investigated in some species.

#### V. TURTLES

Turtles seem to lack turbinals (Parsons, 1959b, 1971a,b; Gauthier *et al.*, 1988; Witmer, 1995), but detailed



**Fig. 19.** (Top) Sagittal views of the skull and the soft tissues of a saltwater crocodile [*Crocodylus porosus*, Ohio University Vertebrate Collection (OUVC) 10899] with three-dimensional illustration of the segmented turbinals shown in lateral and medial views. (Bottom) Six coronal sections along the nasal cavity at positions identified by numbers in the top left image. Raw micro-computed tomography (micro-CT) data from Lawrence Witmer and Joshua Krech (MorphoSource ID number 000073608).

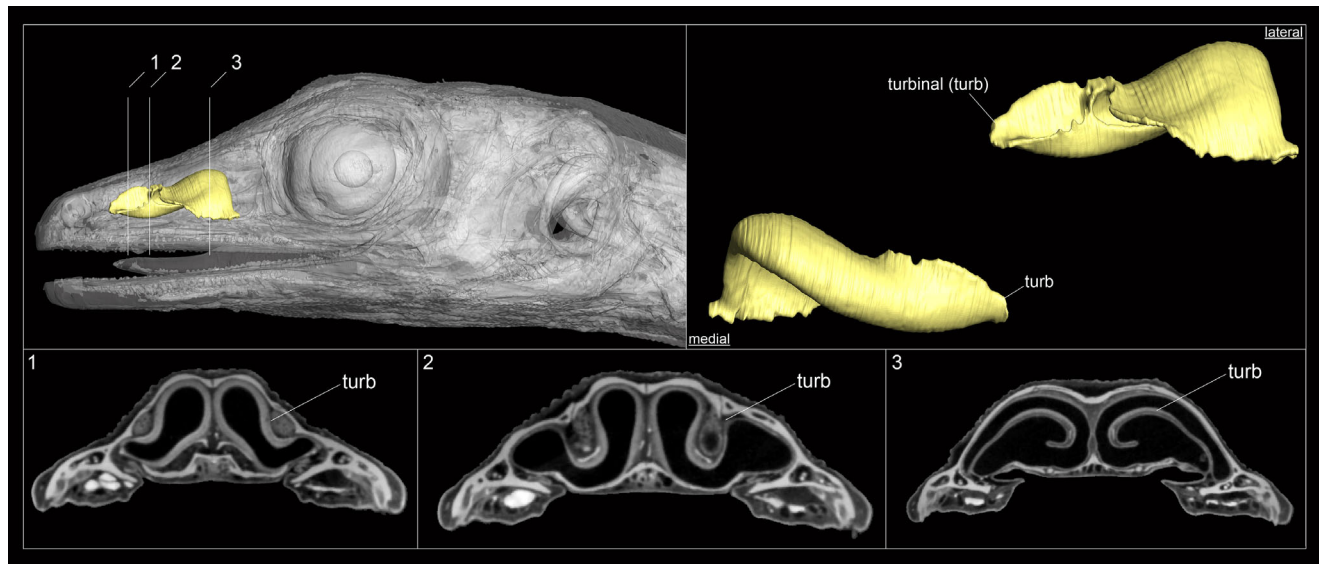
comparative studies are needed to confirm this. Some authors reported the presence of ‘laterale Grenzfalte’, also named as the ‘conchal ridge’ that is suggested to be a rudimentary turbinal or the ‘Muschelwulst’ that has been compared to the squamate turbinal (e.g. Parsons, 1967; Witmer, 1995). Similarities with the turbinal of the Philippine bent-toed gecko *Cyrtodactylus philippinus* (Squamata, see Section VI.1 and Fig. 20) suggest that in the Asiatic softshell turtle *Amyda cartilaginea* (Trionychidae) the so-called ‘olfactory region’ of Parsons (1971b fig. 4H referred to therein as *Trionyx cartilagineus*) may be a potential turbinal. Parsons (1959b) and Witmer (1995) suggested a ridge on the lateral wall of the olfactory region of *Testudo graeca* (‘laterale Grenzfalte’ in Witmer, 1995) may be analogous to a turbinal. However later examinations rejected this hypothesis (Parsons, 1967; Q. Martinez, personal observations in *Testudo hermanni*). Despite the apparent absence of turbinals, turtles have an olfactory recess line with olfactory epithelium containing large Bowman’s glands (Parsons, 1967, 1971b). Interestingly, in turtles there may be a trade-off between the relative surface areas covered by the olfactory and vomeronasal epithelia: aquatic turtles tend to feature a reduced olfactory epithelium and an increased vomeronasal epithelium (Parsons, 1971b).

## VI. LEPIDOSAURIA (SNAKES, LIZARDS AND KIN)

### (1) Squamata

In lizards, when present, there is normally only one cartilaginous turbinal (Fig. 20; Gaupp, 1900; Stebbins, 1948; Parsons, 1959b, 1967; Witmer, 1995; Bourke *et al.*, 2014) but a second turbinal is known at least in *Heloderma suspectum* (Bernstein, 1999). A medial and lateral lamella projecting from the single turbinal was also described in an early juvenile stage of *Lacerta agilis* (Gaupp, 1900). This single turbinal is mostly covered by olfactory epithelium that also lines some parts of the roof and walls of the nasal cavity. Most studies consider the lizard turbinal as an olfactory turbinal, but this is debated (Stebbins, 1948; Bellairs, 1949; Parsons, 1967; Geist, 2000; Bourke *et al.*, 2014; Owerkowicz *et al.*, 2015). Indeed, in some species, the antero-ventral part of the turbinal is lined with respiratory epithelium (Stebbins, 1948; Parsons, 1959b). In this case, the turbinal may have a dual function. Important variations exist in the morphology of this turbinal and reduction or potential loss have been documented in some Chamaeleonidae, Phrynosomatidae (e.g. *Uma notata*), Dactyloidae (e.g. loss in *Anolis carolinensis*), Crotaphytidae (*Crotaphytus*) and Iguanidae (*Dipsosaurus*; Stebbins, 1948; Parsons, 1967; Saint Girons, 1976). This pattern was associated with an





**Fig. 20.** (Top) Sagittal views of the skull and the soft tissues of *Cyrtodactylus philippinus* [University of Florida (UF) 50940] with three-dimensional illustration of the segmented turbinal shown in lateral and medial views. (Bottom) Three coronal sections along the nasal cavity at positions identified by numbers in the top left image. Raw micro-computed tomography (micro-CT) data from Edward Stanley (MorphoSource ID number 000364235).

arboreal lifestyle despite the fact that not all these species are arboreal, and that some arboreal species have a highly developed olfactory region (Parsons, 1967). Among Iguania, Saint Girons (1976) described important reductions in some arboreal and insectivorous species.

To our knowledge, the few studied snakes (e.g. *Leptodeira* and *Vipera*) have a single turbinal (Fig. 21, Table S2) mostly covered by olfactory epithelium on its postero-dorsal part and by respiratory epithelium on its antero-ventral part (Peyer, 1912; Brock, 1929; Parsons, 1959b). Some fully aquatic snakes (Acrochordidae and Hydrophiinae) may have lost the turbinal or have a non-functional olfactory epithelium whereas some less-aquatic taxa (Laticaudinae and Homalopsinae) may only feature a slightly reduced olfactory epithelium. The olfactory epithelium of semi-aquatic (= amphibious) taxa such as Natricinae may be more similar to that of their terrestrial relatives (Parsons, 1967; Gabe & Saint Girons, 1973; Saint Girons, 1976). Interestingly, aquatic snakes may have a well-developed vomeronasal organ (Saint Girons, 1976).

## (2) Rhynchocephalia

Despite some debate, the tuatara (*Sphenodon punctatus*) may have two turbinals: a caudal and rostral turbinal; they may be incompletely separated (Table S2; Parsons, 1959b, 1967; Witmer, 1995; Bernstein, 1999).

## VII. LISSAMPHIBIA (EXTANT AMPHIBIANS)

Many studies affirmed that Lissamphibia lack turbinals (Stebbins, 1948; Parsons, 1959b; Parsons & Williams, 1963; Gauthier *et al.*, 1988) but studies on the main olfactory

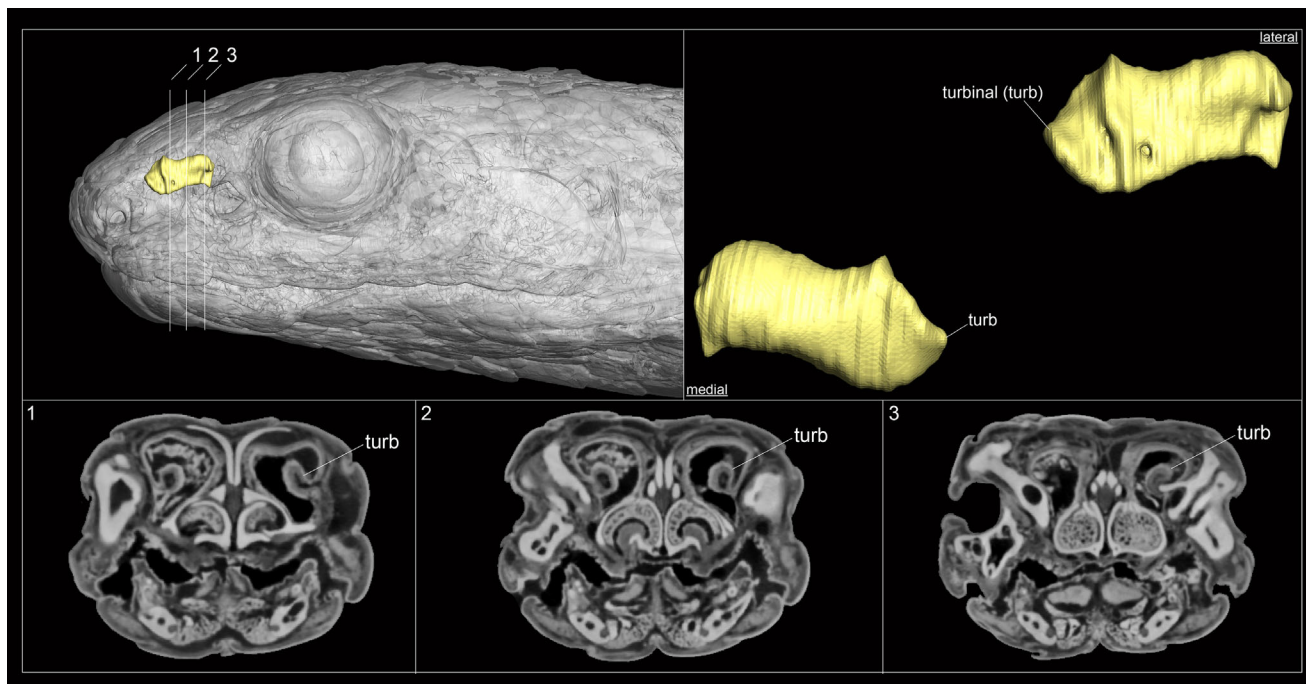
apparatus of Lissamphibia remain rare; their olfactory system is less studied than their vomeronasal organ. However, the morphology of the nasal septum and the relative position of the nasal sac (= the area covered by olfactory epithelium, also referred to as the olfactory sac and ‘*eminencia olfactoria*’) varies among Lissamphibia (Pusey, 1943; Stephenson, 1951; Parsons & Williams, 1963; Dilkes, 1993).

### (1) Anura

To our knowledge, there is no mention of turbinals in Anura. However, comparative studies are lacking.

### (2) Caudata (= Urodela)

Witmer (1995) mentioned that De Beer (1937) identified a rudimentary turbinal in *Ambystoma*. This observation may refer to the longitudinal ridges identified by Eisthen *et al.* (1994) which they defined as a ‘non-described’ structure in terrestrial vertebrates. These ridges, probably not turbinals, are covered by non-sensory epithelium that lose their vascularisation in adult stages (Eisthen *et al.*, 1994). In *Salamandra salamandra*, we could not identify a turbinal (Q. Martinez, personal observations), and this may also apply to many other Caudata. Interestingly, the nasal cavity of the axolotl (*Ambystoma mexicanum*) contains functional olfactory epithelium (Eisthen *et al.*, 1994) which contradicts previous observations reporting the absence of Bowman’s glands in neotenic urodela (Parsons & Williams, 1963; Parsons, 1967; Saint Girons, 1976).



**Fig. 21.** (Top) Sagittal views of the skull and the soft tissues of a Mexican small-headed rattlesnake [*Crotalus intermedius*, University of Florida (UF) 52552] with three-dimensional illustration of the segmented turbinal shown in lateral and medial views. (Bottom) Three coronal sections along the nasal cavity at positions identified by numbers in the top left image. Raw micro-computed tomography (micro-CT) data from Edward Stanley (MorphoSource ID number 000445155).

### (3) Gymnophiona

To our knowledge, there is no mention of turbinals in Gymnophiona. Apparently, olfactory epithelium is highly developed in this clade (Saint Girons, 1976). Similarly to observations for some snakes (see Section VI.1), some fully aquatic Typhlonectidae (*Chthonerpeton indistinctum* and *Typhlonectes natans*) have reduced olfactory epithelium and an increase in extent of the vomeronasal epithelium. In *Dermophis mexicanus*, we identified a structure that may be interpreted as a potential turbinal (Fig. 22) and Schmidt & Wake (1990) found it to be covered by sensory epithelium. This potential turbinal may be considered as part of the *duct olfactor* which may be connected to the vomer (Seydel, 1895).

## VIII. QUANTITATIVE APPROACHES AND METHODOLOGICAL ISSUES

Improved access to CT technology has allowed many quantifications of the surface area of turbinals (e.g. Van Valkenburgh *et al.*, 2004, 2011, 2014; Green *et al.*, 2012; Martinez *et al.*, 2018, 2020, 2023a,b; Lundeen & Kirk, 2019; Wagner & Ruf, 2019; Peri *et al.*, 2020; Lundeen & Kay, 2022; Melin *et al.*, 2022). As often with quantitative approaches, the methodology used in data acquisition as well as in subsequent analysis may impact the results. For

olfaction, significant issues assigned to methodological differences were observed in estimates of numbers of cells and olfactory neurons (Saint Girons, 1976; Hansen, 2007) as well as in the number of OR genes. Because turbinals are numerous, thin, and intricate structures, their segmentation (using CT data) may also impact quantification of their surface area in at least three ways. (i) Different methods to segment turbinals exist and the employed methodology is not necessarily specified (e.g. how to segment the roots of the turbinals and isolate them from their attachment; see Martinez *et al.*, 2023b). What is segmented may also be unclear. As an example, ‘ethmoturbinals’ is sometimes used as a synonym for olfactory turbinals. However, in this case, it is not possible to decipher if interturbinals and frontoturbinals were considered. The inclusion or the exclusion of the semi-circular lamina is another example (Martinez *et al.*, 2023a). (ii) The quality of the scans can affect surface area estimation. Quality is difficult to judge from a published article because it is not only described by resolution. As an example, noisy scans or with a narrow range of grey values may overestimate the surface area of turbinals. (iii) The smoothing parameters used to generate the segmented surface also impact quantitative estimations. Unfortunately, this parameter cannot be standardised since it also depends on the quality of the scans and the software applied. Such artifacts are expected to be less problematic when comparing phylogenetically distant species, as with increasing phylogenetic distance, more differences are expected in the overall shape of a given structure.



**Fig. 22.** (Top) Sagittal views of the skull and the soft tissues of a Mexican burrowing caecilian [*Dermophis mexicanus*, amphibian, University of Florida (UF) 144682] with three-dimensional illustration of the segmented turbinal shown in lateral and medial views. (Bottom) Three coronal sections along the nasal cavity at positions identified by numbers in the top left image. Raw micro-computed tomography (micro-CT) data from Jaimi Gray (MorphoSource ID number 000408376).

As a result, in order to be valid, an intra-specific comparison of turbinal surface area will need to be extremely rigorous in the process of data acquisition. Furthermore, the use of the surface area of all turbinals (respiratory and olfactory turbinals) to scale the surface area of the turbinals (i.e. correct for size) may limit these methodological artifacts. However, prior to applying such size correction, the relation to the body-size proxies needs to be checked as well as the absence of trade-offs between the turbinal of interest and the overall turbinals (Martinez *et al.*, 2020, 2023b). Therefore, in a quantitative approach, we recommend that studies do not merge data segmented by different teams, especially when data are not corrected by the surface area of all the turbinals.

The use of size correction for sensory-related structures has been heavily debated (e.g. Smith & Bhatnagar, 2004; Martinez *et al.*, 2023a). Indeed, from a functional perspective, the absolute size of a sensory-related structure is probably relevant. As an example, if olfactory turbinal surface area is hypothesised to be a proxy for the number of olfactory neurons, then the absolute surface area may be more likely to reflect olfactory performance. On the other hand, when comparing phylogenetically distant species or where there is high variability in terms of size (e.g. rodents), the results are likely to reflect species size. Alternatively, future analyses should be implemented using both raw and size-corrected data (Martinez *et al.*, 2023a). Various proxies can be used to correct the surface area of turbinals for size, for example skull or condylobasal lengths, body mass, the volume of the nasal cavity, the surface area of all turbinals (respiratory and

olfactory turbinals) or the geometric mean (defined as  $\sqrt{\text{skull length} \times \text{skull width}}$ ).

A final consideration should be the condition of the turbinals. As an example, for small mammals, the anterior part of the respiratory turbinals is generally damaged in museum skulls that have undergone manual skeletonisation. It may be very difficult to be certain that the anterior part is not damaged since it may extend to only a few millimeters. We therefore recommended checking these skull-based CT-data with at least one CT based on an ethanol-preserved head in order to confirm the morphology of respiratory turbinals in the most anterior part.

## IX. FUTURE DIRECTIONS

At least five major limitations have hampered turbinal-related studies: (i) the absence of clear turbinal homology between distant lineages; (ii) the absence of clear histological mapping of epithelia types along the turbinals of numerous clades; (iii) the difficulty of sampling specimens destructively (before the advent of CT technology); (iv) the low number of scans from contrast-enhancement stained specimens (e.g. diceCT) available for non-mammalian species; and (v) the fact that CT segmentation is labour intensive and time-consuming.

In recent years, diceCT data have become increasingly available due to initiatives such as the open Vertebrate Thematic Collections Network (Blackburn *et al.*, 2024). Advances

in such methodologies (Metscher, 2009; Pauwels *et al.*, 2013; Gignac *et al.*, 2016; Gabner *et al.*, 2020) have allowed efficient estimation of gross nasal epithelial cover (Yohe, Hoffmann & Curtis, 2018; Yohe *et al.*, 2022; Smith *et al.*, 2021*b*). As an example, the olfactory epithelium (or mucosa) of the olfactory turbinals is known to be thicker than non-olfactory epithelium (e.g. Negus, 1958) and Smith *et al.* (2021*a,b*) demonstrated that this difference is also visible with diceCT data and can be distinguished, isolated and quantified (Fig. 8). More recently, Smith *et al.* (2022) demonstrated that this methodology can also be applied to the venous system associated with the turbinals. This represents a huge step forward, allowing new investigations. As an example, Parsons (1971*b*, p. 332) noted for the olfactory epithelium of turtles, that: ‘It would be extremely difficult to measure the surface area of such a complex cavity accurately’ (see also Paulli, 1900*a,b,c*). Smith *et al.* (2022) recommended using classical histology for at least one specimen in order to compare it with the diceCT data to prevent invalid extrapolations. In the near future, deep-learning technology may considerably reduce segmentation time (e.g. Lösel *et al.*, 2020; Herbst *et al.*, 2021). Therefore, a strong focus may be placed on developmental and comparative histology (or related methods) in order to improve our knowledge about turbinal homology and the epithelial covering of the different areas.

From a functional perspective, the task remains huge. For decades, findings about the absolute and relative size of various olfactory-related structures from the nasal cavity (including olfactory turbinals) have been interpreted in the light of potential olfactory capabilities (e.g. see discussion in Smith *et al.*, 2004). However, as for many other anatomical structures, clear functional correlates remain rare. A similar statement may be made for more recent work using turbinal data (e.g. Van Valkenburgh *et al.*, 2004, 2011, 2014; Green *et al.*, 2012; Martinez *et al.*, 2018, 2020, 2023*b*; Wagner & Ruf, 2019, 2021; Yohe *et al.*, 2022). To our knowledge, no study has yet tested the potential relationship between olfactory performance [e.g. olfactory sensitivity and olfactory discrimination (see Laska, 2017, and Martinez *et al.*, 2024*a*)] and the various metrics related to olfactory turbinals. It must be an urgent priority to study the co-variation and the potential relations between the different olfactory-related proxies (see Section II.6*b*). In addition to the potential proxies we discussed previously (e.g. olfactory epithelium cover, receptor density, receptive range, degree of neural connectivity, number and expression levels of functional OR genes), it would also be useful to study turbinal shape in relation to airflow dynamics (e.g. Craven *et al.*, 2010; Ranslow *et al.*, 2014; Bourke & Witmer, 2016; Pang *et al.*, 2016). As an example, in phyllostomid bats, the size of the olfactory recess (Eiting *et al.*, 2014*b*) impacts olfactory detection whereas there is no clear link between the pattern of airflow in the nasal cavity and foraging ecology (Eiting, Perot & Dumont, 2015). Due to the difficulty of finding homologous landmarks on the turbinals, only one

study has attempted to quantify morphological changes in turbinals using geometric morphometrics (Curtis *et al.*, 2020). Such works could unlock new perspectives: for example, some turbinal variation may be associated with other functions such as redirecting the air or even participating in nasophonation [= nasal echolocation (Curtis & Simmons, 2017; Curtis *et al.*, 2020)]. Such issues regarding function also apply to the respiratory turbinals and to the respiratory process itself, involving heat and moisture conservation as well as protection of the lower respiratory tract.

## X. CONCLUSIONS

- (1) We reviewed the current state of knowledge on turbinals in tetrapods and provide synonyms and correspondences of turbinals from about 80 publications. This review aims to provide a complete toolbox for future work on turbinals and more generally on the tetrapod skull.
- (2) Future efforts should focus on the understanding of turbinal homology, first for early developmental stages and then comparing these with adults. A particular focus should be given to non-mammalian species where turbinal homology remains poorly understood. Evolutionary developmental studies may also help to clarify if turbinals have evolved convergently in mammals and birds.
- (3) From a functional perspective, the epithelial cover of the turbinals need to be mapped in species from different clades. This is key to assigning the different turbinals to their functional category and therefore to be able to use them in quantitative analyses. The development of contrast-enhancement staining methods (e.g. diceCT), now allow this to be carried out relatively easily.
- (4) We recommend that future research tests directly the functional significance of the turbinals. This may be addressed by testing potential correlations with performance as well as with other potential proxies. For the surface area of the olfactory turbinals, correlations may be tested with olfactory sensitivity and discrimination capabilities. Other potential proxies for consideration may be the extent of olfactory epithelium, receptor density, degree of receptive range of the olfactory receptors, degree of neural connectivity, as well as genomic proxies such as the number of functional olfactory receptor genes, their composition and their expression levels. For the respiratory turbinals, studies should also consider other proxies such as ventilation rate and gap width of the respiratory tract.
- (5) With the recent technological innovations, we are able to explore these peculiar structures as never before. This is also sparking renewed interest in turbinals as well as in comparative anatomy in general. As stated by Van Valkenburgh, Smith & Craven (2014, p. 1982): ‘it is an especially exciting time to study the nose’. Almost a decade later, the same smell is in the air.

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### XIII. SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**Fig. S1.** Alternative interpretations of the turbinal homology of the platypus [*Ornithorhynchus anatinus*, Museum of Vertebrate Zoology (MVZ) 32885] shown in Fig. 16.

**Table S1.** Synonyms and correspondences of mammalian turbinates terminologies between this review and other studies as well as among other studies.

**Table S2.** Synonyms and correspondences of turbinates terminologies between this review and other studies as well as between the other studies themselves; see legend to Table S1 for abbreviations; (Wit) = Witmer (1995).

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