


Nasal turbinates of the dicynodont *Kawingasaurus fossilis* and the possible impact of the fossorial habitat on the evolution of endothermy

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Abstract

The nasal region of the fossorial anomodont *Kawingasaurus fossilis* was virtually reconstructed from neutron-computed tomographic data and compared with the terrestrial species *Pristerodon mackayi* and other nonmammalian synsapsids. The tomography of the *Kawingasaurus* skull reveals a pattern of maxillo-, naso-, fronto- and ethmoturbinal ridges that strongly resemble the mammalian condition. On both sides of the nasal cavity, remains of scrolled maxilloturbinals were preserved that were still partially articulated with maxilloturbinal ridges. Furthermore, possible remains of the lamina semicircularis as well as fronto- or ethmoturbinals were found. In *Kawingasaurus*, the maxilloturbinal ridges were longer and stronger than in *Pristerodon*. Except for the nasoturbinal ridges, no other ridges in the olfactory region and no remains of turbinates were recognized. This supports the hypothesis that naso-, fronto-, ethmo- and maxilloturbinals were a plesiomorphic feature of synsapsids, but due to their cartilaginous nature in most taxa were, in almost all cases, not preserved. The well-developed maxilloturbinals in *Kawingasaurus* were probably an adaptation to hypoxia-induced hyperventilation in the fossorial habitat, maintaining the high oxygen demands of *Kawingasaurus*' large brain. The surface area of the respiratory turbinates in *Kawingasaurus* falls into the mammalian range, which suggests that they functioned as a countercurrent exchange system for thermoregulation and conditioning of the respiratory airflow. Our results suggest that the environmental conditions of the fossorial habitat led to specific sensory adaptations, accompanied by a pulse in brain evolution and of endothermy in cistecephalids, ~50 million years before the origin of endothermy in the mammalian stem line. This supports the Nocturnal Bottleneck Theory, in that we found evidence for a similar evolutionary scenario in cistecephalids as proposed for early mammals.

KEYWORDS

Dicynodontia, endothermy, nasal anatomy, Nocturnal Bottleneck, turbinates

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1 | INTRODUCTION

Higher metabolic rates and mechanisms for the regulation of body temperature (endothermy) are two of the most important innovations in vertebrates, allowing animals to maintain their vital functions more independently of climatic conditions. A widely held view is that endothermy evolved independently in the synapsid and diapsid lineages (e.g., Benton, 2021; Crompton et al., 2015; Kemp, 2006a; Lovegrove, 2017; Padian & de Ricqlès, 2020). However, the recent discovery of the biochemical mechanism of muscle nonshivering thermogenesis in mammals and birds (Nowack et al., 2017, 2019) led to the hypothesis that whole-body endothermy had already evolved in the common ancestor of mammals and birds (Grigg et al., 2022).

Compared with ectotherms, endotherms are generally characterized by a higher basal metabolic rate (BMR) and body temperature, a constant core body temperature, as well as a greatly elevated maximum aerobic metabolic rate (Kemp, 2006a). It should be noted here that several intermediate thermophysiological conditions also exist. However, the term 'endothermy' is used in this study, in the sense of high metabolic rates or so-called whole-body (tachymetabolic) endothermy (see Grigg et al., 2022).

Questions about the advantages of an endothermic physiology have not been completely answered, especially when taking into account that daily food requirements of endotherms are some tenfold higher than in ectotherms (Bennett & Ruben, 1979; Benton, 2021; Lovegrove, 2017). However, it is reasonable to hypothesize that endotherms are more active and alert, particularly at lower ambient temperatures, which enables them to live in cold climates and to adapt to a wider range of ecological niches than ectotherms (Benton, 2021).

1.1 | Hypotheses about the origin of endothermy

The origin of endothermy in synapsids has been controversially discussed and numerous initial selective pressures were proposed that might have led to higher metabolic rates. Much of the debate focused on the problem of whether thermoregulation or a higher aerobic capacity was the primary evolutionary step towards an endothermic physiology, and most hypotheses can be assigned either to the 'thermoregulation first' or to the 'aerobic capacity first' group (Hopson, 2012; Kemp, 2006a). A third category of theories did not focus only on a single selective pressure, but considered the whole organism with respect to its metabolic physiology (e.g., Kemp, 2006a, 2006b, 2007a, 2007b; Lovegrove, 2017; Newham et al., 2022). As these hypotheses were already reviewed in detail by Kemp (2006a), Hopson (2012), Benton (2021), Grigg et al. (2022) and Newham et al. (2022), only a short overview is given here.

One idea that considered thermoregulation as the primary function is the 'hypothesis of miniaturization' (Hopson, 1991; Kemp, 2005; Lovegrove & Seymour, 2019; McNab, 1978). It states that large-bodied inertial homoeotherms evolved from small ectotherms. Those animals retained constant body temperature during

later evolutionary miniaturization through a corresponding increase of metabolic heat production and better insulation of the body surface.

The 'brain-size hypothesis' discusses the need of a constant body temperature and the high energetic expenditure for precise functioning of a relatively enlarged brain as the initial selective pressure for endothermy (e.g., Allman, 1990, 2000; Hulbert, 1980; Jerison, 1971).

Another idea belonging to the 'thermoregulation first hypotheses' was proposed by Crompton et al. (1978) and Taylor (1980), and is known as the 'Nocturnalization hypothesis'. It is based on the assumption that maintenance of a constant body temperature was essential for early mammals to be active at night and to occupy a nocturnal habitat. Interestingly, Angielczyk and Schmitz (2014) investigated the scleral rings and orbit dimensions of 24 Carboniferous-to-Jurassic nonmammalian synapsid species and came to the conclusion that nocturnality evolved several times independently in the synapsid lineage. They suggested endothermy as a possible evolutionary advantage of early mammals in cooler night environments. By contrast, Lovegrove (2019) argued that through becoming night active, early mammals avoided overheating, evaporative water loss and poor sperm quality (Benton, 2021).

Alternatively, the 'parental care model' of Farmer (2000, 2003) proposed that temperature regulation was important as it increased parental ability in early mammalian evolution. Accordingly, the initial selective pressure was closely linked with the ability to maintain a higher incubation temperature for the developing offspring. Farmer (2000, 2020) and Groenewald et al. (2001), who found 18–20 skeletons of the cynodont *Trirachodon* in a cast of a terminal chamber of a burrow system, pointed out that complex social behaviour such as extended parental care was closely linked with the elaboration of the brain and endothermy.

The 'aerobic capacity first' hypotheses considered elevated aerobic metabolism as the primary step towards an endothermic physiology. The first version is known as the 'aerobic capacity model' of Bennett and Ruben (1979) and Ruben (1995). They concluded that the principal factor in the evolution of endothermy was the increase in aerobic capacities supporting the sustained activity of endotherms. Another idea is the 'assimilation capacity model' of Koteja (2000), in which he proposed that the evolution of endothermy was driven by selection for intense posthatching parental care, probably from feeding the offspring, which required an increased capacity of the visceral organs supporting high rates of daily energy expenditures.

Finally, Hopson (2012) suggested changes in the foraging mode in the transition from basal synapsids ('pelycosaur') to therapsids as the most important driving force of endothermy. He claimed that the shift from an ancestral 'sit and wait' foraging of ectotherms to a more active, energy-intensive 'widely foraging' mode led to an increased aerobic capacity and the ability to sustain high levels of foraging activity.

An idea that can be assigned to the 'whole organism' hypotheses is the Nocturnal Bottleneck Theory. It was first proposed by Walls (1942), who compared the visual systems of extant sauropsids and

mammals. He concluded that early eutherian mammals underwent an episode of nocturnality, escaping the predation of diurnal dinosaurs, followed by a reversion to a diurnal lifestyle in many species in the Cenozoic (Gerkema et al., 2013). Later studies also included circadian organization, activity patterns, palaeontological data, physiology and genetic evidence for a nocturnal phase in early mammalian evolution (e.g., Gerkema et al., 2013; Hall et al., 2012; Heesy & Hall, 2010).

Another hypothesis considering the whole organism is Kemp's 'correlation progression model'. Kemp's idea was that all structures of organisms were deeply and inextricably embedded within the complex functioning of the whole (Kemp, 2006a, 2006b, 2007a, 2007b). Consequently, the evolution of endothermy can be best described as 'correlated progression' of character evolution, leading to higher levels of metabolic activity and homeostatic regulation.

Lovegrove (2017) distinguished three pulses in the evolution of endothermy in birds and mammals: Phase 1 occurred from the Permian to Triassic and was characterized by the appearance of large bodied homeotherms, which evolved parental care and several adaptations for conquering dry land. Phase 2, from the Early Triassic to the Jurassic, was marked by extreme body-size miniaturization, the evolution of enhanced body insulation, encephalization, thermoregulatory control and increased ecomorphological diversity. Finally, in Phase 3, which persisted from the Cretaceous to the Cenozoic, the evolution of terrestrial cursoriality in mammals and adaptations to cooler climates led to new pulses in the evolution of endothermy. Recently, Newham et al. (2022) proposed another view of the evolution of mammalian endothermy and split synapsid physiological evolution into five primary phases from the late Palaeozoic to the Cenozoic. Furthermore, several hypotheses discussed the possible influence of external perturbations, such as changes in climate or in the composition of atmospheric gases, on the evolution of endothermy.

Geochemical studies revealed that atmospheric oxygen reached a maximum of more than 30% at the end of the Carboniferous. During the Permian, it dramatically decreased, to reach a minimum of only ca. 12%–15% in the Early Triassic (Berner, 2006, 2001; Berner & Canfield, 1989). Interestingly, the origin of therapsids in the Mid-Permian falls in the so-called late Palaeozoic oxygen pulse, which is considered to have led to a wider divergence of tetrapods and other groups, to an increase in body size, to higher activity levels, as well as to higher oxygen-use and metabolic capacities (Graham et al., 1995, 1997).

It seems reasonable that the hypoxic and hypercapnic atmospheric conditions during the Permian-Triassic Mass Extinction (PTME) event impacted greatly on the evolution of vertebrates. Burrowers such as *Lystrosaurus* were able to withstand the harsh environmental conditions of the PTME, because they probably had a greater aerobic scope, were preadapted to hypoxia and hypercapnia (Laaß et al., 2010; Retallack et al., 2003), and better protected against extreme temperature fluctuations and arid environmental conditions (Botha-Brink, 2017).

Interestingly, Benton (2021) proposed that the shift from sprawling to a more erect posture in vertebrates near the Permian-

Triassic Boundary (PTB) did not happen in a steady or gradual manner in multiple lineages, but that the PTME killed off all the sprawling lineages. Other studies discussed possible selective advantages of endothermy in Mammaliaforma in coping with the progressively cooler Triassic climate (Araújo et al., 2022).

1.2 | Possible indicators for endothermy in extinct species

Endothermy requires a set of morphological and physiological features of an organism (Kemp, 2006a; Lovegrove, 2017). Unfortunately, most of them are related to soft-tissue anatomy, which were usually not preserved in the fossil record. These include, for example, the cardiovascular system, a higher oxygen capacity of the blood cells, an increased number of mitochondria and the insulation of the body by fur or feathers. Consequently, in most cases, only skeletal and other features from the fossil record are discussed as indicators for endothermy.

Several studies investigated the differentiation of teeth as a possible indication for more efficient food processing (e.g., Bennett & Ruben, 1986; Brink, 1957) and also the role in the evolution of endothermy of the secondary palate (Brink, 1955; Kemp, 1982), which separates air and food passages, and allows continuous breathing during eating. A further consequence of a secondary palate is an elaboration of the space in the nasal cavity, which is an important prerequisite for the elaboration of turbinates (Crompton et al., 2017).

Other authors focused on the origin of the diaphragm in synapsid evolution (e.g., Brink, 1955; Kemp, 1982; Lambertz et al., 2016). A diaphragm, which is absent in sauropsids, enabled synapsids continuous breathing during locomotion (Benton, 2021). However, diaphragms are not preserved in the fossil record, but the reduction of lumbar ribs in the thorax of extinct species is regarded as an indication for its presence. The origin of the diaphragm is also closely related to locomotion and the posture of the limbs. The body posture as a possible indicator of endothermy was already proposed by Bakker (1971) and Carrier (1987). While reptiles can only breathe or walk, but not both, which is known as Carrier's Constraint, due to their parasagittal erect posture, gait and the diaphragm, mammals are able to breath and run at the same time (Benton, 2021). As pointed out by Benton (2021), all medium-sized and larger tetrapods shifted from a sprawling to a more erect posture across the PTB, which was accompanied by significant changes in locomotion, respiration and energetic costs.

Skeletal dimensions and posture of extinct animals can also be used to infer variables of cardiovascular physiology (Seymour, 1976, 2016; Grigg et al., 2022). For example, great vertical distances between the heart and the top of the body are, at the same time, indicators of both high arterial blood pressures and endothermy in extinct animals, because the cardiovascular system must be capable of driving the vertical blood column in the body (Seymour, 2016; Grigg et al., 2022).

Another source of information is the size of long-bone foramina through which the blood vessels passed, which are indicative of the blood flow in extinct animals. As endothermy requires a much greater blood flow and oxygen consumption, the size of long-bone foramina may provide information about the metabolic status of extinct animals (Hu et al., 2020, 2021; Knaus et al., 2021). Such information can also be inferred from osteohistology, which is based on the observation that the bones of modern endotherms are usually characterized by higher growth rates and the presence of fibrolamellar bone, which is absent in most ectotherms (e.g., Bakker, 1972; de Ricqlès, 1974, 1976; Legendre et al., 2016; Olivier et al., 2017).

Newham et al. (2020) investigated the incremental tooth cementum of stem mammals with synchrotron X-ray computed tomography and measured femoral nutrient foramina, and used these features as proxies for estimating the basal and maximum metabolic rates.

It is also generally possible to estimate body temperatures of extinct species from the stable oxygen isotope ratios of bones, teeth or eggshells (e.g., Barrick & Showers, 1994; Barrick et al., 1996; Dawson et al., 2020; Rey et al., 2017), but the method is controversial, due to the possible influence of diagenetic effects on the results (Trueman et al., 2003).

Furthermore, features of the neuroanatomy, such as brain size (e.g., Allman, 1990; Benoit et al., 2017; Gillooly & McCoy, 2014; Hopson, 1979, 1980; Isler & van Schaik, 2006; Kemp, 2009; Mink et al., 1981; Rowe et al., 2011), and the loss of the parietal foramen in mammalian ancestry (Benoit et al., 2015, 2016; Roth & Roth, 1980), came into focus. In ectotherms, the pineal organ is responsible for thermoregulation and is associated with the epiphysial complex as a detector of the environmental temperature. Consequently, the loss of the parietal foramen is an indication that animals became more independent from external heat sources and the thermoregulatory mechanisms of ectotherms were probably replaced by others (Benoit et al., 2015, 2016).

Several authors recognized small foramina in the snout region of late Permian and early Triassic therocephalians and cynodonts, which they interpreted as indications of vibrissae and/or the presence of fur (Brink, 1957; Watson, 1931). In fact, possible remains of hair were preserved in coprolites of late Permian age (Bajdek et al., 2016; Smith & Botha-Brink, 2011). Benoit et al. (2017) used another approach and investigated the snout region of nonmammalian synapsids by means of X-ray tomography. They found evidence for a true infraorbital canal only in derived cynodonts, which they interpreted as indicators of a mobile rhinarium and whiskers (Benton, 2021).

Recently, another feature of the neuroanatomy was proposed by Araújo et al. (2022) as a possible indicator for endothermy. The authors found morphological differences between the endolymph-filled semicircular ducts of the inner ears of endo- and ectotherms resulting from differences in the viscosity of the endolymph and different requirements for biomechanical function.

There is, however, little consensus as to whether these features are reliable indicators of endothermy or not, which is also reflected in the different results obtained by using different methods. Hillenius (1992) showed that several skeletal features were, at best, weak

indications for an endothermic physiology or were even not necessarily correlated with endothermy.

A widely held view is that respiratory turbinates in the nasal cavity of mammals and birds are among the strongest indicators for endothermy (Hillenius, 1992, 1994; Ruben, 1995, 1996; Ruben et al., 2012). However, Owerkowicz et al. (2015) showed that in birds, in contrast to mammals, turbinates in the nasal cavity only play a minor role in saving moisture and heat. Through elongation of the neck, the air flow through the lungs and driven by lightening of the cranial skeleton, the avian trachea become a major site of respiratory heat and water conservation. Furthermore, simply constructed preconchae, which are situated in the main respiratory airflow but covered with olfactory epithelium, were also developed in crocodiles (Owerkowicz et al., 2015). However, the anatomy of the nasal cavity may provide important information about the metabolic status of extinct animals, in particular in the mammalian lineage.

1.3 | Evolution of the nasal cavity in nonmammalian synapsids

The evolution of the nasal cavity in nonmammalian synapsids was closely associated with the development of the secondary palate, which enables uninterrupted breathing and feeding (Bennett & Ruben, 1986; Hillenius, 1994) and a better capacity for suckling and swallowing food (Maier, 1999). By elongation of the secondary palate, the choana shifted to a more caudal position, which resulted in the separation of the main respiratory airflow from the oral cavity (Bennett & Ruben, 1986).

A secondary palate probably evolved at least three times independently among nonmammalian therapsids, that is, in dicynodonts, therocephalians and cynodonts (Rubidge & Sidor, 2001; Sidor, 2003). Furthermore, Sidor (2003) considered the small shelf formed by the palatine and maxilla (crista choanalis) of the biarmosuchian *Lycaenodon longiceps* as an early stage in the development of a secondary palate. Maier et al. (1996) interpreted bony ridges and the vomerine pad as supporting structures of a soft secondary palate in the therocephalians *Promoschornychus* and *Olivieria*, but this is disputed (see Crompton et al., 2015). However, there is consensus that a secondary palate was present at least in the epicynodont grade (Crompton et al., 2015; Parrington & Westoll, 1940; Rubidge & Sidor, 2001).

A further consequence of the elongation of the secondary palate was a great expansion of the respiratory part of the nasal cavity, which therewith provided sufficient space for the elaboration of the respiratory turbinates (Crompton et al., 2015; Hillenius, 1992, 1994; Ruf et al., 2014). Respiratory turbinates are thin, scrolled bony or cartilaginous walls covered with respiratory epithelium. In mammals, these are the maxilloturbinates (mxt) as well as the rostral part of the nasoturbinates (Ruf et al., 2014). In contrast, the ethmoturbinates are located in the caudal part of the nasal cavity away from the main respiratory airflow. These delicate sheets of bones are covered with olfactory epithelium.

Respiratory turbinates function as a countercurrent exchange system for airflow conditioning in endotherms. They warm, humidify and filter the inhaled air and cool the exhaled air (Schmidt-Nielsen, 1981). As endotherms must take up more oxygen to maintain their BMR, which is about an order of magnitude higher than in ectotherms (Graham et al., 1997), their respiratory rates are higher. As shown by Hillenius (1992), respiratory turbinates substantially reduce respiratory water loss by condensation of water on the cool epithelial surface of the turbinates during exhalation. Most mammalian turbinates are complex structures (e.g., Macrini, 2012; Paulli, 1900a, 1900b, 1900c; Rowe et al., 2005), which have a considerably increased surface area. Respiratory turbinates in the mammalian nasal cavity function as a protective mechanism that prevents desiccation from respiratory water loss.

During mammalian ontogenetic development, the cartilaginous turbinates of the juveniles ossify to become delicate bony structures in the adults. Consequently, they have only little potential for fossil preservation, which might explain their absence in most early mammals and nonmammalian synapsids (Hillenius, 1992, 1994; Owerkowicz et al., 2015). Nevertheless, it has been widely accepted that the nasal cavity of nonmammalian synapsids contained a system of cartilaginous turbinates. This view is supported by the presence of bony ridges on the inner walls of the nasal cavity, which were interpreted as sites for the attachment of the turbinates (e.g., Bendel et al., 2018; Crompton et al., 2015, 2017; Franco et al., 2021; Hillenius, 1992, 1994; Kemp, 1979; Kerber et al., 2020, 2023; Pusch et al., 2019, 2020; Ruben et al., 2012). The pioneer work on the anatomy of the mammalian nasal skeleton was by Zuckerkandl (1887) and Paulli (1900a, 1900b, 1900c).

Nasoturbinal ridges (ntr) were already recognized on the undersides of the nasals and frontals in the nasal cavity of the sphenacodontid pelycosaur *Dimetrodon* (Romer & Price, 1940), as well as in numerous nonmammalian therapsids (e.g., Bendel et al., 2018; Brink, 1960; Cluver, 1971; Crompton et al., 2015, 2017; Fourie, 1974; Maier et al., 1996; Hillenius, 1994; Kemp, 1969, 1979; Kerber et al., 2020, 2023; Pusch et al., 2019, 2020; Ruf et al., 2014; Sigurdson, 2006; Sigurdson et al., 2012). Furthermore, several studies, which were based on X-ray computed tomography, focused on the nasal anatomy of modern mammals (e.g., Crompton et al., 2017; Macrini, 2012; Rowe et al., 2005; Ruf, 2020; Ruf et al., 2021; Van Valkenburgh et al., 2004).

Ridges for the attachment of respiratory turbinates were only reported from the mammalian stem line, in advanced theriodonts (Crompton et al., 2017; Hillenius, 1994; Ruben et al., 2012; Tatarinov, 2000). It should be noted that Hopson (2012) doubted the presence of respiratory turbinal ridges in the therocephalian *Glanosuchus* and in the cynodont *Massetognathus* described by Hillenius (1994). According to Hillenius (1994), the ridge in *Glanosuchus* was formed by the ventral edge of the nasal bone, which projects into the nasal cavity along its contact with the maxilla. Therefore, Hopson (2012) supposed that the described ridges were a result of slight distortion of the bones forming the nasal cavity. However, Sigurdson (2006), who serially sectioned a therocephalian

snout, and Pusch et al. (2020), who investigated a skull of the therocephalian *Lycosuchus*, did not recognize maxilloturbinal ridges (mxtr).

In cynodonts, maxilloturbinal ridges were found in *Thrinaxodon*, *Galesaurus* and probably in *Massetognathus* and *Probainognathus* (Crompton et al., 2015, 2017; Fourie, 1974; Hillenius, 1994; Pusch et al., 2019), but they were absent in *Procynosuchus* (Kemp, 1979), *Brasilitherium* (Ruf et al., 2014) and the basal mammaliomorph *Pseudotherium argentinus* (Wallace et al., 2019). Tatarinov (2000) reported possible remains of ossified maxilloturbinals from a late Permian theriodont from Russia.

Ossified turbinates were likely also present in Mammaliaformes. For example, Wallace et al. (2019) found a disarticulated, scrolled bone in the nasal cavity of the basal mammaliomorph *Pseudotherium argentinus* near the expected location of the mammalian maxilloturbinals. Kermack et al. (1981) reconstructed ossified turbinates of the mammaliaform *Morganucodon* but their reconstruction was questioned by Crompton et al. (2015) and Ruf et al. (2014). Furthermore, turbinates are known from the late Jurassic docodont *Haldanodon* (Lillegraven & Krusat, 1991) and the tritheledontid *Elliotherium* (Crompton et al., 2017).

Besides this, the mammalian nasal cavity also has important functions for olfaction. The olfactory region is the posterior part of the mammalian nasal cavity, which is caudoventrally partially separated from the main respiratory airflow by the lamina terminalis (Ruf et al., 2014). The olfactory part of the mammalian nasal cavity also contains turbinal bones that are covered with olfactory epithelium. These are the ethmoturbinals and the caudal part of the nasoturbinals, which are responsible for collecting odour molecules from the airflow.

Among nonmammalian synapsids, possible ethmoturbinal ridges (etr) were already observed on both sides of the nasoturbinal ridges in the pelycosaur *Dimetrodon* (Hillenius, 1994, Figure 9). The earliest evidence of remnants of partially ossified naso- and ethmoturbinals comes from the nonmammalian cynodont *Brasilitherium riograndensis* (Ruf et al., 2014). Nevertheless, only little information about the anatomy of the olfactory part of the nasal cavity of nonmammalian synapsids comes from the fossil record.

1.4 | The metabolism of dicynodonts

The metabolism of dicynodonts has been controversially discussed, as divergent results have been obtained when different methods were used.

Currently, four groups of hypotheses on the evolution of endothermy exist: It evolved (1) independently in dicynodonts and mammaliaforms (e.g., Faure-Brac & Cubo, 2020; Laaß et al., 2010; Olivier et al., 2017; Rey et al., 2017; Whitney & Sidor, 2020); (2) in almost all nonmammalian synapsids including dicynodonts shortly after the Synapsida-Sauropsida split (Knaus et al., 2021); (3) only in the mammalian stem line (e.g., Araújo et al., 2022; Crompton et al., 2017; Newham et al., 2020, 2022); or (4) endothermy was a plesiomorphic feature of Amniota (Grigg et al., 2022).

The first hypothesis of a convergent evolution of endothermy in dicynodonts is supported by several lines of evidence. First, dicynodonts independently evolved a secondary palate (e.g., Angielczyk & Walsh, 2008; Cluver, 1971; Hillenius, 1994; Rubidge & Sidor, 2001; Toerien, 1953), which was an important precondition for the separation of air and food passage and the elaboration of the nasal cavity and turbinates. However, the secondary palate of dicynodonts was also intimately associated with their highly derived feeding system, specifically as part of the supporting structure for the keratinous rhamphotheca. Due to this, several functional aspects of its role in the evolution of endothermy are less clear than in the mammalian stem line.

Further support comes from bone histology (Faure-Brac & Cubo, 2020; Olivier et al., 2017). Rey et al. (2017) investigated apatite stable oxygen isotope compositions ($\delta^{18}\text{O}_p$) of bones and teeth of several Permo-Triassic therapsids and found that cynodonts and dicynodonts independently acquired constant elevated thermo-metabolism, respectively, within the Eucynodontia and Lystrosauridae + Kannemeyeriiformes clades.

Whitney and Sidor (2020) analysed growth patterns of *Lystrosaurus* tusks from Antarctica and found periodical zones of stress followed by periods of reactivation of metabolic activity that strongly resembled the torpor patterns of modern endotherms.

Another argument for a convergent evolution of endothermy in dicynodonts is also the enlarged, mammal-like brain, with a degenerated pineal organ in the dicynodont *Kawingasaurus* (Laaß & Kaestner, 2017). This is supported by several studies that concluded that the function of a large, energetically expensive brain requires an elevated metabolism (e.g., Allman, 1990; Gillooly & McCoy, 2014; Hopson, 1979; Isler & van Schaik, 2006; Kemp, 2009; Mink et al., 1981; Rowe et al., 2011). Benoit et al. (2017) went so far as to estimate body temperatures of nonmammalian synapsids on the basis of the relationship between relative brain size and body temperature of Gillooly and McCoy (2014). Interestingly, Benoit et al. (2017) reported a body temperature of 34.1°C for *Kawingasaurus* (Benoit et al., 2017, Figure 11), which is in the mammalian range. However, in Table 2 of their paper, they mention another body temperature for *Kawingasaurus*, which is in contradiction to the value in their Figure 11 and to their main conclusions.

Finally, an investigation of a skull of the dicynodont *Lystrosaurus* using neutron tomography revealed possible maxilloturbinates in the respiratory part of the nasal cavity (Laaß et al., 2010).

Considering the size of long-bone foramina in nonmammalian synapsids, which lay in the range of those of modern mammals, endothermy probably evolved in nonmammalian synapsids shortly after the separation of synapsids and diapsids (Knaus et al., 2021).

By contrast, Crompton et al. (2017) investigated the nasal cavities of non-mammaliaform cynodonts to nonmammalian mammaliaforms and came to the conclusion that only late nonmammalian mammaliaforms developed ossified turbinates for water conservation, as would be advantageous for high metabolism. Furthermore, they hypothesized that cartilaginous turbinates, which were most

likely present in other nonmammalian synapsids, probably prevented overheating during the hot climate in Early Triassic.

Araújo et al. (2022) came to similar conclusions by applying another method. Their approach is based on a functional correlation between inner-ear biomechanics and metabolic status. Increased body temperatures decrease endolymph viscosity in the semicircular ducts of the inner ear, which are essential for motor coordination, navigation and spatial awareness, especially for endotherms with increasing activity. As pointed out by the authors, adaptations to maintain optimal functionality of the sense of balance are reflected in morphological changes of the bony canals of the semicircular ducts, which makes it possible to apply the method to extinct species. As a proxy to evaluate the probability of endothermy, they introduced the thermo-motility index (TMI), which reflects the morphological characteristics of the semicircular canals. Apart from many modern and fossil vertebrates, Araújo et al. (2022) also investigated 16 species of anomodonts including *Kawingasaurus*. As a result, the authors concluded that most dicynodonts, including *Kawingasaurus*, had a low probability of endothermy (TMI = 0.27).

Benoit et al. (2016) came to a similar conclusion, having recognized a gradual and convergent loss of the photoreceptive function of the pineal organ and degeneration of the third eye in the mammalian stem line. However, the authors also found considerable variability of the pineal foramen in dicynodonts, including its complete loss in *Kawingasaurus* and some other taxa.

With respect to these highly divergent results from dicynodonts, a description of the nasal anatomy of *Kawingasaurus* might be helpful to shed new light on the discussion of the metabolic status of these animals.

2 | MATERIAL AND METHODS

2.1 | Material

The subject of this study was the skull of the dicynodont *Kawingasaurus fossilis* with the inventory number GPIT-PV-117032 (formerly GPIT/RE/9272) from the collection of the Eberhard-Karls Universität in Tübingen (Figure 1). This specimen was already the subject of studies by Laaß (2015a), and Laaß and Kaestner (2017).

The skull was derived from the Usili Formation of the Ruhuhu region, Kingori, in Tanzania. According to Angielczyk et al. (2014), the Usili Formation of Tanzania roughly correlates with the South African *Cistecephalus* Assemblage Zone of the Karroo Basin, which is of late Permian age. The basal skull length measured from the tip of the snout to the condyles is 40.5 mm.

Tomographic data and a three-dimensional (3D) model of the skull of *Pristerodon mackayi* from previous investigations by Laaß (2015b, 2016) were included in this study for comparison. The skull of *P. mackayi* is housed in the collection of the Museum of Natural History in Berlin under the inventory number MB.R. 985. The basal skull length measured from the tip of the snout to the condyles is 78 mm.

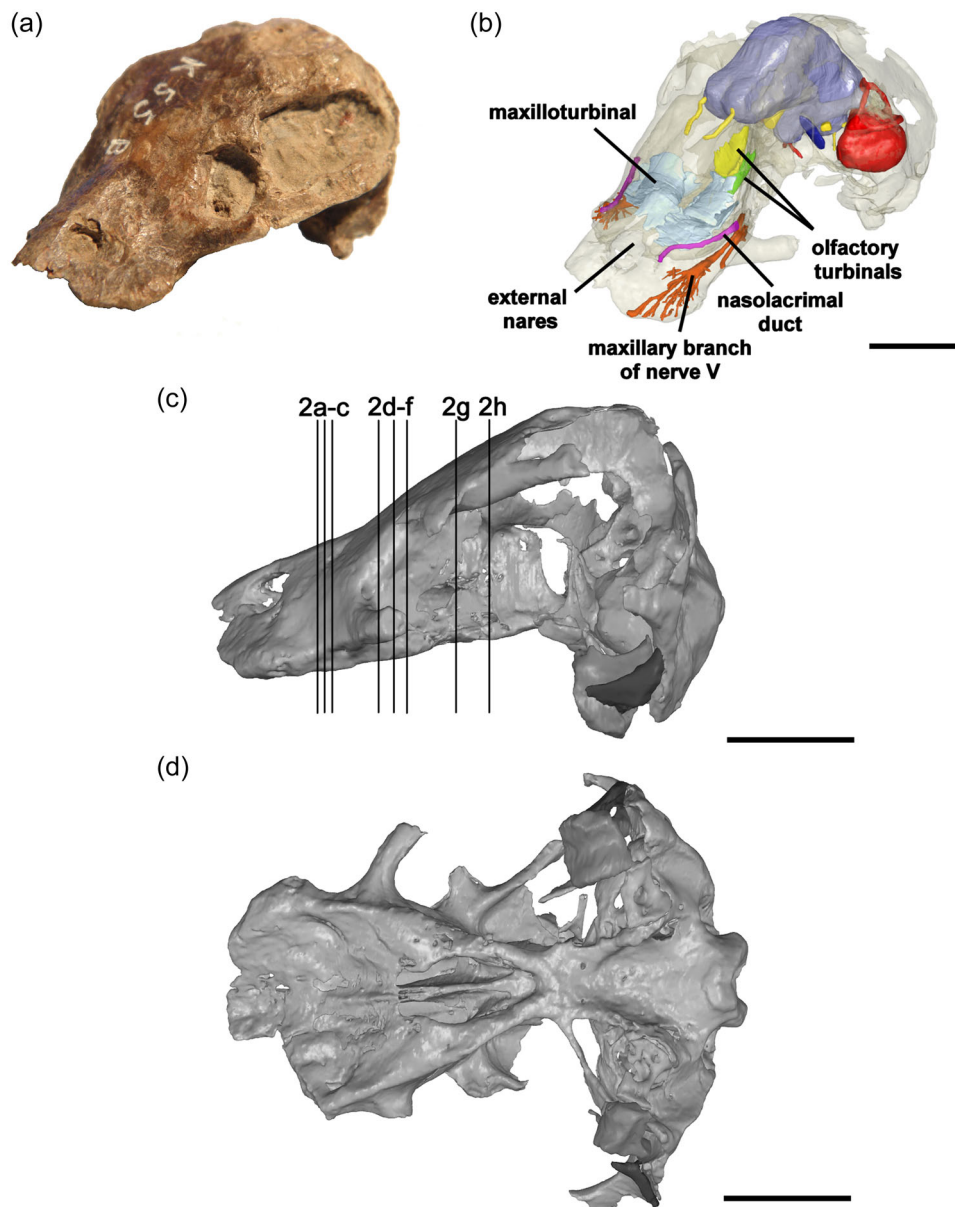


FIGURE 1 The skull of *Kawingasaurus fossilis* (GPIT-PV-117032). (a) Photograph of the specimen. (b) Virtual three-dimensional model of the skull. (c) Lateral view. The lines indicate the positions of the transversal sections in Figure 2. (d) Ventral view. All scale bars represent 10 mm.

2.2 | Neutron tomography and reconstruction of the tomographic volume

This work is based on neutron tomography experiments performed at the ICON instrument (Kaestner et al., 2011) at the Swiss Spallation Neutron Source at Paul Scherrer Institut in Villigen, Switzerland. Further details about the neutron tomographic experiments on the skull of *K. fossilis* (GPIT-PV-117032) and *P. mackayi* (MB.R. 985) were described by Laaß (2015a, 2015b, 2016), Laaß et al. (2017), and Laaß and Kaestner (2017).

The projection data from the neutron tomography scan was reconstructed using the open-source reconstruction tool MuhRec (Kaestner, 2011). The reconstruction processing chain involved normalization, outlier removal and ring removal (Münch et al., 2009)

followed by filtered back-projection. A TV-2 based denoising filter (Burger et al., 2006) was applied to the reconstructed data using the open-source image processing tool KipTool (Carminati et al., 2019). This filter has very good noise-suppression capacity without harming relevant anatomical features in the images.

2.3 | Virtual reconstruction and visualization of internal cranial structures

The visibility of internal cranial structures of low contrast to the matrix, such as the remains of turbinal bones in the tomographic slices, was improved by applying filter plugins of the software ImageJ, such as the FFT Bandpass Filter for reduction of artefacts

and the CLAHE Filter for enhancing local contrast. The underlying method is the Contrast Limited Adaptive Histogram Equalization method described by Zuiderveld (1994). For the bandpass filter, the settings 'filter large structures down to 40 pixels; filter small structures down to 3 pixels; suppress stripes: none; and tolerance of direction: 5%' were applied. The settings for the CLAHE Filter were 'blocksize: 99; histogram bins: 256; and maximum slope: 1.20'.

The 3D modelling and visualization of the tomographic slices was carried out using the software AMIRA 5.4 (FEI Visualization Sciences Group; <http://www.vsg3d.com/>) following the method of Laaß (2015a, 2016), and Laaß and Schillinger (2015). Structures of interest, such as the bones of the skull, endocranial cavities and canals of nerves and blood vessels, were vectorized slice by slice with the segmentation tool of AMIRA. After smoothing and polygon reduction, the regions of interest (ROI) were saved as Wavefront files (OBJ). After this, the Wavefront files were reassembled, coloured and integrated into 3D PDF files with the software Simlab Composer 2014 SP1 (Simlab Soft; <http://www.simlab-soft.com/>). Volumes and surface areas of ROIs were determined with the measuring tools of AMIRA and are summarized in Supporting Information: Table S1.

3 | RESULTS

3.1 | General remarks

The nasal cavity of *Kawingasaurus* is described using representative tomographic slices (Figures 2 and 3) whose positions are marked in Figure 1c. For comparison, additional slices are also presented for *Pristerodon* (Figure 4a–c). Furthermore, selected features discussed below are summarized in Supporting Information: Table S1.

Similar to other dicynodonts, *Kawingasaurus* and *Pristerodon* possessed a secondary palate (Figures 1d, 4) that was mainly formed by the caudally elongated premaxillary. As a result, the respiratory passage in *Kawingasaurus*, which is formed ventrally by the elongated premaxilla, laterally by the palatines and dorsally by the lateral wings of the vomer (lwv) (the transverse lamina, tl), is partially separated from the rest of the nasal cavity.

In *Kawingasaurus*, the respiratory part of the nasal cavity was formed rostrally by the premaxilla, dorsally by the nasals and laterally by the maxillaries and septomaxillaries. Ventrally, it is separated from the oral cavity by the premaxilla, the maxillaries and palatines (see also Cox, 1972). The olfactory part of the nasal cavity was dorsally and laterally formed by the nasals and frontals and ventrally by the transverse laminae. A cribriform plate, which separates the mammalian olfactory part of the nasal cavity from the brain cavity (Kielan-Jaworowska et al., 2004), was neither recognized in *Kawingasaurus*, nor in *Pristerodon*.

In contrast to *Pristerodon*, which possessed well-developed maxillary recesses (Barry, 1967; see also Figures 4 and 6b), the nasal cavity of *Kawingasaurus* was not expanded by paranasal sinuses. Maxillary sinuses were described from numerous dicynodonts such

as *Lystrosaurus* (Benoit et al., 2018; Cluver, 1971), *Diictodon feliceps* (Agnew, 1959; Benoit et al., 2018; Sollas & Sollas, 1914), *Cistecephalus* (Benoit et al., 2018; Keyser, 1973), *Rastodon procurvidens* (Simão-Oliveira et al., 2019), *Patranomodon nyaphulii*, *Eodicynodon oosthuizeni*, *Abajudon kaayai*, *Compsodon helmoedi*, *Myosaurus gracilis*, and *Oudenodon bainii* (Benoit et al., 2018).

3.2 | Internal anatomy of the nasal cavity and comparisons

As in other nonmammalian synapsids, *Kawingasaurus* and *Pristerodon* possessed nasolacrimal ducts that extend from the lacrimal foramen in the orbit to the region of the septomaxillary foramen (e.g., Cluver, 1971; Hillenius, 2000; Ruf et al., 2014). In both taxa, only the anterior-most and the posterior parts of the nasolacrimal ducts were covered by bone (Figures 2c,f, 4a,b, f–i and 5e). The rest of the ducts lie in a sulcus ventral to the mxtr on the inner wall of the nasal cavity (Figure 2a–e; marked by dotted lines in Figures 4f–i and 5e).

In the nasal cavity of *Kawingasaurus*, several ridges were recognized: First, there is a pair of nasoturbinar ridges on the undersides of the nasals, which run from the region near the external nares to the olfactory region of the nasal cavity (or) (Figure 2a–d). Similar ridges also occur in *Pristerodon* (Figure 4a,b), in *Lystrosaurus* (Cluver, 1971), and *Dicynodontoides* (Kemp, 1969). Among other groups of nonmammalian synapsids, nasoturbinar ridges were also reported, for example, from the sphenacodontid pelycosaur *Dime-trodon* (Hillenius, 1994; Romer & Price, 1940), the titanosuchid dinocephalian *Jonkeria* (Boonstra, 1968), the gorgonopsians *Leontoccephalus*, and *Arctognathus* (Hillenius, 1994; Kemp, 1969), and the therocephalians *Akidognathus* (Brink, 1960) and *Moschowhaisia* (Tatarinov, 1963).

In *Kawingasaurus*, prominent maxilloturbinal ridges on both sides of the nasal cavity were recognized (Figures 2a–f and 3). As shown in the virtual 3D model in Figure 5c–e, the mxtr ran from the vicinity of the external naris through almost the entire respiratory part of the nasal cavity.

The maxilloturbinal ridges in *Pristerodon* (Figure 4a,b,h) were shorter and weaker than in *Kawingasaurus*. So far, maxilloturbinal ridges were unknown from dicynodonts and only described from representatives of the mammalian stem line (Crompton et al., 2017; Hillenius, 1994; Ruben et al., 2012).

Remarkably, slightly curved structures (mxt) on both sides of the nasal cavity in *Kawingasaurus* were preserved (Figures 2a–f and 3). It can be ruled out that these curved structures were sclerotic plates or any other bones that were displaced into the nasal cavity, as was recognized in a burnetiid skull described by Day et al. (2018). The orbits of *Kawingasaurus* are small, being only 6–7 mm in diameter. The structures in question have a length of up to 8.5 mm from rostral to caudal (Figures 5g,h and 7). As already described by Laaß and Kaestner (2017), the delicate bones surrounding the brain cavity are largely undamaged and undistorted. The same is true for the nasal cavity (Figure 2).

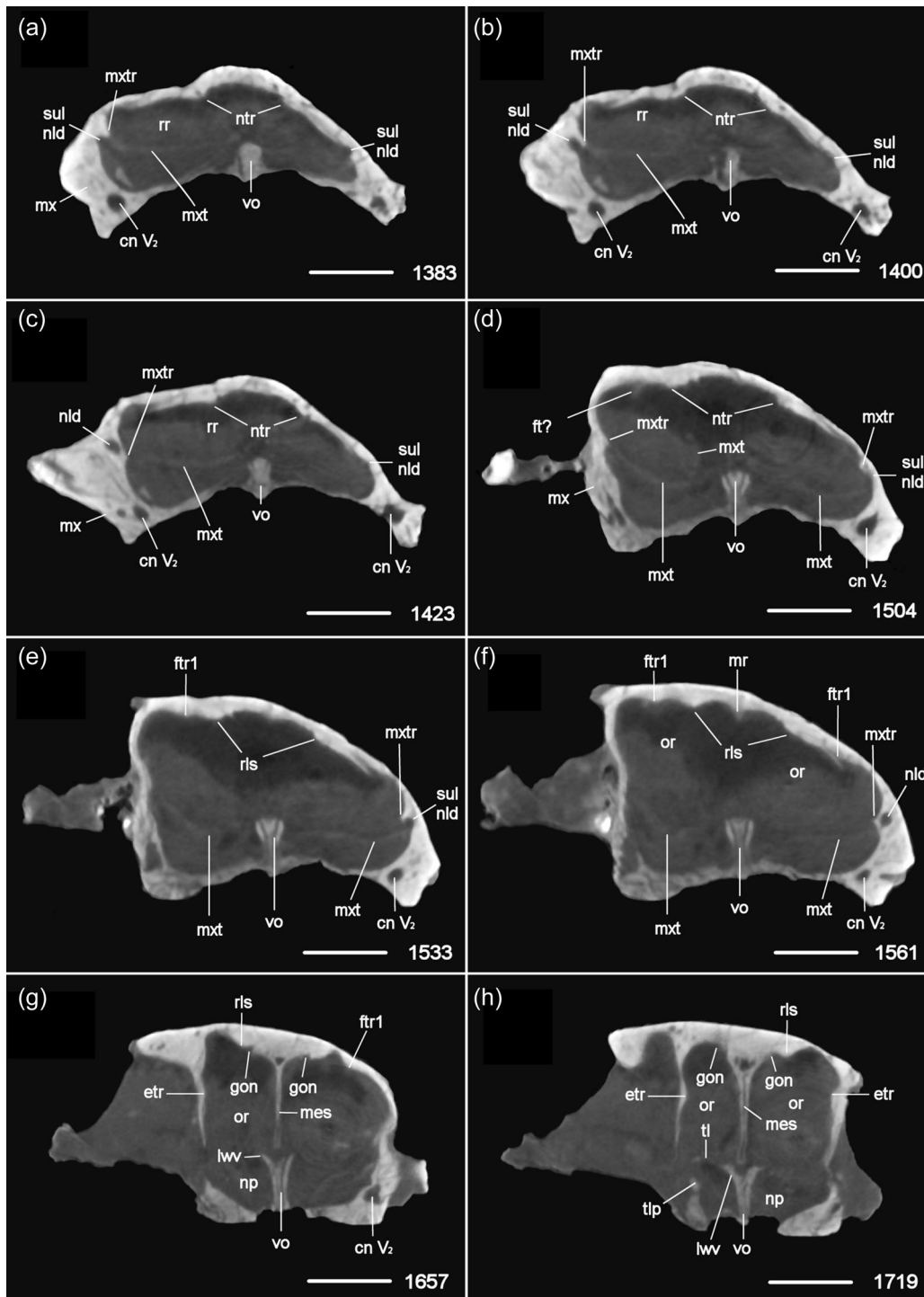


FIGURE 2 Representative tomographic slices through the nasal cavity of *Kawingasaurus fossilis* (GPIT-PV-117032). The number in the right corner on each tomographic image is that of the slice in the tomographic image stack. (a–d) Sections through the respiratory part of the nasal cavity, showing maxilloturbinal and nasoturbinal ridges. Note the presence of maxilloturbinals on both sides. (e–h), Sections through the olfactory part of the nasal cavity. Note the presence of possible ethmoturbinal ridges (et) and the lateral wings of the vomer that, together with the transverse laminae of the palatines form the pair of nasopharyngeal passages. Abbreviations: cn V₂, canal of the maxillary branch of cranial nerve V; et?, possible remains of ethmoturbinal; etr, ethmoturbinal ridge; ftr1, ftr2, ridges of possible frontoturbinals 1 and 2; gon, groove of the olfactory nerve; lwv, lateral wing of the vomer; mes, mesethmoid; mr, median ridge; mx, maxillary; mxt, maxilloturbinal; mxtr, ridge of the maxilloturbinal; nld, nasolacrimal duct; np, nasopharyngeal passage; ntr, ridge of the nasoturbinal; or, olfactory region of the nasal cavity; rls, ridge of the lamina semicircularis; rr, respiratory region; sul nld, sulcus of the nasolacrimal duct; tl, transverse lamina; tlp, transverse lamina of the palatine; vo, vomer. All scale bars represent 5 mm.

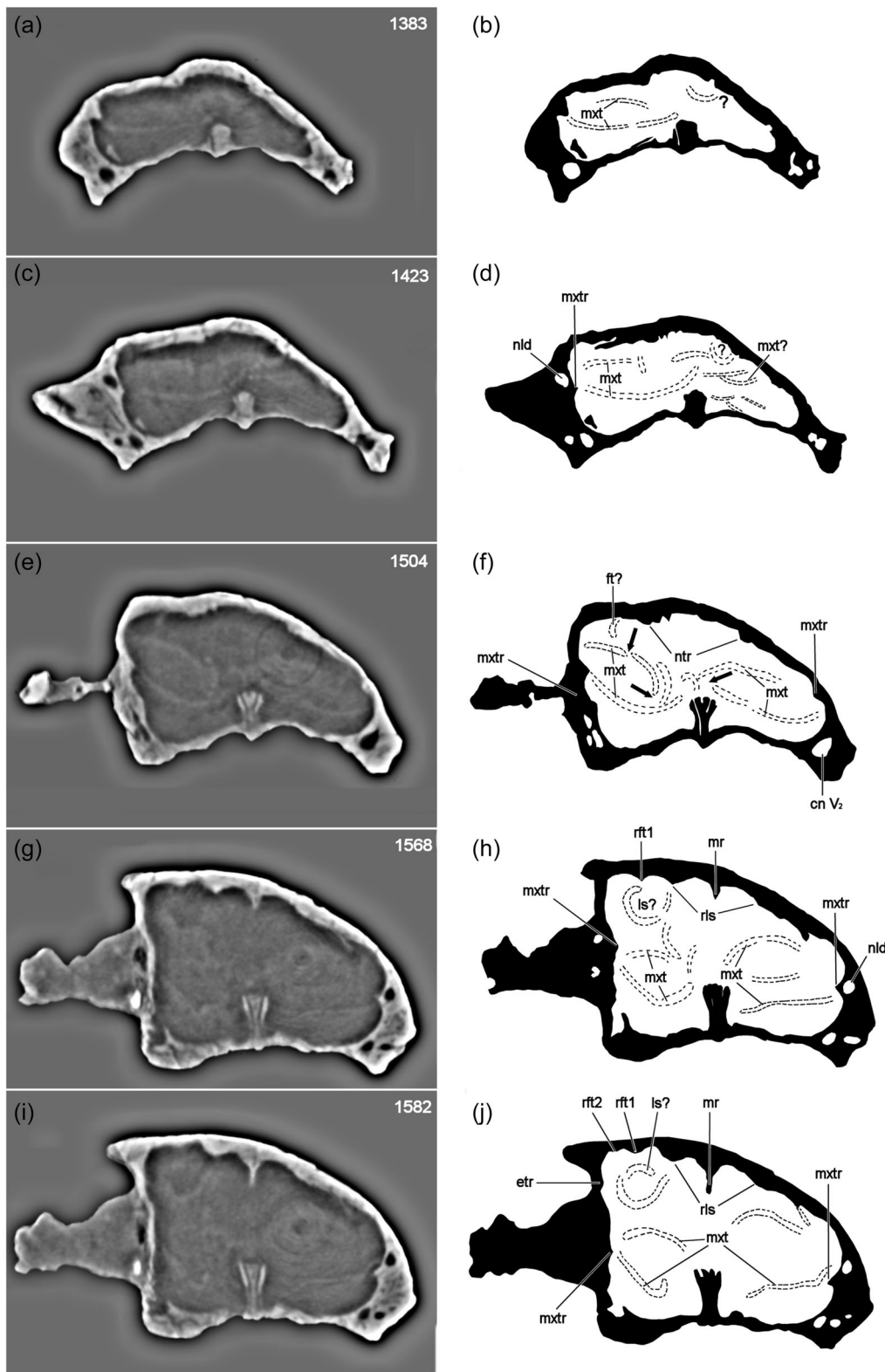


FIGURE 3 Sketches of the turbinates in the nasal cavity of *Kawingasaurus fossilis* (GPIT-PV-117032). To increase the visibility of structures of weak contrast to the background, the tomographic slices in (a), (c), (e), (g) and (i) were filtered by an FFT Bandpass Filter and a filter to enhance local contrast. The arrows in (f) mark breaks in the turbinates, which indicates poor ossification. The number in the right corner on each tomographic image is that of the slice in the tomographic image stack. Abbreviations: cn V₂, canal of the maxillary branch of cranial nerve V; etr, ethmoturbinal ridge; ft, possible remains of a frontoturbinal; ls, lamina semicircularis; mr, median ridge; mxtr, maxilloturbinal; mxtr, maxilloturbinal ridge; nld, nasolacrimal duct; ntr, nasoturbinal ridge; rft1, rft2, possible frontoturbinal ridges 1 and 2; rls, possible ridge of the lamina semicircularis.

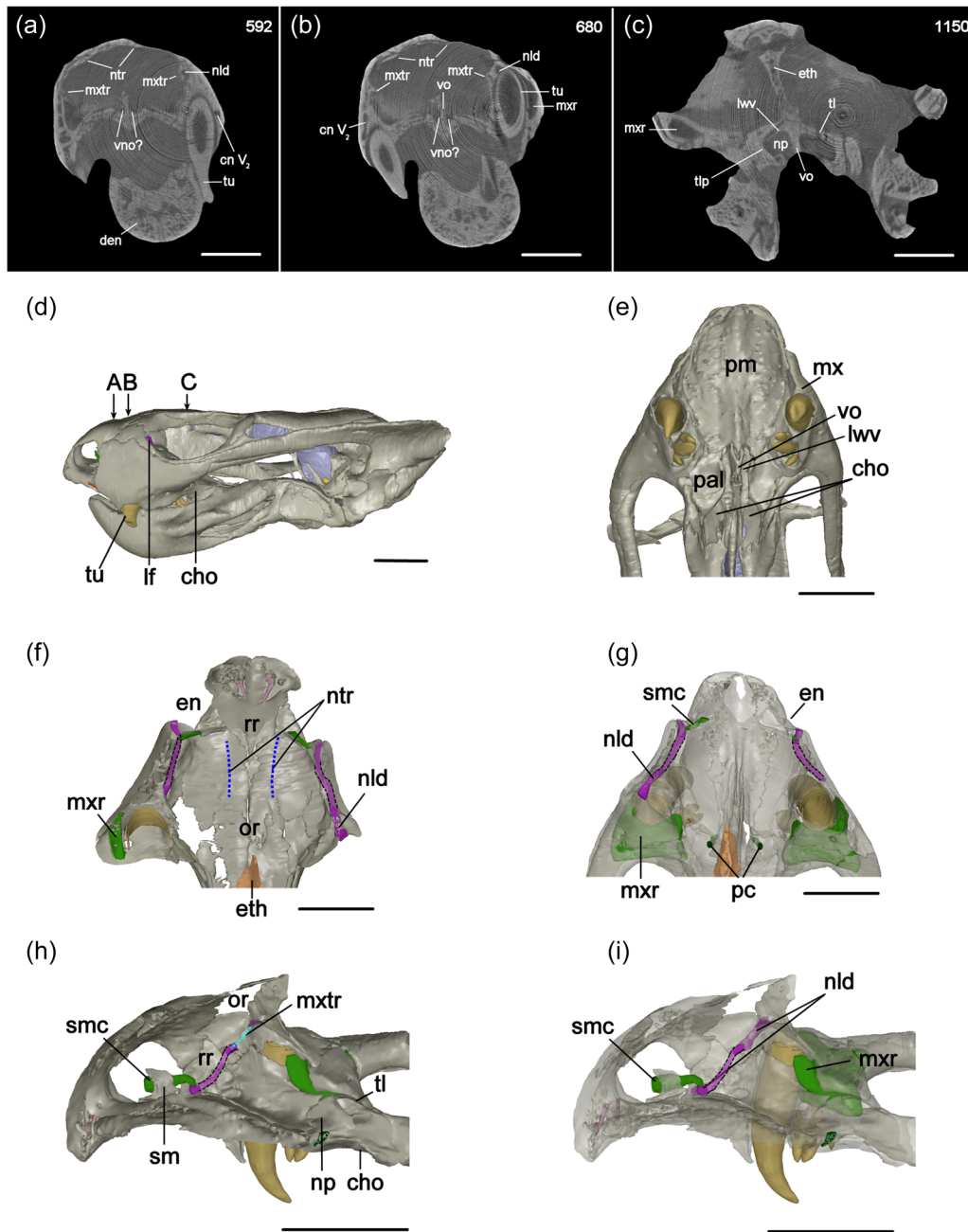


FIGURE 4 Virtual three-dimensional (3D) reconstruction of the skull of *Pristerodon mackayi* (MB.R. 985). The number in the right corner on each tomographic image is that of the slice in the tomographic image stack. (a, b) Tomographic slices through the respiratory part of the nasal cavity. Note the presence of naso- and maxilloturbinal ridges. (c) Section through the posterior part of the nasal cavity. Note the nasopharyngeal passages, which are covered by the lateral wings of the vomer and the palatines. (d) Virtual 3D model of the skull showing the positions of the tomographic slices (a–e). (e) Virtual 3D model of the skull showing the secondary palate. (f, g) Virtual transverse sections through the nasal cavity. The nasolacrimal ducts are coloured in violet and the parts that were not covered by bone are stippled. The nasoturbinal ridges are stippled in blue. (h, i) Sagittal sections through the nasal cavity. The nasolacrimal ducts are coloured in violet and the parts that were not covered by bone are stippled. The course of the bony mxtr is stippled in light blue. Abbreviations: cho, choana; den, dentary; en, external naris; lf, lacrimal foramen; lwv, lateral wing of the vomer; mx, maxillary; mxr, maxillary recess; mxtr, maxilloturbinal ridge; nld, nasolacrimal duct; np, nasopharyngeal passage; ntr, ridge of the nasoturbinal; or, olfactory region of the nasal cavity; pal, palatine; pm, premaxillary; pc, palatine canal; rr, respiratory region of the nasal cavity; sm, septomaxilla; smc, septomaxillary canal; tl, transverse lamina; tlp, transverse lamina of the palatine; tu, tusk; vo, vomer. All scale bars represent 10 mm.

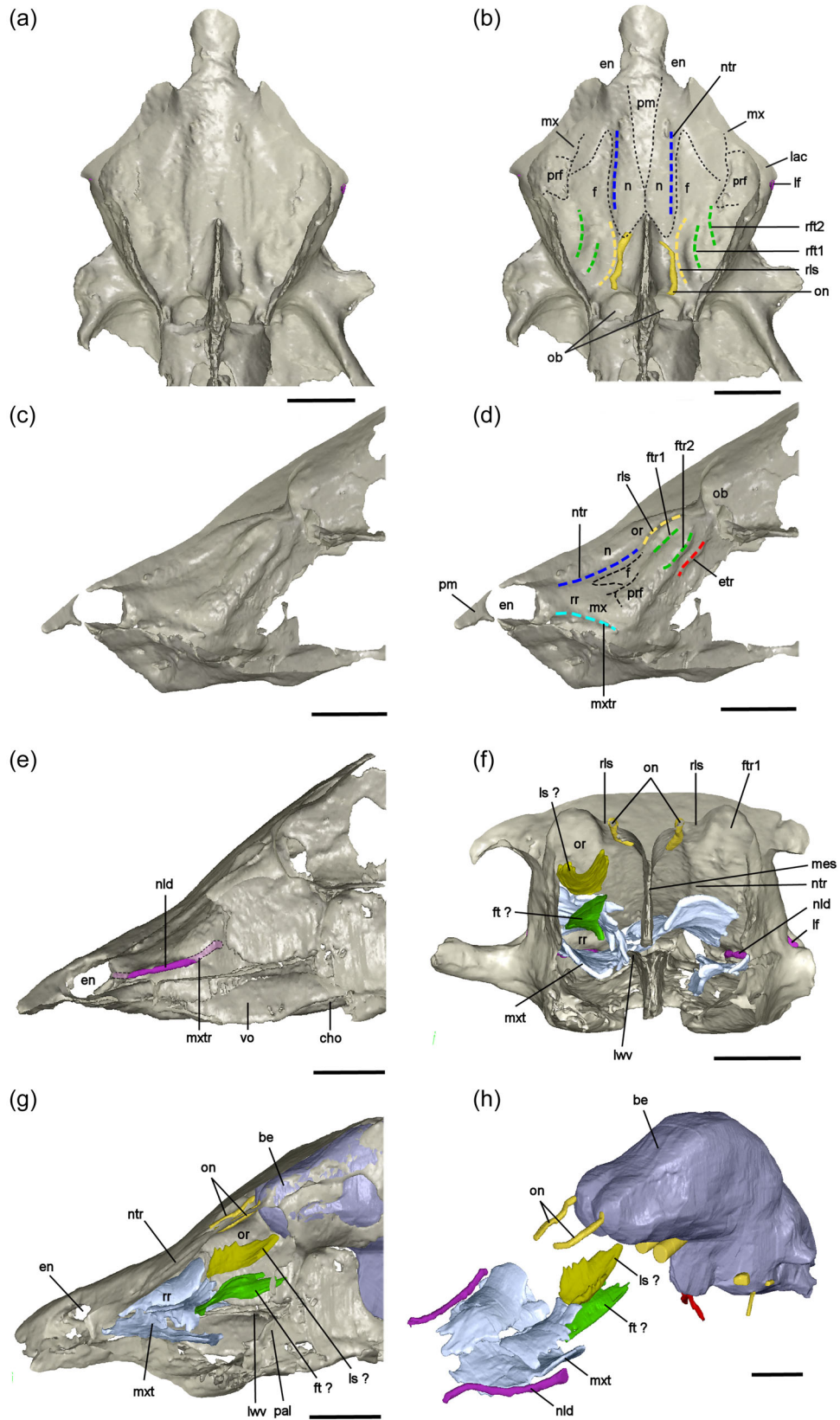


FIGURE 5 (See caption on next page).

An important observation is that the structure on the left side of the nasal cavity was still associated with the maxilloturbinal ridge. Symmetrically, on the right side of the nasal cavity, a corresponding structure was also evident, which obviously had been slightly moved to the floor of the nasal cavity (Figures 2d–f and 3). The attachment of the left structure to the maxilloturbinal ridge strongly suggests that they represent maxilloturbinals. The 3D reconstructions in Figure 5f–h revealed a relatively simple construction consisting of scrolled sheets of bone. However, it cannot be ruled out that the turbinals were originally more complex and only the strong main branches were preserved due to their better fossilization potential. In *Pristerodon*, mxt were not recognized (Figure 4a,b).

In Figure 2, the contrast between the mxt in *Kawingasaurus* and the rock matrix is much lower than the contrast between dermal bones and the matrix. This might be an indication that the mxt were either poorly ossified or cartilaginous. However, the presence of several breaks in the turbinals rather suggests a poor ossification (Figure 3e,f, marked by arrows), because cartilaginous structures would react more flexibly to diagenetic compression.

A reason that such delicate organic structures with low contrast to the matrix could be visualized, might be that in contrast to X-rays, neutrons often produced a better contrast in or between organic structures and the matrix, as demonstrated by Schillinger et al. (2018, Figure 4), who applied both methods to the same specimen of fossil teeth.

More caudally, four other ridges (ridge of the lamina semicircularis [rls], ridges of possible frontoturbinals 1 and 2 [ftr1, ftr2], etr) were recognized in the olfactory part of the nasal cavity of *Kawingasaurus* (Figures 2e–h and 5a–d,f). The first pair of ridges (rls) is parallel to the mesethmoid (mes) (Figures 2e–g and 5b). Corresponding ridges also occur in the cistecephalid *Kembawacela kitchingi* (Angielczyk et al., 2019; Figure 8a). Rostrally, these ridges in *Kawingasaurus* are almost continuous with the nasoturbinal ridges (Figures 5b, 7b). This is reminiscent of the condition in modern mammals, where the lamina semicircularis is continuous with the nasoturbinal (Schrenk, 1989; Voit, 1909; Ruf, 2020). Remarkably, on the left side of the nasal cavity, near the possible ridge of the lamina semicircularis, another possible remainder of a scrolled turbinal was recognized (Figure 3i), which could be part of the lamina semicircularis.

More laterally, two other ridges (ftr1 and ftr2) were present (Figures 2e–g and 3g–j). As shown in Figure 5b, they are located on

the undersides of the frontals, which suggests that they were sites for attachment of frontoturbinals. Similar ridges were also found by Cluver (1971, Figure 30) on the ventral side of the frontals in *Lystrosaurus*. Finally, a fourth ridge is located on the lateral wall of the nasal cavity. Its location indicates that it was probably the site for attachment of an ethmoturbinal (Ruf, 2020).

Similar ridges are also known from other synapsids such as sphenacodontid pelycosaur, gorgonopsians, therocephalians, cynodonts, mammaliaforms, and mammals (e.g., Hillenius, 1994; Kemp, 1969). For example, Romer and Price (1940) also found a nasoturbinal ridge in *Dimetrodon*, as well as four ridges in the olfactory portion of the nasal cavity. In *Pristerodon*, no ridges in the olfactory portion of the nasal cavity were recognized.

In *Kawingasaurus* (Figure 2g,h), a nasal septum was developed that divided the nasal cavity into a right and a left part. This ossified nasal septum is interpreted here as the mesethmoid. According to Ruf et al. (2014), the ossification of the mesethmoid started in the dorsal part of the nasal septum and then spread into the periphery. The same condition was recognized here: in Figure 2f, the dorsal part of the probably cartilaginous nasal septum began to ossify as a small median ridge (mr) on the underside of the roof of the nasal cavity. More caudally (Figure 2g,h), the mesethmoid became more and more ossified from dorsal to ventral. Median ridges, as possible sites for attachment of a cartilaginous nasal septum, were also described from the dicynodonts *Sangusaurus parringtonii* (Angielczyk et al., 2018) and *Rastodon procurvidens* (Simão-Oliveira et al., 2019), and from most cynodonts (e.g., Franco et al., 2021; Kerber et al., 2020; Ruf et al., 2014).

It should be noted that on both sides of the mesethmoid, distinctive grooves (groove of the olfactory nerve) were visible (Figures 2g,h and 5b,f). Corresponding structures, preserved as ridges on a natural endocast of the interior skull roof (ridge and rami of the olfactory nerve), are also present in the cistecephalid *K. kitchingi* (Angielczyk et al., 2019) (see Figure 8). Following Benoit et al. (2018), the authors interpreted them as ophthalmic canals of the trigeminal nerves. Similar grooves on the ventral side of the roof of the nasal cavity flanking the mesethmoid also occur in *Brasilitherium*. However, Ruf et al. (2014) tentatively interpreted them as the grooves of the olfactory nerves. This can be confirmed here, because Figures 5b and 8b show that the grooves enter the brain cavity and continue to the region of the olfactory bulbs, which corresponds to the mammalian condition for the olfactory nerve (cranial nerve I). The

FIGURE 5 Virtual three-dimensional (3D) reconstruction of the skull of *Kawingasaurus fossilis* (GPIT-PV-117032) showing the turbينات in the nasal cavity. (a) Coronal section through the nasal cavity. (b) Interpretation of the possible homologues of the turbinal ridges. The stippled black lines show the approximate location of the sutures between the bones forming the nasal cavity. (c) Parasagittal section through the nasal cavity. (d) Interpretation of the possible homologues of the turbinal ridges. Stippled black lines as in (b). (e) Course of the nasolacrimal duct and association to the mxtr. The parts of the duct that were enclosed by bones are stippled. (f, g) Transverse and parasagittal sections through the nasal cavity, showing the remains of the turbinate system. (h) 3D model of the turbinate system and related soft-tissue structures. Abbreviations: be, brain endocast; cho, choana; en, external naris; etr, ethmoturbinal ridge; f, frontal; lf, lacrimal foramen; lvv, lateral wing of the vomer; mes, mesethmoid; mx, maxillary; mxt, maxilloturbinal; mxtr, ridge of the maxilloturbinal; n, nasal; nld, nasolacrimal duct; ntr, ridge of the nasoturbinal; ob, casts of the olfactory bulbs; on, olfactory nerve reconstructed; or, olfactory region of the nasal cavity; prf, prefrontal; rft1, rft2, possible frontoturbinal ridges 1 and 2; rls, possible ridge of the lamina semicircularis; rr, respiratory region; vo, vomer. All scale bars represent 5 mm.

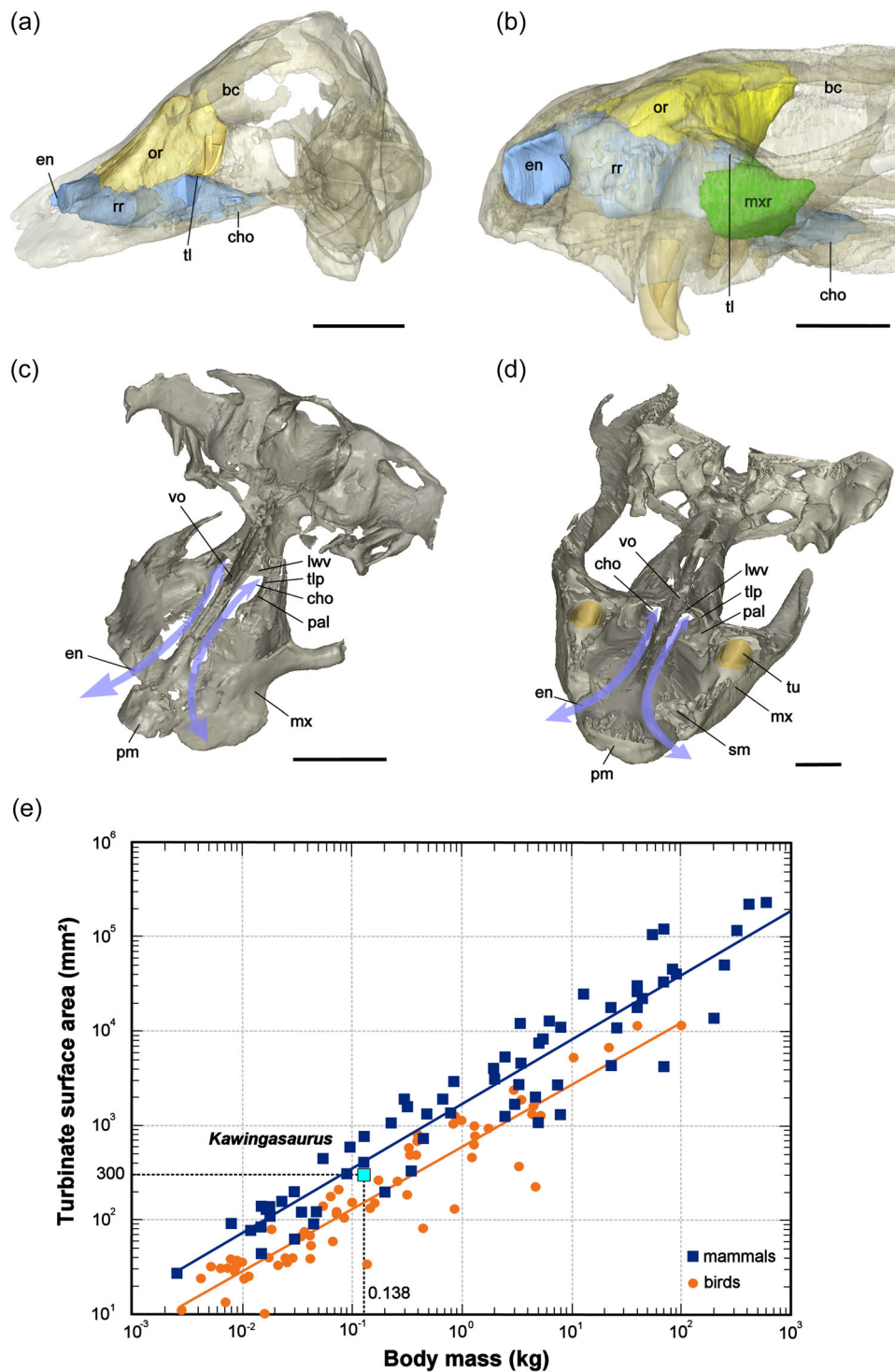


FIGURE 6 Structure of the nasal cavities and respiratory airflow of *Kawingasaurus* and *Pristerodon*. (a) Respiratory (light blue) and olfactory region (yellow) of the nasal cavity of *Kawingasaurus* and (b) *Pristerodon*. Additionally, *Pristerodon* possessed maxillary recesses, which were connected with the respiratory portion of the nasal cavity. (c) Oblique view into the opened nasal cavity of *Kawingasaurus*. The blue arrows visualize the airflow through the respiratory portion of the nasal cavity. (d) Oblique view into the opened nasal cavity of *Pristerodon*. The blue arrows are as in (c). (e) Scaling relationship of the respiratory turbinate surface area on body mass in mammals (blue squares), birds (orange circles) and *Kawingasaurus* (light blue square). Note that the turbinate surface area of *Kawingasaurus* falls into the mammalian range. Modified from Owerkowicz et al. (2015, Figure 9.4A). Abbreviations: bc, brain cavity; cho, choana; en, external naris; etr, ethmoturbinal ridge; lwv, lateral wings of the vomer; mx, maxilla; mxr, maxillary recess; mxtr, maxilloturbinal ridge; ntr, ridge of the nasoturbinal; or, olfactory region of the nasal cavity; pal, palatine; pm, premaxilla; rr, respiratory region of the nasal cavity; sm, septomaxilla; tl, transverse lamina; tlp, transverse lamina of the palatine; tu, tusk; vo, vomer. All scale bars represent 10 mm.

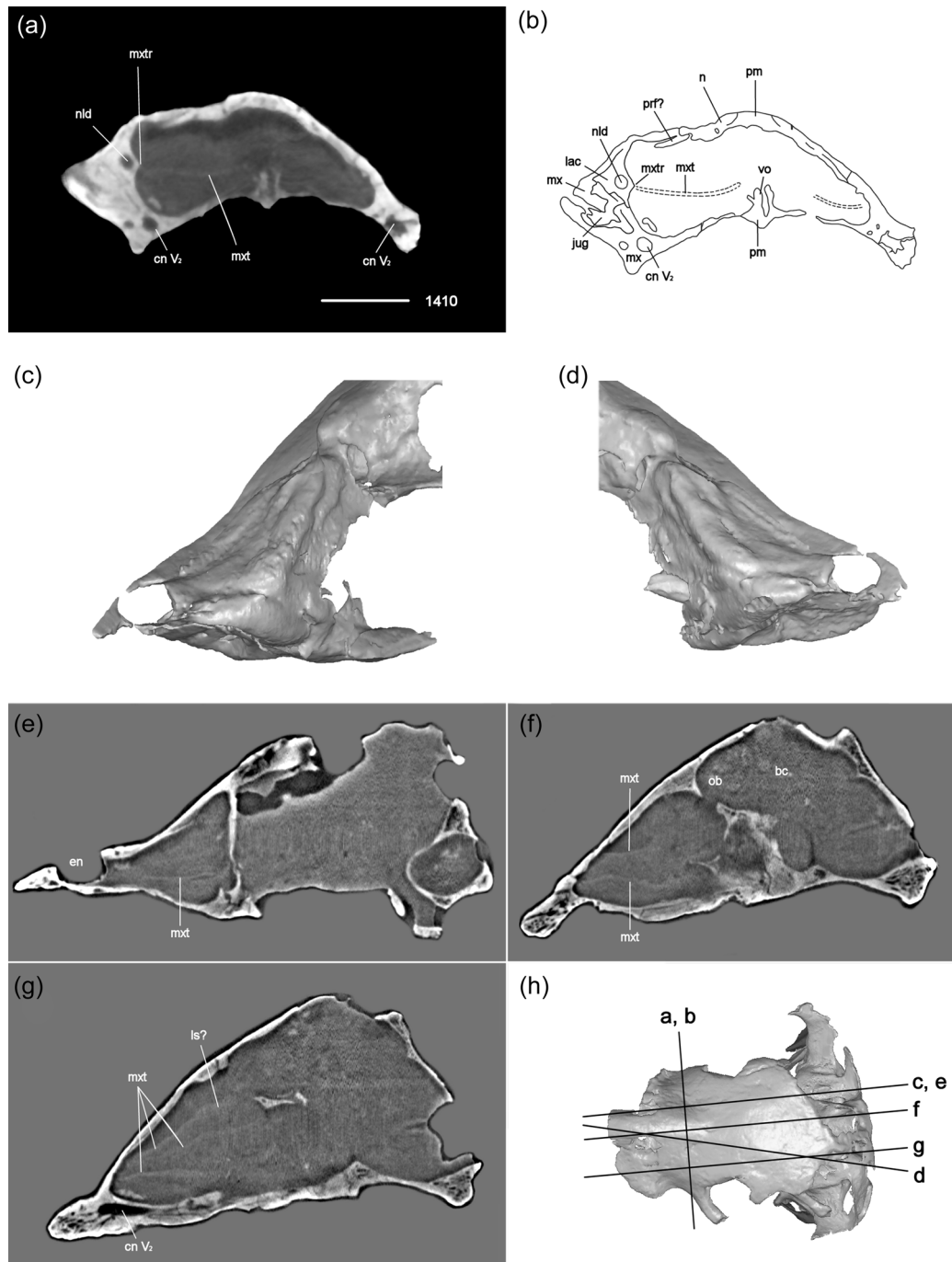


FIGURE 7 Additional slices through the nasal cavity of *Kawingasaurus fossilis* (GPIT-PV-117032). The tomographic slices in (e–g) were filtered by an FFT Bandpass filter to increase the visibility of structures of weak contrast to the background. (a) Tomographic slice that shows the part of the nasolacrimal duct that runs through the lacrimal bone. (b) Interpretative sketch of (a) showing the bones that form the nasal cavity. Note that the nasolacrimal duct runs within the body of the lacrimal. (c, d) Virtual sections through the three-dimensional model of the *Kawingasaurus* skull, showing the medial surface of the right (c) and the left maxilla and surrounding bones (d) in the nasal cavity. Note the course of the mxtr. (e–g) Sagittal slices through the nasal cavity. Note the delicate traces of turbinals. (f) The lines indicate the positions of the sections (c–e). Abbreviations: bc, brain cavity; cn V₂, canal of the maxillary branch of cranial nerve V; en, external naris; jug, jugal; lac, lacrimal; ls, possible remains of the lamina semicircularis; mxt, maxilloturbinal; mxtr, ridge of the maxilloturbinal; n, nasal; nld, nasolacrimal duct; ob, casts of the olfactory bulbs; prf, prefrontal; pm, premaxilla; vo vomer.

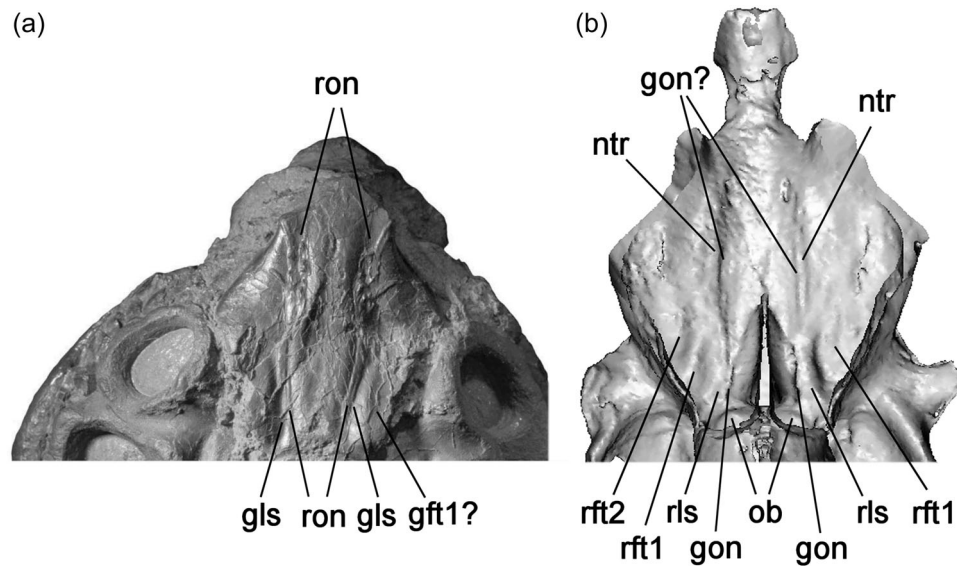


FIGURE 8 Anatomy of the interior skull roof of *Kembawacela kitchingi* and *Kawingasaurus fossilis* compared. (a) Natural endocast of *K. kitchingi* (from Angielczyk et al., 2019). (b) Virtual section through the skull of *Kawingasaurus*, which shows the underside of the skull roof. Note that grooves on the endocast appear as ridges on the skull roof and vice versa. Abbreviations: gon, groove of the olfactory nerve; ift1, impression of the frontoturbinal ridge 1; ils, impression of the ridge of the lamina semicircularis; ntr, nasoturbinal ridge; ob, olfactory bulb; rft1, ridge of frontoturbinal 1; rft2, ridge of frontoturbinal 2; rls, ridge of the lamina semicircularis; ron, ridge and rami of the olfactory nerve.

trigeminal nerve, however, left the brain in all probability through the trigeminal notch, which was formed in dicynodonts by the anterodorsal process and the pila antotica (e.g., Castanhinha et al., 2013; Cluver, 1971; Kemp, 2009; Laaß & Kaestner, 2017; Surkov & Benton, 2004).

It is evident that the olfactory region of the nasal cavity (or) in *Kawingasaurus* was greatly expanded dorsolaterally into the orbito-temporal region (Figures 2g,h, 5f,g and 6a). It has about the same volume as the respiratory region (Supporting Information: Table S1). For comparison, in *Pristerodon* the olfactory part has only about half the volume of the respiratory region (Figure 6b and Supporting Information: Table S1). Furthermore, *Kawingasaurus* and *Pristerodon* possessed nasopharyngeal passages (np) on the ventral floor of the nasal cavity, which were separated by transverse laminae from the olfactory region of the nasal cavity (or). The transverse laminae were built by the lateral wings of the vomer and the transverse laminae of the palatines (Figures 2g,h and 4c). The respiratory airflow through the nasal cavity is visualized in Figure 6c,d.

4 | DISCUSSION

4.1 | General remarks

The nasal anatomy of *Kawingasaurus* and *Pristerodon* reveals a mosaic pattern of ancestral and derived, mammal-like features. The nasal openings of *Kawingasaurus* and *Pristerodon* were separated from each other by a broad internarial process of the premaxillaries, which according to Ruf et al. (2014) is the basal condition in synapsids. The derived condition can only be recognized in cynodonts and mammals,

where the internarial process was reduced. This was probably closely correlated with the development of flexible, motile outer cartilages and the formation of a rhinarium (Higashiyama et al., 2021; Maier, 1980, 2002). In contrast, in all probability *Kawingasaurus* and *Pristerodon* possessed a horny beak that included the nasal openings (see also Benoit et al., 2018; Cluver, 1971; Cox, 1998; Jasinoski & Chinsamy-Turan, 2012; Sullivan & Reisz, 2005; Watson, 1960).

Due to the presence of the secondary palate, the nasal and oral cavities in *Kawingasaurus* and *Pristerodon* were largely separated from each other, which enabled continuous breathing during food processing and the elaboration of the turbinate system, which is discussed in the following sections.

4.2 | Possible homologies of the turbinates

The pattern of ridges for attachment of possible maxillo-, naso-, fronto- and ethmoturbinates in the nasal cavity of *Kawingasaurus* strongly resembles the mammalian bauplan (Figure 9). Some of these ridges, maxillo- and nasoturbinal ridges, also occur in *Pristerodon* (Figure 4).

The interpretation of the ridge in the respiratory portion of the nasal cavities of *Kawingasaurus* and *Pristerodon* as maxilloturbinal ridge is well supported by the fact that it runs on the inner walls of the maxilla and lacrimal in proximity to the nasolacrimal duct, as in most modern mammals (Evans & Christensen, 1979; Hillenius, 1994; Nickel et al., 1979).

To date, it is still uncertain whether the maxilloturbinal is a plesiomorphic feature or not. On the one hand, maxilloturbinal ridges were only reported from cynodonts and mammals (Hillenius, 1994;

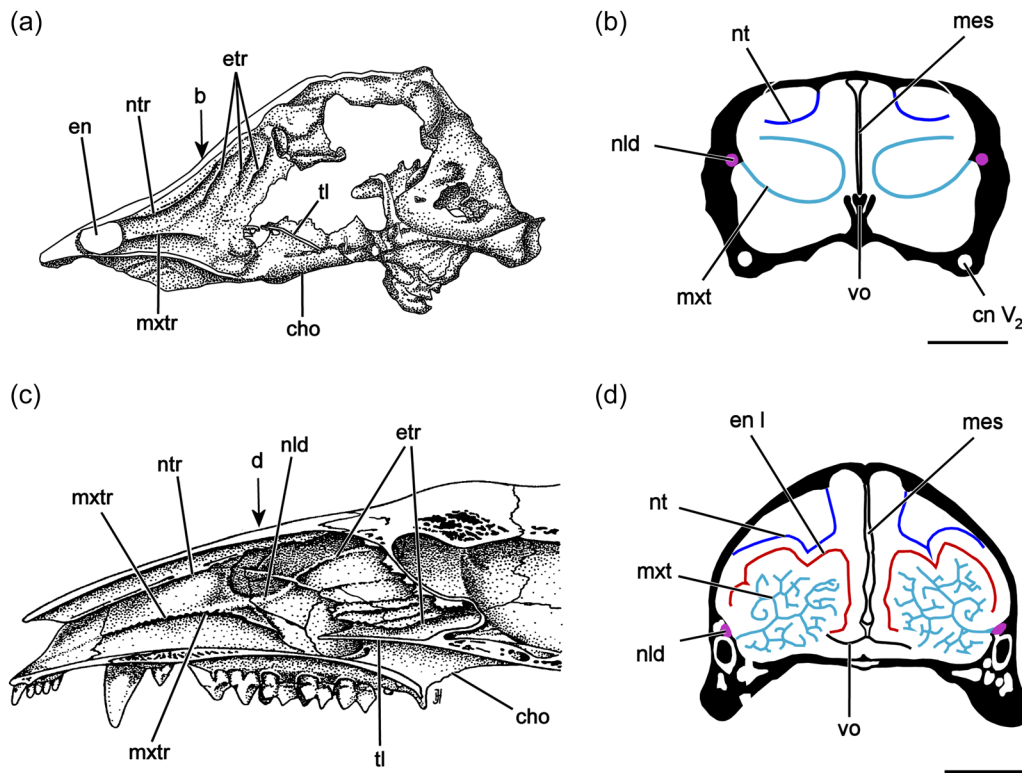


FIGURE 9 Morphology of the turbinate systems of *Kawingasaurus* and modern mammals compared. (a) Sagittal section through the *Kawingasaurus* skull showing the turbinal ridges. (b) Coronal section through the skull at the caudal region of the respiratory part of the nasal cavity. At this level, the close relationship between nasolacrimal duct and mxtr is clearly visible, because the nld is enclosed by bones and the naso- and mxtr are well developed. The position of the section in (b) is marked in (a) by an arrow. The turbinals are coloured. (c) Sagittal section through the skull of the marsupial *Didelphis virginiana* showing the turbinal ridges in the nasal cavity. The turbinal bones were removed. Modified from Hillenius (1994). (d) Coronal section through the respiratory part of the nasal cavity of the marsupial *Didelphis virginiana*, showing the turbinal skeleton and the position of the nasolacrimal ducts. Redrawn from Figure 11 of Macrini (2012), which shows the caudal part of the respiratory portion of the nasal cavity similar to the position in (b). The position of the section is marked in (c) by an arrow. Abbreviations: cho, choana; cn V₂, canal of the maxillary branch of cranial nerve V; en, external naris; en I, endoturbinale I; etr, ethmoturbinal ridge; mes, mesethmoid; mxtr, maxilloturbinal; mxtr, maxilloturbinal ridge; nld, nasolacrimal duct; nt, nasoturbinal; ntr, nasoturbinal ridge; tl, transverse lamina; vo, vomer. Scale bars represent 5 mm.

Ruben et al., 2012; Ruf et al., 2014), but on the other hand similar conchae are also present in other amniote groups. Most authors (e.g., Moore, 1981; Parsons, 1970; Starck, 1979) considered the maxilloturbinal as a phylogenetically ancient feature that is homologous to the reptilian concha and the concha media of birds. de Beer (1937) regarded the maxilloturbinal as homologous to the ancient amniote and synapsid concha ectochoanal. Its absence in basal synapsids was usually explained by their possible cartilaginous nature that precluded fossil preservation (e.g., Kemp, 2006a; Owerkowicz et al., 2015; Parsons, 1967; Ruf et al., 2014). This is supported by the development of the nasal cartilages of modern mammals that, if at all, ossify late during ontogeny (Crompton et al., 2017). Alternatively, Hillenius (1992) interpreted the maxilloturbinal as a neomorphic acquisition of therapsids that originated during the transition to endothermy. However, the discovery of maxilloturbinal ridges in the nasal cavities of *Kawingasaurus* and *Pristerodon* suggests that the maxilloturbinal was in all probability already present at least in the common ancestor of dicynodonts and mammaliaforms, which supports the traditional view of de Beer (1937) and Starck (1979).

The reason that remains of maxilloturbinals in *Kawingasaurus* are preserved but absent in *Pristerodon* might be the different degree of ossification of the turbinals. In *Pristerodon*, the turbinate system was in all probability cartilaginous, which is supported by the fact that the turbinal ridges are less developed than in *Kawingasaurus* or are even absent.

Naso- and ethmoturbinal ridges were already found in pelycosaurs and, therefore, interpreted as plesiomorphic features (Hillenius, 1994). This is supported by the current study with respect to the occurrence of nasoturbinal ridges in *Kawingasaurus* and *Pristerodon* and by the occurrence of several ridges in the olfactory region of *Kawingasaurus* (Figure 9).

The interpretation of the ridges on the ventral sides of the nasals as nasoturbinals is supported by their location dorsally from the maxilloturbinal, which is also the condition in mammals (Figure 9c; Ruf, 2020; Schrenk, 1989; Voit, 1909). Moreover, the well-preserved internal wall of the olfactory region of the nasal cavity (or) of *Kawingasaurus* revealed that the most medial pair of ridges in the olfactory region was almost confluent with the nasoturbinal ridges

(Figures 5b and 8), as is also often found in modern mammals (Ruf, 2020). This supports their interpretation as sites for attachment of the lamina semicircularis. Furthermore, two pairs of ridges were situated on the undersides of the frontals (Figure 5b), which might be an indication that they are probably homologues of the mammalian frontoturbinal ridges 1 and 2.

The mammalian turbinate system is, however, usually not only complex, but also houses numerous highly branched specific turbinas, which complicates considerations of the homology of these structures.

4.3 | Olfaction

The nasal cavities of *Kawingasaurus* and *Pristerodon* were partially divided into respiratory and olfactory portions (Figure 6a,b), which is also known from cynodonts, mammaliaforms and mammals (Crompton et al., 2015, 2017; Ruf et al., 2014). Due to the caudal position of the choana, the respiratory part of the nasal cavity in both taxa was enlarged, but to different degrees (Figures 4, 5 and 6a,b). While the olfactory region of *Kawingasaurus*' nasal cavity occupied almost the same volume as the respiratory part, in *Pristerodon* it had only half the volume of the respiratory region. (Figure 6a,b and Supporting Information: Table S1).

Similar results were obtained when comparing the dimensions of the olfactory bulbs. Accordingly, in *Kawingasaurus* the length of the dorsal surface of the olfactory bulb casts (3.7 mm) corresponds to 18.3% of the length of the dorsal surface of the whole endocranial cast (20.26 mm; Laaß & Kaestner, 2017). In *Pristerodon*, the olfactory bulbs occupy only 5.9 mm of the whole length of the endocast (47.2 mm), which corresponds to 12.5% (Laaß, 2015b). For comparison, the relatively largest olfactory bulbs in nonmammalian synapsids were reported from *Brasilitherium riograndensis*, which occupied 34.5% of the length of the dorsal surface of the whole endocranial cast (Rodrigues et al., 2013).

The absence of sites for attachment of olfactory turbinas in *Pristerodon*, in contrast to the well-developed fronto- and ethmo-turbinal ridges in the olfactory portion of the nasal cavity of *Kawingasaurus*, suggests more elaborate and well-developed olfactory turbinas in *Kawingasaurus* and a greater importance of olfaction in this species. A well-developed sense of smell is a typical sensory adaptation of modern fossorial mammals (Francescoli, 2000).

4.4 | Functions of the respiratory turbinates in *Kawingasaurus*

The maxilloturbinas are a unique feature of mammals. They warm, humidify and filter the inhaled air, cool the exhaled air (Hillenius, 1992, 1994; Schmidt-Nielsen, 1981) and contribute to 'selective brain cooling' (Baker, 1982; Elkhawad, 1992; Jessen, 2001; Valkenburgh et al., 2004). The question arises whether the maxilloturbinas of dicynodonts had similar functions.

As shown in previous studies (e.g., Cox, 1972; Laaß, 2015a; Laaß & Kaestner, 2017; Macungo et al., 2022), *Kawingasaurus* inhabited a subterranean habitat. *Pristerodon* was likely a terrestrial dicynodont, which is supported by the more erect body posture (Ray, 2006; Ray & Chinsamy, 2003), and its specific sensory adaptations to life above ground (Angielczyk & Schmitz, 2014; Laaß, 2016).

Burrowers are much more affected by dust than terrestrial species. Therefore, modern subterranean species possess filtering mechanisms in the nose to protect the lungs against particles arising from their scratching or head digging in the substrate (Hildebrand et al., 2003). The nasal openings of burrowers are usually narrow and can often be closed by nose flaps (Hildebrand et al., 2003). Additionally, they are often well moistened to fix dust particles before they can reach the upper air passage or the lungs (Hildebrand et al., 2003). Respiratory turbinates also contribute filtering dust, bacteria and other particles from the inhaled air by capturing them with the humid epithelium, which is moistened by fluid from the nasolacrimal duct (Negus, 1956, 1958; Walker & Wells, 1961). Several studies revealed that *Kawingasaurus* not only used its strong forelimbs for digging, but also its head (Cox, 1972; Kammerer, 2021; Laaß, 2015a; Laaß & Kaestner, 2017; Macungo et al., 2022). This suggests that filtering the inhaled air was more important in the fossorial habitat than above ground, which might be one explanation for the well-pronounced maxilloturbinas in *Kawingasaurus*.

Furthermore, maxilloturbinas are also interpreted as an adaptation to high respiratory rates, because they significantly reduce respiratory water loss (Hillenius, 1992, 1994; Ruben, 1995, 1996). High respiratory rates may be correlated with hypoxia (Huey & Ward, 2005; Retallack et al., 2003), with endothermy (Hillenius, 1992, 1994; Hillenius & Ruben, 2004), or with both.

As *Kawingasaurus* inhabited a fossorial habitat, it was exposed to the specific atmosphere of a burrow. Studies of gas composition in burrows of modern subterranean mammals revealed low oxygen concentrations, between 14% and 18.4%, and high carbon-dioxide concentrations, between 0.22% and 6%, or even more (e.g., Boggs et al., 1984; Darden, 1972; Kuhnen, 1986; McNab, 1966). Extreme hypoxic and hypercapnic conditions were also recorded in burrows of the mole rat *Spalax ehrenbergi* (Arieli, 1979; Shams et al., 2005). In contrast, other studies found atmospheric conditions in burrows that did not deviate significantly from above-ground conditions (Burda et al., 2007 and references therein). However, gas compositions in burrows may differ considerably, depending on soil type, porosity, ventilation, burrow architecture, seasonal effects, temperature, humidity, rain and the activity level of the animal (Arieli, 1979; Burda et al., 2007; Shams et al., 2005; Weissberger et al., 2009).

A common strategy of burrowers to compensate for low oxygen concentrations is hyperventilation (e.g., Arieli & Ar, 1979; Barros et al., 2004; Boggs et al., 1984; Crompton et al., 2017; Pichon et al., 2015; Tomasco et al., 2010). As pointed out by Crompton et al. (2017), hypoxia-induced hyperventilation increases the risk of heat- and water loss from the respiratory tract. Consequently, the maxilloturbinas of *Kawingasaurus* were likely to have been an adaptation to low-oxygen conditions in the fossorial habitat, an

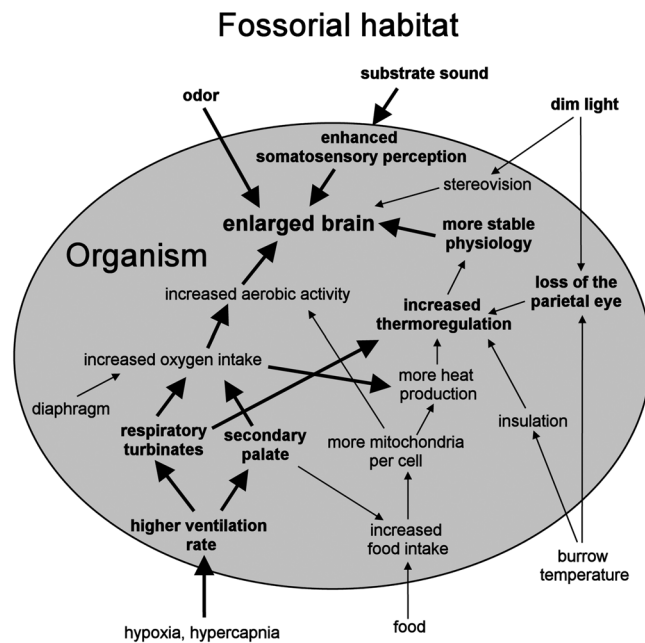


FIGURE 10 The potential influence of the fossorial habitat on the evolution of structures and functions responsible for, or affected by, endothermic temperature physiology of an animal. Illustration inspired by Figure 3 of Kemp (2006a).

important evolutionary innovation towards a continuous, rhythmic respiration and a more efficient respiratory system (Graham et al., 1997; Retallack et al., 2003; see also Figure 10). This would support the hypothesis of Retallack et al. (2003), according to which the respiratory system of burrowing therapsids was preadapted to hypoxic and hypercapnic conditions, resulting in a selective advantage to survive the PTME. However, cistecephalids did not survive the PTME.

Did the maxilloturbinates of *Kawingasaurus* only prevent hypoxia-induced water loss, or were they also functionally correlated with endothermy? A first argument for a thermoregulatory function is the ossification of the turbinates in *Kawingasaurus*, which enhanced the efficiency of conserving heat and water at rest, as well as the ability to dissipate heat during thermal stress (Crompton et al., 2017). Furthermore, the surface area of the turbinates in *Kawingasaurus* falls in the mammalian range (Figure 6e) and, therefore, was large enough to play a major role for thermoregulation and endothermy (see Owerkowicz et al., 2015). Otherwise, the relatively constant low temperature in burrows suggests that the turbinates in *Kawingasaurus* functioned rather in heat- and water conservation than in decreasing body temperature. Decreasing body temperature, including selective brain cooling, was probably only important during phases of energy-expensive activities such as digging.

A further, indirect argument for thermoregulation in the nasal cavity is the absence of the parietal foramen in *Kawingasaurus*, which suggests an increased independency from external heat sources and the presence of alternative mechanisms for thermoregulation under low-light conditions (Figure 10; Benoit et al., 2015, 2016). This

function was most likely taken over by the respiratory turbinates. Other possible sites for thermoregulation and water conservation along the respiratory tract are the avian tracheae, but due to the short neck, similar adaptations are unlikely for *Kawingasaurus*.

A *Kawingasaurus* was one of the smallest dicynodonts. Miniaturization favoured the origin of thermoregulatory mechanisms to compensate the higher heat loss of small animals, which was especially important for night-active species (e.g., Hopson, 1991; Kemp, 2005; McNab, 1978). Otherwise, it is also known that regulation of body temperature and insulation of the body are less important for burrowers than for night-active, nocturnal species, because burrows usually provide a stable microclimate with almost constant temperature (Burda et al., 2007). Studies of modern subterranean mammals also revealed lower BMRs and body temperatures, and a higher thermal conductance than in ground-dwelling species (Barros et al., 2001, 2004; Sedláček, 2007 and references therein). The reasons for this phenomenon are subject of debate. According to Sedláček (2007), three hypotheses exist: The first is the 'thermal stress hypothesis', according to which a reduced BMR minimizes the risk of overheating in burrows (McNab, 1966). The second is the 'respiratory stress hypothesis' that explains the lower BMR with the hypoxic and hypercapnic conditions in burrows (Arieli, 1979; Darden, 1972). The third is the 'cost-of-burrowing hypothesis'. It proposes that a lower BMR compensates for the enormous energetic demands of subterranean foraging and represents an energy saving mechanism (Vleck, 1979).

Finally, the most convincing argument for a thermoregulatory function of the respiratory turbinates and higher metabolic rates in *Kawingasaurus* is the enormous size of its brain compared to other nonmammalian synsids (e.g., Laaß & Kaestner, 2017). Several studies showed that encephalization is necessarily accompanied by elevated metabolic rates, because of the high energetic demands of neuronal tissues (e.g., Isler & van Schaik, 2006; Mink et al., 1981; Rowe et al., 2011). As shown by Laaß and Kaestner (2017), the Encephalization Quotient (EQ = 0.51) of *Kawingasaurus* is two to three times higher than that of other therapsids and falls in the range of the quotients of mammaliaforms and Mesozoic mammals. No ectotherm exists with a similar EQ. It is therefore unlikely that *Kawingasaurus*' brain could function without a stable physiology, a constant body temperature and thermoregulation, which was in all probability supported by the respiratory turbinates (Figure 10). The elaboration of *Kawingasaurus*' brain, however, can be well explained with the sensory specializations for underground life, such as a well-developed tactile sense, olfaction and probably stereovision (Laaß & Kaestner, 2017).

A further point to discuss concerns possible functional differences of the respiratory turbinates between burrowing and terrestrial species. As already mentioned, the maxilloturbinal ridges in *Kawingasaurus* were much stronger than in *Pristerodon*. For probably the same reason, the slightly ossified turbinates were only preserved in *Kawingasaurus*, but absent in *Pristerodon* due to their cartilaginous nature.

A functional interpretation of the weak respiratory turbinal ridges in *Pristerodon* is difficult. However, *Pristerodon* was most likely

an animal that lived above ground (Laaß, 2016), which is supported by the anatomy and posture of the digits (Ray, 2006; Ray & Chinsamy, 2003), and sensory adaptations such as tympanic hearing in the low-frequency range of the terrestrial habitat (Laaß, 2016) and photopic vision (Angielczyk & Schmitz, 2014). As a terrestrial species, *Pristerodon* was likely more frequently exposed to temperature variations than *Kawingasaurus*, which might be an reason for the importance of thermoregulation. Interestingly, Kemp (2006a, 2006b) proposed that therapsids evolved mechanisms of thermoregulation and a higher BMR in the Mid-Permian that resulted in a higher tolerance to temperature variations and enabled them to colonize a wider range of climate zones than their ectothermic ancestors, the pelycosaurids. However, a parietal foramen was still present in *Pristerodon*, which suggests that it probably still relied on the thermoregulatory mechanisms of ectotherms. To what extent the more erect posture was an indication for a higher activity level and endothermy is uncertain. Furthermore, there is no sign for brain expansion ($EQ = 0.18$; Laaß, 2015b). On the other hand, *Pristerodon* possessed a secondary palate, which is an important precondition for higher ventilation rates.

In summary, it can be concluded that the respiratory turbinates in *Kawingasaurus* were most likely an adaptation to higher respiration rates induced both by hypoxia and the increased oxygen demands of the large brain and of endothermy. As discussed above, several lines of evidence indicate that the respiratory turbinates functioned in thermoregulation, reduction of respiratory water loss and air filtering. In the terrestrial species *Pristerodon*, the role of the maxilloturbinates remains less clear.

4.5 | Implications for the metabolism of dicynodonts

What does the anatomy of the nasal cavities of *Kawingasaurus* and *Pristerodon* tell us about the metabolism of dicynodonts?

Endothermy probably evolved independently in mammaliaforms and dicynodonts (see Section 1.4), namely in Triassic Lystrosauridae and Kannemeyeriiformes (e.g., Laaß et al., 2010; Olivier et al., 2017; Rey et al., 2017; Whitney & Sidor, 2020). Our study supports this hypothesis and reveals that endothermy evolved not only in Triassic dicynodonts, but also in Permian cistecephalids. Interestingly, lystrosaurids and cistecephalids were burrowers and lived under similar environmental conditions, which probably led to similar adaptations to underground life and convergent evolution of endothermy in both dicynodont clades.

However, it cannot be excluded that endothermy already evolved in a first pulse shortly after the Synapsida-Sauropsida split (Knaus et al., 2021) or even in early Amniota (Grigg et al., 2022), probably triggered by temperature fluctuations during the late Palaeozoic ice age (e.g., Isbell et al., 2012; Montañez & Poulsen, 2013). If this is correct, the differences in the nasal anatomy of *Pristerodon* and *Kawingasaurus* can be explained by different metabolic rates in these species. If so, cistecephalids and

lystrosaurids underwent a second phase in the evolution of endothermy, accompanied by adaptations to life underground of the visual, olfactory and respiratory systems, and the elaboration of the brain, which in many respects is comparable to the Nocturnal Bottleneck in early mammalian evolution.

In contrast, Araújo et al. (2022) argued that the semicircular canal morphology of the inner ears of dicynodonts including *Kawingasaurus* only suggest a low probability for endothermy. However, the functional morphology of the digits of dicynodonts revealed that burrowing was, to various degrees, part of their behavioural regime (Kümmell, 2009; Ray, 2006; Ray & Chinsamy, 2003) and some species such as *Kawingasaurus* were even fossorial (Cox, 1972; Laaß, 2015a; Laaß & Kaestner, 2017). Studies of the semicircular-canal morphology of modern mammals revealed that the sense of balance is less important for burrowers, due to the restricted head rotations and the decreased requirements for motor coordination underground. According to the 'canonical model' of semicircular canal orientation, the plane of each semicircular canal is ideally orthogonal to the planes of the other two ipsilateral canals, so that all three canals of the inner ear intersect at 90° angles (Berlin et al., 2013). Remarkably, the greatest deviations from this ideal condition were recognized among fossorial mammals such as *Notoryctes*, *Chrysochloris*, *Talpa*, and *Heterocephalus* (Berlin et al., 2013), and aquatic mammals such as *Trichechus* and *Tursiops* (Ekdale, 2013). Consequently, this phenomenon evolved independently in different mammalian clades, which were all characterized by restricted or slow head rotations. Such behaviour requires less sensitivity of the semicircular canals (Berlin et al., 2013), which might be an indication of a degenerated sense of balance.

Interestingly, the semicircular-canal morphology of *Kawingasaurus* also shows large deviations from the 'ideal' condition. For example, the angle between the anterior and the lateral semicircular canal is only 53° (Laaß, 2015a), which is near the lowest value known from placental mammals, in which the angle ranges between 52.2° and 122° (Berlin et al., 2013; Ekdale, 2013). Taking this into consideration, the question arises whether the approach of Araújo et al. (2022) can be applied to *Kawingasaurus* and other burrowing dicynodonts to infer their metabolic status.

Furthermore, Araújo et al. (2022) mentioned that their approach is less suited for predicting the metabolic status of a single species than the metabolism of a clade. In many respects, *Kawingasaurus* reveals an unusual anatomy among dicynodonts (e.g., brain size, ossification of the braincase, loss of the parietal foramen, vestibule inflation), which suggests that it is an 'outlier' of the group.

5 | SUMMARY AND CONCLUSIONS

This study of the nasal cavities of *Kawingasaurus* and *Pristerodon* provided first evidence of maxilloturbinal ridges in dicynodonts, as well as the remains of a well-developed turbinate system that strongly resembles the mammalian condition (Figure 9). It consists of

a pair of naso- and maxilloturbinals in the respiratory part of the nasal cavity and four pairs of olfactory turbinals. The olfactory turbinals we tentatively interpret as the sites of attachment of the lamina semicircularis, of the frontoturbinals 1 and 2, and of ethmoturbinals.

The presence of maxilloturbinals supports a convergent origin of endothermy in dicynodonts. As possible explanations for the evolution of endothermy in *Kawingasaurus*, the influence of the fossorial habitat was discussed. We concluded that hypoxic conditions underground induced higher ventilation rates, which likely favoured a rhythmic respiration and a more efficient respiratory system. Additionally, the maxilloturbinals most likely served for thermoregulation and water conservation, and were in all probability functionally correlated with higher metabolic rates (Figure 10). This is supported by the absence of the parietal foramen, the presence of a secondary palate and by the enormous size of *Kawingasaurus*' brain compared with those of other nonmammalian synapsids. The elaboration of discrete regions of the brain resulted from a sensory shift to somatosensation, olfaction and stereovision as an adaptation to the fossorial habitat (Figure 10). The EQ, which falls into the range of Mesozoic endothermic mammals, suggests that *Kawingasaurus*' brain could only function in concert with a stable physiology and higher metabolic rates to satisfy the high energetic demands of the neuronal tissues.

AUTHOR CONTRIBUTIONS

Michael Laaß: Conceptualization; data curation (equal); formal analysis; investigation; methodology; software; validation; visualization; writing original draft; writing—review and editing. **Anders Kaestner:** neutron tomographic experiment; data processing (equal); review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available on request from the corresponding author. The data are not publicly available due to privacy or ethical restrictions. Additional data (Supporting Information: Table S1) is provided as an online supplement to this article.

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