Comparative Anatomy and Systematic Implications of the Turbinal Skeleton in Lagomorpha (Mammalia)

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ABSTRACT
In order to elucidate the systematic relevance of the turbinal skeleton in Lagomorpha the ethmoidal regions of 6 ochotonid, 21 leporid, and 2 outgroup species (Sciurus vulgaris, Tupaia sp.) species were investigated by high-resolution computed tomography (μCT). Number and shape of turbinals correspond to major clades and to several genera. All Lagomorpha under study have a deeply excavated nasoturbinal that is continuous with the lamina semicircularis; a feature likely to be an autapomorphy of lagomorphs. In particular, the olfactory turbinals (frontoturbinals, ethmoturbinals, and interturbinals) provide new systematic information. The plesiomorphic lagomorph pattern comprises two frontoturbinals, three ethmoturbinals, and one interturbinal between the two frontoturbinals. Ochotonidae are derived from the lagomorph groundplan by loss of ethmoturbinal III; an interturbinal between the two frontoturbinals is an autapomorphy of Leporidae. Pronolagus is apomorphic in having a very slender first ethmoturbinal, but shows a puzzling pattern in decreasing the number of turbinals. Pronolagus rupestris and Romerolagus diazi have independently reduced their turbinals to just two fronto- and two ethmoturbinals, which is the lowest number among the sampled lagomorphs. In contrast, the more derived leporid genera under study (Oryctolagus, Caprolagus, Sylvilagus, and Lepus) show a tendency to increase the number of turbinals, either by developing an ethmoturbinal IV (Caprolagus hispidus, Lepus arcticus) or by additional interturbinals. Intraspecific variation was investigated in Ochotona alpina, Oryctolagus cuniculus, and Lepus europaeus and is restricted to additional interturbinals in the frontoturbinal recess of the two leporids. Anat Rec, 297:2031–2046, 2014. © 2014 Wiley Periodicals, Inc.

Key words: ethmoidal region; nasal cavity; turbinals; Lagomorpha; Mammalia; comparative anatomy; systematics

Anatomical Abbreviations: et I-IV = ethmoturbinal I-IV; etr = ethmoturbinal recess; ft 1-2 = frontoturbinal 1-2; fr = frontal; fr = frontoturbinal recess; it = interturbinal; lh = lamina horizontalis; ls = lamina semicircularis; ma = maxillary; ma = maxillary sinus; mt = maxilloturbinal; na = nasal; ns = nasal septum; nt = nasoturbinal; pa = palatine; pm = premaxillary.
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The skeleton of the nasal conchae (turbinals, turbinals) is a complex system that can be used for systematic and functional morphological purposes in mammals. Detailed descriptions of internal nasal structures in prenatal and early postnatal stages based on histological serial sections exist for a wide range of mammalian orders and species (e.g., Voit, 1909; Reinbach, 1952a, 1952b; Spatz, 1964; Maier, 1980; Schrenk, 1989; Mess, 1997; Frahnert, 1998; Goebbel, 1998; Ruf, 2004). Although these data form the fundamental background for understanding adult structures and elucidating homologies (Maier, 1993), they include ontogenetic stages in which the nasal structures are not fully developed (and ossified). Systematic interpretations based on prenatal stages are difficult for species when the adult turbinal morphology is unknown. In contrast, adult crania are poorly understood because of the technical limitations of investigating internal cranial structures by histology. Historically, to study the adult skeleton, specimens had to be destroyed. The work of Paulli (1900a, 1900b, 1900c) is one of the rare cases when fully ossified specimens were examined. In his study, he presents about 100 species from several orders, based on juvenile and adult specimens which were investigated with macroscopic techniques. In recent years, nondestructive imaging techniques, such as high-resolution computed tomography (μCT) have been established for investigating the mammalian nasal cavity (e.g., Clifford and Wittmer, 2004; Van Valkenburgh et al. 2004; Rowe et al. 2005; Van Valkenburgh et al. 2011; Macrini, 2012). However, comprehensive comparative studies of the turbinal skeleton of adult mammals to elucidate systematic relationships are still rare.

This is particularly the case in the order Lagomorpha (Fig. 1), which comprises the two families Leporidae (hares, rabbits; 11 genera, 61 species) and Ochotonidae (pikas; 1 genus, 30 species) (Hoffmann and Smith, 2005). While the sister–group relationship of Ochotonidae and Leporidae is clearly supported, the internal systematics of the former and several basal genera of the latter (Protroropus, Poelagus, Nesolagus, Romerolagus, Bunolagus) as well as of the problematic polytypic genus Lepus are still unresolved (e.g., Dice, 1929; Hamers-Casterman et al. 1979; Corbet, 1983; Halanych et al., 1999; Stoner et al., 2003; Matthee et al., 2004; Robinson and Matthee, 2005; Wible, 2007; Palacios et al., 2008). For example, Halanych and Robinson (1999) postulate a sister–group relationship of Romerolagus and Bunolagus based on cytochrome b and 12S rDNS analyses, which is difficult to bring in line with the recent geographic distribution of these species (Romerolagus = Mexico, Bunolagus = South Africa). Romerolagus, Bunolagus, and Pronolagus were classically assigned as palaeeolagine-like, of which only the latter is known by fossil remains from the Plio-Pleistocene of South Africa (López Martínez, 2008). The DNA supermatrix approach by Robinson and Matthee (2005) reveals a sister–group relationship between Romerolagus, as an ancient lineage (see also Matthee et al., 2004), and a clade comprising Oryctolagus, Caprolagus, Bunolagus, Pentalagus, Brachylagus, Sylvilagus, and Lepus; Poelagus, Pronolagus, and Nesolagus form the sister-clade to both of these. The sister–group relationship of the African genus Pronolagus and the Asian genus Nesolagus also needs to be discussed against the background of paleobiogeography given a Chinese origin of the latter (Matthee et al., 2004; Jin et al., 2010). Robinson and Matthee (2005) review several different phylogenies based on morphological characters. It appears that several homoplastic features occur especially in leporids, whose genera evolved most probably within several short radiation events (Corbet, 1983; Dawson, 1958; Hibbard, 1963; Halanych and Robinson, 1999; Robinson and Matthee, 2005; López Martínez, 2008).

Cranial morphology is one major key to elucidate systematic problems. To date the focus of cranial investigations in lagomorphs has been largely restricted to external skull anatomy, dentition, and topography of cranial arteries (e.g., DuBrul, 1959; Bugge, 1974; López Martínez, 1985; Averyanov, 1999; Martin, 2004; Wible, 2007; Palacios et al., 2008; Koenigswald et al., 2010). Although a considerable number of publications on the nasal cavity in lagomorphs exist, these works have been restricted to a limited number of species: Ochotona rufescens and Ochotona roylei (prenatal to postnatal: Insom et al., 1990), Ochotona sp. (prenatal: Frahnert, 1998), Oryctolagus cuniculus (prenatal: Voit, 1909; de Beer and Woodger, 1930; Frick and Heckmann, 1955; adult: Paulli, 1900c), Lepus europaeus (adult: Paulli, 1900c; Caboni-Racynska, 1964); Lepus capensis (prenatal: Eloff, 1950).

Furthermore, to date, the use of two different terminologies for the turbinal structures of the lateral and
posterior part of the ethmoidal region have hindered comparative and systematic analyses of these features across a broader array of taxa (see Rowe et al., 2005; Maier and Ruf, 2014). Most investigations are based on the terminology established by Paulli (1900a, 1900b, 1900c): these are the endo- and ectoturbinals. However, the topography, ontogeny, and homology of these structures have not been sufficiently considered. As these two types of turbinals are simply numbered, especially the ectoturbinals allow no homology among different species, because they cover two different types of turbinals: frontal turbinals and interturbinals. Furthermore, the crista or lamina semicircularis, which is not a turbinal at all given its ontogenetic origin, represents the first endoturbinal according to Paulli (1900a, 1900b, 1900c). The terminology used in the present study was predominantly provided by Voit (1909) and others (e.g., Reinbach, 1952a, 1952b). It identifies structures based on their ontogeny and thus allows distinct homologies as well as phylogenetic examination. The frontoturbinals belong to the frontoturbinal recess of the pars lateralis of the ethmoid region; the ethmoturbinals are located in the pars posterior or ethmoturbinal recess. In both recesses interturbinals, which have a less medial extension, can occur. The lamina semicircularis is the medial wall of the maxillary sinus and frontoturbinal recess and thus not a turbinal sensu strictu. The posterior portion of the nasoturbinal, the fronto- and ethmoturbinals as well as dorsal parts of the lamina semicircularis are covered by olfactory epithelium, whereas the anterior turbinals (anterior part of nasoturbinal, maxilloturbinal, and atrioturbinal) are covered by respiratory epithelium for moistening and warming inspired air (Allison and Turner Warwick, 1949; Le Gros Clark, 1951; Ruf, 2004).

Here for the first time a comprehensive comparative morphological analysis of the turbinal skeleton in Lagomorpha covering most genera based on μCT of adult specimens is provided and discussed against the background of recent phylogenies (e.g., Robinson and Matthee, 2005).

MATERIALS AND METHODS

Macerated skulls of adult Ochotonidae (6 species) and Leporidae (21 species) were scanned with the μCT scanner von tome x s (GE phoenix x-ray), which is housed in the Steinnmann-Institut für Geologie, Mineralogie und Paläontologie at Universität Bonn, Germany. Selected species of Rodentia and Scandentia, i.e., Sciurus vulgaris and Tupaia sp., were used for outgroup comparison in addition to data on further species from literature. To investigate intraspecific variation in the turbinal skeleton, five specimens of Ochotona alpina, eight specimens of Oryctolagus cuniculus, and eleven specimens of Lepus europaeus were included in the study. Table 1 provides a detailed taxa list and the voxel size (resolution) of μCT scans.

The species were taxonomically classified according to Wilson and Reeder (2005), thus Lepus groenlandicus is now L. arcticus. Pronolagus rupestris specimen 1037 was assigned to P. cf. saundersiae due to the place of collection, which was the Cape of Good Hope (see Skinner and Smithers, 1990).

Based on the μCT data, virtual 3D models of the turbinal skeleton were rendered with the software Avizo 6.1-8.1 (Visualization Sciences Group, FEI, Bordeaux, France) using the manual segmentation tool. The anatomical terminology (see list of anatomical abbreviations below) was used according to Voit (1909) and Reinbach (1952a, 1952b).

To elucidate the systematic potential of the turbinal skeleton in lagomorphs, major characters such as number, loss or addition of turbinals as well as morphological features of the turbinals, and the lamina semicircularis are mapped onto a phylogeny by Robinson and Matthee (2005), that is based on DNA sequences derived from five nuclear introns and two mitochondrial genes. However, as most of the investigated species of this study are not part of the phylogeny of Robinson and Matthee (2005), a simplified cladogram restricted to the investigated genera is used.

RESULTS

Maxilloturbinal

The maxilloturbinal shows a very similar morphology in all investigated lagomorphs. It extends laterally to the lamina of the nasoturbinal and posteriorly into the pars posterior of the ethmoidal region. The maxilloturbinal is very tall in cross section, and shows a complex pattern of several longitudinal medial ridges (Figs. 2A, 4–8). In Caprolagus and Lepus, the maxilloturbinal has a tremendous ventral extension and obviously increased surface area (Figs. 7, 8). The complex pattern of the maxilloturbinal is also present in Sciurus and Tupaia, though it is a more slender structure in the latter (Fig. 9).

Nasoturbinal and Lamina Semicircularis

In all examined lagomorphs the nasoturbinal and the lamina semicircularis are partially in contact or even fused and in several species the suture is mostly obliterated (Figs. 5, 7). Thus, in several species, the posterior limitation of the nasoturbinal and its supporting ridge on the nasal bone had to be estimated. Furthermore, the proximal part of the nasoturbinal that most probably represents the nasal ridge, as well as the lamina semicircularis, are deeply excavated and form a recess that opens into the ethmoidal recess (Figs. 2A, 4–8). In Sciurus the nasoturbinal is also a tall lamella but no excavation is present and it is separated from the lamina semicircularis by a distinct gap. The same pattern holds true for Tupaia though the nasoturbinal is a very slender lamina and shifted ventrally (Fig. 9).

The lamina semicircularis is a pronounced structure in lagomorphs. It is sickle shaped and its posterior border is laterally scrolled. This is especially the case in Leporidae rather than in Ochotonidae. In the former the dorsal lamina of the lamina semicircularis is scrolled posterior to the hiatus semilunaris (entrance to the maxillary sinus) and the ventral lamina forms a distinctly scrolled processus uncinatus inside the maxillary sinus (Figs. 2B, 3–8). In ochotonids the dorsal lamina is straight and the processus uncinatus of the ventral lamina is relatively short (Figs. 2C, 4A). The lamina semicircularis of the outgroup taxa under study also has a distinctly scrolled dorsal lamina; the straight processus uncinatus inside the maxillary sinus is much more pronounced in Tupaia than in Sciurus, where it is quite short (Fig. 9).
Frontoturbinal Recess

All investigated species of Ochotona have two frontoturbinals inside the frontoturbinal recess (Figs. 2C, 4A). These turbinals are quite slender lamellae and frontoturbinal 1 is a double scroll, whereas frontoturbinal 2 forms a single ventral scroll (Fig. 2C).

In contrast, the frontoturbinal recess in Leporidae houses three turbinals in most species: two frontoturbinals and one interturbinal (see “Discussion”) in between (Figs. 3, 4C, 6–8); generally these three turbinals are double scrolls. However, there are certain exceptions from this pattern among the leporids. In all examined species of Pronolagus and in Romerolagus, only the two frontoturbinals are present and the interturbinal is extremely reduced (Pronolagus cf. saundersiae) or missing (Figs. 4E, 5).

Similarly, in one of the eight investigated individuals of...
Oryctolagus, the interturbinal between the two frontoturbinals is lacking and another specimen shows only a very small interturbinal.

Additional interturbinals occur in Oryctolagus, Sylvilagus, and Lepus and are often simple scrolls or straight lamellae. In one specimen of Oryctolagus, an additional small interturbinal is present between frontoturbinal 2 and ethmoturbinal I (Fig. 7A). Sylvilagus graysoni has a very small and short second interturbinal between frontoturbinal 2 and ethmoturbinal I and Sylvilagus transitionalis has a similar interturbinal between the lamina semicircularis and the first frontoturbinal (Fig. 6). In Sylvilagus floridanus the interturbinal between the two frontoturbinals is reduced to a small and straight lamella.

The genus Lepus shows a puzzling pattern with additional small interturbinals in the frontoturbinal recess. Lepus arcticus has a second small interturbinal between frontoturbinal 1 and the larger interturbinal (Fig. 7E). Lepus timidus, Lepus tolai, Lepus sinensis, and Lepus townsendii have an additional smaller interturbinal...
Fig. 3. µCT cross sections through the pars posterior of the ethmoidal region of selected leporids. A *Sylvilagus floridanus* A592107, B *Lepus americanus* A592295. Left turbinals are highlighted by the color code used in this study. Not to scale. Abbreviations: see text.
between frontoturbinal 2 and the lamina horizontalis, which supports the ethmoturbinals (Fig. 8C, E). *Lepus americanus* shows a small third interturbinal between the lamina semicircularis and the first frontoturbinal (Fig. 3B). In *Lepus europaeus* additional interturbinals occur in seven of the 11 examined individuals. In six specimens, a small interturbinal is present between frontoturbinal 2 and ethmoturbinal 1 (Fig. 8A) that ends on the latter in five of them. In two individuals, a small straight interturbinal is also present between the lamina semicircularis and frontoturbinal 1. Another specimen has one additional small and straight interturbinal between the lamina semicircularis and frontoturbinal 1. The size of the interturbinal between the two frontoturbinals varies also in the examined specimens from short and straight to very pronounced and double scrolled. *Sciurus* and *Tupaia* both have only two distinct frontoturbinals that are double scrolls (Fig. 9).

**Ethmoturbinal Recess**

In all lagomorphs under study the first ethmoturbinal has only one proximal ridge and is divided anteriorly
into two lamellae. The anterior lamella extends into the pars anterior of the nasal cavity (Figs. 4–8).

The ethmoturbinal recess of all investigated species of *Ochotona* houses two ethmoturbinals and one interturbinal in between (Figs. 2C, 4A). The anterior lamella of ethmoturbinal I points anterodorsally (Fig. 4B). Ethmoturbinal II is a tall structure with a large laterally scrolled dorsal lamella and a very small ventral one; thus the basal ridge of ethmoturbinal II appears to be shifted ventrally (Fig. 4B). The interturbinal is smaller than both ethmoturbinals and is dorsally scrolled (Fig. 3B).

The leporid genus *Pronolagus* shows a variable pattern in the ethmoturbinal recess. *Pronolagus rupestris* has only two ethmoturbinals, *Pronolagus randensis* has three ethmoturbinals, and *Pronolagus cf. saundersiae* has three ethmoturbinals and an interturbinal between the first and second ethmoturbinal (Fig. 5). Ethmoturbinal I in the examined species of *Pronolagus* is remarkably slender with a short posterior lamella (Fig. 5B, D, F). Both parts are separated by a gap that continues almost to the posterior end. Ethmoturbinal II is quite tall and dorsally scrolled, whereas ethmoturbinal III is...
very small (Fig. 5). *Romerolagus* is the second leporid genus with a reduced number of ethmoturbinals. Only ethmoturbinals I and II are present, and an interturbinal is missing (Fig. 4E, F). Ethmoturbinal II is a double scroll.

Almost all other investigated leporid species share a similar and larger number of turbinals in the ethmoidal recess, that is also characteristic of the outgroup taxa under study: three ethmoturbinals and one interturbinal between ethmoturbinal I and II (Figs. 3B, 6–9).

However, there is some variation. Both *Caprolagus* and *Lepus arcticus* have a fourth ethmoturbinal, that is very slim and small in the former but a distinct structure in the latter (Fig. 7C–F). In *Poelagus*, ethmoturbinals II and III and the interturbinal in the ethmoturbinal recess are remarkably slender (Fig. 4B, C). In two individuals of *Oryctolagus* the interturbinal in the ethmoidal recess is remarkably reduced and in *Sylvilagus floridanus*, the interturbinal between ethmoturbinals I and II is lacking (Fig. 3A). *Sylvilagus graysoni* as well as *Lepus oiiostolus* have a second small and short interturbinal between the common interturbinal and ethmoturbinal II (Figs. 6C, 8C).

Fig. 6. Virtual 3D models of the turbinal skeleton of the leporid *Sylvilagus*. A, B *Sylvilagus nuttalli* A594342; C, D *Sylvilagus graysoni* A581790, maxilloturbinal not preserved; E, F *Sylvilagus transitionalis* A590905. A, C, E lateral view; B, D, F medial view. Scale bars equal 5 mm. Abbreviations: see text.
DISCUSSION

It is evident that certain patterns of the turbinal skeleton in the investigated lagomorphs correspond to certain clades and genera (Table 2, Fig. 10). First, all lagomorphs have a highly complex maxilloturbinal situated laterally to the nasoturbinal. As this pattern is also present in Sciurus and Tupaia it may represent a plesiomorphic character for Lagomorpha (see Frahnert, 1998). From the early ontogeny of Oryctolagus and Ochotona it is known that the anlage of the maxilloturbinal is a simple, tall infold of the lower paries nasi with an almost smooth medial surface that has small ridges (cartilage and soft tissue) that foreshadow the complex surface of later ontogenetic stages (Voit, 1909; Frahnert, 1998). In many rodents (e.g., muroids) the maxilloturbinal remains a simple infold throughout ontogeny, but in some, such as Sciurus and Castor, it shows a similar, more complex adult morphology as in lagomorphs (Frahnert, 1998; Ruf, 2004). Thus, the polarization of
the complexity of the maxilloturbinal among Glires is still controversial.

Second, a continuous nasoturbinal and lamina semicircularis including the cavity inside the former is not known from the outgroup members among Euarchontoglires and therefore represents an autapomorphic feature of Lagomorpha. Concerning the morphology of the ventral lamina of the lamina semicircularis, the ochotonid species are similar to the outgroup taxa, whereas all leporids under study have an enlarged and scrolled ventral lamina, which is thus an autapomorphic feature of Leporidae.

The frontoturbinal and ethmoturbinal recesses house a variable number of olfactory turbinals in the species under study. However, a general pattern is observed in many small mammals including Sciurus and many other rodents as well as Tupai a (Pauli, 1900a, 1900b, 1900c; Frahnert, 1998; Ruf, 2004; pers. observ.): two frontoturbinals, three ethmoturbinals and one interturbinal between ethmoturbinal I and II. Thus, this pattern, which is present in many of the investigated species, is supposed to be plesiomorphic for the lago- morph groundplan (see also Maier and Ruf, 2014).
All ochotonid species under study show the plesiomorphic pattern in the frontoturbinal recess as already described in perinatal stages (Insom et al. 1990; Frahnert, 1998). The ethmoturbinal recess is derived in lacking the third ethmoturbinal. The reduced number of ethmoturbinals might be related to the small size of ochotonids although similar sized members of the outgroup show the plesiomorphic pattern. A reduced number of turbinals is also present in small-sized as well as in larger species of leporids (see below). However, the reduction in number of turbinals in Ochotonidae certainly evolved independently from leporid species with reduced ethmoturbinals. Neither intrageneric nor intraspecific (Ochotona alpina) variation could be observed in the number of turbinals.

In contrast, almost all leporids under study have an additional turbinal between the two frontoturbinals, which is an autapomorphic feature of Leporidae. Evidence from early ontogeny of the frontoturbinal recess and its associated structures clearly indicate that this turbinal is not a true frontoturbinal but an interturbinal. In an early fetal Oryctolagus only two frontoturbinals are present, whereas a later fetal stage shows the low ridge of an additional turbinal between both frontoturbinals (Voit, 1909; Frick and Heckmann, 1955). An early fetal stage of Lepus capensis shows only two frontoturbinals and three ethmoturbinals (Eloff, 1950). However, a small ridge between the two frontoturbinals clearly indicates the presence of the growing interturbinal (Eloff, 1950: fig. 4G).

As is well known from several ontogenetic studies on the ethmoidal region of mammals, frontoturbinals and ethmoturbinals always develop from anterior to posterior and it is very unlikely that additional major turbinals can appear later in ontogeny between these structures (Schrenk, 1989; Mess, 1997; Frahnert, 1998; Ruf, 2004). If this is the case, then these additional turbinals are always interturbinals.

Interestingly, the more basal leporid clades all show independently derived patterns in terms of a decrease in number of olfactory turbinals. Given recent phylogenies (e.g., Stoner et al., 2003; Matthee et al., 2004; Robinson and Matthee, 2005), these reductions are homoplastic features. The noticeably slender olfactory turbinals in Poelagus marjorita represent an autapomorphic feature of this species. The genus Pronolagus is united by having a very slender first ethmoturbinal, but shows a variable pattern ranging from a reduced number of interturbinals (in Pronolagus c.f. saundersiae) to the complete loss of all interturbinals and ethmoturbinal III in Pronolagus rupestris. However, the distribution of the number of frontoturbinals, interturbinals, and ethmoturbinals within Pronolagus does not fit proposed intrageneric phylogenies (Matthee et al., 2004; Robinson and Matthee, 2005). Romerolagus diazi is the second leporid genus that shows a very reduced number of turbinals.
just two frontoturbinals and two ethmoturbinals. This pattern evolved independently from that seen in *Pronolagus rupestris* based on all recent phylogenies (Averianov, 1999; Halanych and Robinson, 1999; Stoner et al., 2003; Matthee et al., 2004; Robinson and Matthee, 2005).

The clade comprising *Oryctolagus*, *Caprolagus*, *Sylvilagus*, and especially *Lepus* is characterized by a tendency to increase the number of turbinals. *Sylvilagus graysoni*, *Caprolagus hispidus*, *Lepus americanus*, and *Lepus arcticus* are the lagomorphs with the greatest number of olfactory turbinals known so far (Table 2). Both *Caprolagus hispidus* and *Lepus arcticus* evolved a fourth ethmoturbinal independently. Though intragenetically and intraspecifically variable, *Oryctolagus*, *Sylvilagus*, and *Lepus* exhibit additional interturbinals in different positions among the fronto- and ethmoturbinals. However, it is evident that these additional structures are restricted to the frontoturbinal recess and the space between ethmoturbinal I and II. Furthermore, the interturbinals between frontoturbinal 1 and 2 and ethmoturbinal I and II, respectively, are highly conserved characters and usually larger than additional interturbinals.

A decrease or increase in the number of turbinals occurs in several clades and might be influenced by body size, phylogeny, and/or climatic and olfactory adaptations. An important step in elucidating these patterns would be a morphometric analysis of turbinal surface areas including additional species (e.g., *Brachylagus*, *Pentalagus*, and *Nesolagus*). This work is ongoing and must be discussed against the background of physical adaptations to certain environments (e.g., Yang, 1990; Katzner et al., 1997, Lovegrove, 2003). However, from the 3D models of the turbinal skeleton of the investigated species it is already evident that there are significant differences among species in the proportion of respiratory and olfactory turbinals. In all examined *Lepus* species, the maxilloturbinal appears to be significantly enlarged. This could reflect adaptations to thermoregulation under harsh climatic conditions as are present in the high-latitude and arid environments that are inhabited by several of the investigated species (e.g., Sheriff et al., 2009, see also VanValkenburgh et al., 2011). The genus *Pronolagus* has remarkably small fronto- and ethmoturbinals that imply a reduced reliance on olfaction. However, only a detailed morphometric analysis of these turbinals considering behavioral data
In summary, the present study clearly shows that the turbinal skeleton in lagomorphs reveals useful characters that can be used for systematic purposes and future phylogenetic analyses. Several features such as the number and shape of turbinals are characteristic of major clades or certain genera and species. It is also evident that the combination of two frontoturbinals, three ethmoturbinals, as well as an interturbinal between the two frontoturbinals and the first two ethmoturbinals, respectively, is a quite common pattern. In contrast, additional interturbinals show a greater level of variability. The striking reduction or increase of turbinals in several species as well as the very enlarged maxilloturbinal in *Lepus* need to be examined in terms of adaptation to climate and behavior as well as variation. Thus, further studies on additional species of leporids as well as morphometric analyses of the turbinal skeleton are needed to elucidate functional correlations of the turbinal skeleton, adaptations to environmental variables, and finally the evolutionary mechanisms that triggered lagomorph diversification.

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