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The turbinal skeleton of *Pentalagus furnessi* (Leporidae, Lagomorpha)

Festschrift in Honour of Professor Dr. Wolfgang Maier
Edited by Ingmar Werneburg & Irina Ruf

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http://zoobank.org/65C65C2B-4806-4F9E-8F0A-72F07DEB1E7F

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Citation: Ruf I (2022) The turbinal skeleton of *Pentalagus furnessi* (Leporidae, Lagomorpha). Vertebrate Zoology 72 423–432. https://doi.org/10.3897/vz.72.e83324

Abstract

The turbinal skeleton inside the nasal cavity supports the respiratory and olfactory epithelia of the mammalian nose and can provide systematic and morphofunctional information. For the first time, the turbinal skeleton of *Pentalagus furnessi* (Amami rabbit) from Japan is described based on µCT scans and virtual 3D reconstructions of two specimens. In general, the turbinal skeleton of *Pentalagus furnessi* resembles the pattern and characters observed in other Leporidae. The maxilloturbinal is highly dendritic, nasoturbinal and crista semicircularis are in close contact and form a common recess, the frontoturbinal recess houses two frontoturbinals and one interturbinal between them, the ethmoturbinal recess houses three ethmoturbinals and one interturbinal between ethmoturbinal I and II. *Pentalagus furnessi* is derived from the leporid grundplan in having a lamina semicircularis with almost straight posterior margin and ventral lamella and in showing a single-scrolled and relatively short interturbinal between frontoturbinal 1 and 2. These characters can be regarded as autapomorphic for the Amami rabbit. Furthermore, the two specimens have an additional small and short interturbinal between frontoturbinal 2 and ethmoturbinal I that shows some variation. This pattern supports previous observations of intraspecific variation of certain interturbinals in *Oryctolagus cuniculus* and some *Sylvilagus* and *Lepus* species. The comparison of the turbinal skeleton of *Pentalagus furnessi* and its possible sister taxon (e.g., *Pronolagus*, *Poelagus* or *Caprolagus*) reveals a puzzling pattern which is discussed.

Key words

Introduction

Pentalagus furnessi (Amami rabbit) is a medium-sized leporid and the only living species of the genus. Today, *Pentalagus furnessi* is restricted to Amami Oshima and Tokunoshima (Ryukyu Islands) in southern Japan and probably arrived at the latter during the early Middle Pleistocene. The species is known from only four frag-

mented extant populations, which in concert with habitat loss and introduction of dogs, cats and *Herpestes javanicus* accounts for the classification "Endangered" by the IUCN. The Amami rabbit differs from all other living Leporidae in having very short ears, small eyes, tail and hindfeet; the claws are significantly longer and used for digging burrows as well as climbing steep slopes; vocalization is comparable to *Ochotona* (Otsuka et al. 1980; Tomida and Otsuka 1993; Yamada et al. 2002; Yamada and Cervantes 2005; Schai-Braun and Hackländer 2016). Although *Pentalagus furnessi* is considered to be one of the most primitive extant lagomorphs it is well nested within Leporidae based on morphological and especially molecular data (e.g., Yamada et al. 2002; Ge et al. 2013; Schai-Braun and Hackländer 2016; Cano-Sánchez et al. 2022).

As an insular species, *Pentalagus furnessi* is enigmatic in several respects but still little is known about its cranial anatomy. While some external cranial and dental studies of *Pentalagus furnessi* exist (e.g., Otsuka et al. 1980; Tomida and Otsuka 1993; Ge et al. 2015), no anatomical descriptions of intracranial structures are available to date.

The mammalian cranium holds important structural complexes for understanding evolution, development and function of the sensory systems, dietary and locomotory adaptations as well as phylogenetic information (e.g., Maier 1993; Wible and Hopson 1993; Spoor et al. 2007; Usui and Tokita 2018; Martin and Koenigswald 2020). In their comprehensive review on the biology, systematics, and evolution of Lagomorpha, Kraatz et al. (2021) propose this order as an excellent model system to study a broad array of functional systems and evolutionary transformations. In this regard it is important to fill gaps of knowledge in lagomorph cranial anatomy.

The present study provides the first anatomical description of intracranial structures in *Pentalagus furnessi* focusing on nasal structures. The turbinal skeleton supports the respiratory and olfactory epithelia and provides phylogenetic as well as morphofunctional information as already demonstrated in several other mammalian orders (e.g., Maier 2000; Smith and Rossie 2008; Van Valkenburgh et al. 2011, 2014; Smith et al. 2012; Ruf 2014, 2020; Ruf et al. 2015, 2021; Martinez et al. 2018, 2020; Wagner and Ruf 2019, 2021). Systematically relevant turbinal characters were described for all extant lagomorph genera except for *Pentalagus*, *Nesolagus*, *Bunolagus*, and *Brachylagus* (Ruf 2014). Thus, the anatomical description of the turbinal skeleton of *Pentalagus furnessi* will help complete this data set for further phylogenetic and morphofunctional studies.

Methods

This study is based on two adult macerated skulls of *Pentalagus furnessi* that are housed in the National Museum of Nature and Science, Tokyo, Japan. Specimen M 12939 was scanned with the µCT scanner (Fraunhofer/
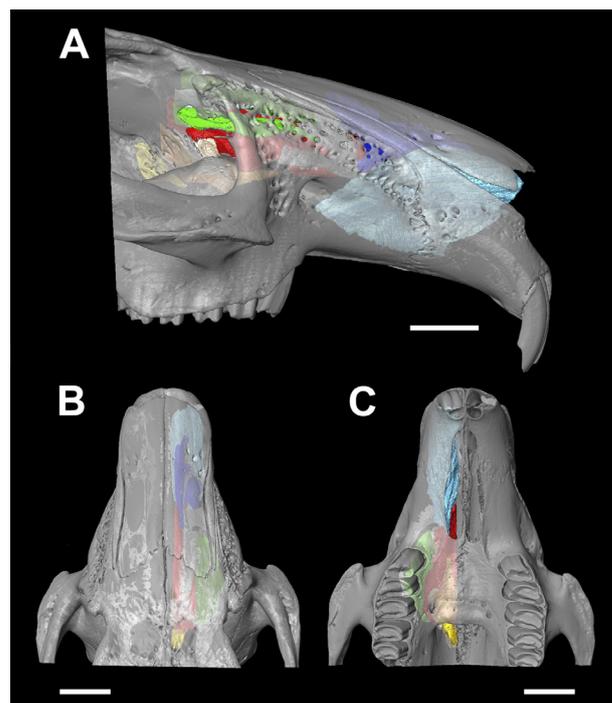
Figure 1. Virtual 3D model of the rostrum and right turbinal skeleton of *Pentalagus furnessi* (M 12940) in **A** right lateral, **B** dorsal and **C** ventral view. The dermal bones are transparent and provide insight into the nasal cavity showing the segmented right turbinals. Colour code refers to Fig. 2. Scale bars: 10 mm.

ProConXray/Feinfocus) housed at the Senckenberg Forschungsinstitut und Naturmuseum Frankfurt, Frankfurt am Main, Germany. Scan parameters are 90 kV, 89 µA, 1500 ms exposure time, 1600 projections, and 0.0252 mm resolution (isotropic voxel size). Specimen M 12940 was scanned at Fraunhofer IIS, Deggendorf, Germany, with a TomoScope HV 500 by Werth Messtechnik GmbH Gießen; scan parameters are 150 kV, 300µA, 666ms exposure time, 1200 projections, and 0.0499 mm resolution (isotropic voxel size). The µCT data were processed with VGStudio MAX 2.2 (Volume Graphics, Heidelberg, Germany) and the virtual 3D model of the turbinal skeleton of M 12940 was manually segmented in Avizo 9.01 (Thermo Fisher Scientific FEI).

Anatomical terminology follows Ruf (2014) and Maier and Ruf (2014), although some other terminologies exists (see Smith and Bonar 2022 and table 1 for further synonyms of turbinal structures therein). Due to the lack of early ontogenetic stages of *Pentalagus furnessi* identification and homology of interturbinals are based on topography, medial extension compared to fronto- and ethmoturbinals as well as developmental patterns of these structures observed in other Lagomorpha and further mammalian species (e.g., Paulli 1900; Voit 1909; Frick and Heckmann 1955; Ruf 2014, 2020; Wagner and Ruf 2019, 2021). For comparative illustration of selected characters, µCT images of *Romerolagus diazi* (10977, Naturhistorisches Museum Basel, Switzerland), *Poelagus marjorita* (28732, Staatliches Museum für Naturkunde Stuttgart, Germany), *Lepus europaeus* (M6335, Institut für Geowissenschaften, Universität Bonn, Germany) and
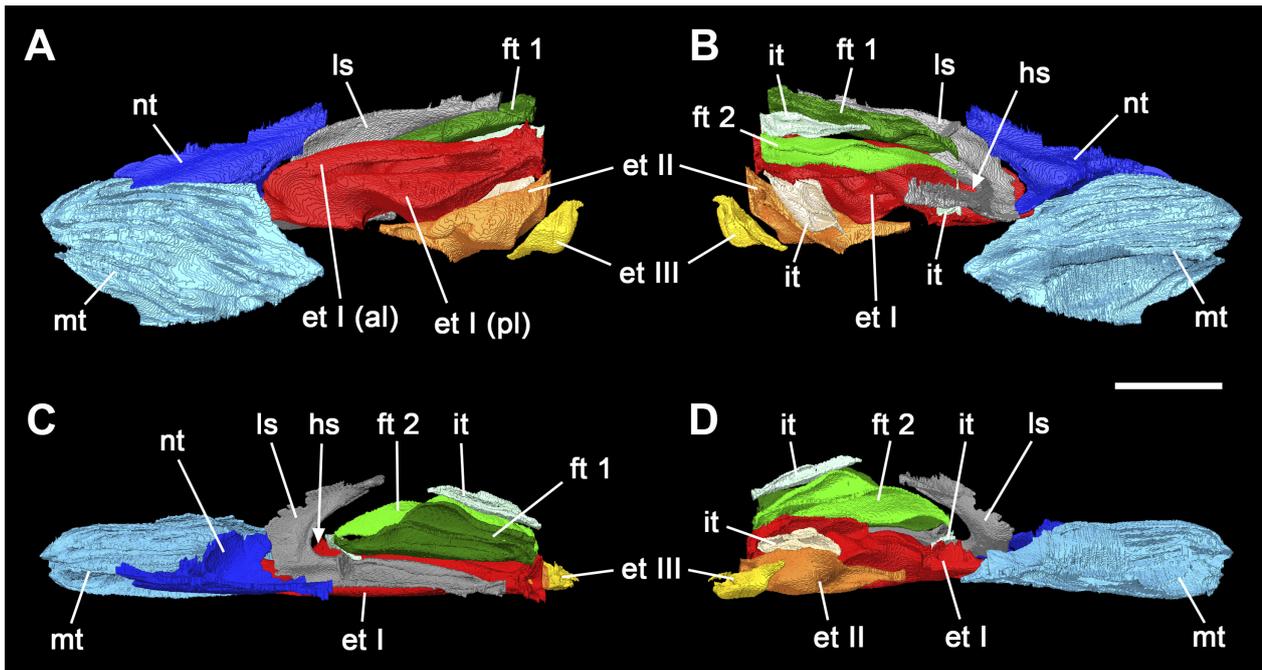
Figure 2. Virtual 3D model of the right turbinal skeleton of *Pentalagus furnessi* (M 12940) in **A** medial, **B** lateral, **C** dorsal and **D** ventral view. Abbreviations: al, anterior lamella; et I–III, ethmoturbinal I–III; ft1-2, frontoturbinal 1–2; hs, hiatus semilunaris; it, interturbinal; ls, lamina semicircularis; mt, maxilloturbinal; nt, nasoturbinal; pl, posterior lamella. Scale bar: 10 mm.

Ochotona alpina (100485, Museum für Naturkunde, Berlin, Germany) were used. For details on scan parameters see Ruf (2014).

Lagomorph phylogeny follows Robinson and Matthee (2005), Ge et al. (2013), and Cano-Sánchez et al. (2022) and is used for grundplan reconstruction in the sense of Hennig (1984) in order to elucidate apomorphic and plesiomorphic characters of the last common ancestor of a respective taxon.

Results

Both studied *Pentalagus furnessi* specimens are very similar in their turbinal morphology. Thus, the anatomical description mainly refers to specimen M 12940, and specimen M 12939 is mentioned for intraspecific differences.

The nasal cavity of *Pentalagus furnessi* is large and extends below the endocranial cavity, where the olfactory bulbs are located (Fig. 1). The pars anterior of the nasal cavity houses the maxilloturbinal and the nasoturbinal. The maxilloturbinal has a great dorsoventral extension and is situated ventrally to the nasoturbinal. Anteriorly the maxilloturbinal extends far into the nasal aperture and posteriorly it ends below ethmoturbinal I (Figs 1A, 2A, B). In cross-section the maxilloturbinal is highly dendritic, i.e., it shows many lamellar ridges and additional outgrowths (epiturbinals). Its ventralmost lamella forms the medial wall of the nasolacrimal canal. The nasoturbinal arises from the nasal ridge of the nasal bone and forms a straight lamella that shows a sickle-shaped posterior

border (Figs 2A, B, 3A). Here, the nasoturbinal is partly in close contact with the lamina semicircularis and thus, both structures form a morphological unit (Fig. 2A, B). In this area both structures are excavated to a recess that continues posteriorly into the pars lateralis of the nasal cavity (Fig. 3B).

The lamina semicircularis is sickle-shaped reflecting the posterior border of the nasoturbinal and forms the anteromedial wall of the pars lateralis as well as of the hiatus semilunaris (Fig. 2B, C). Its long dorsal lamella becomes laterally rolled up and merges with the lamina cribrosa; its ventral part is much shorter and forms a straight and distally slightly thickened lamella in the upper part of the maxillary sinus (processus uncinatus) (Fig. 4). The part that forms the anterior border of the hiatus semilunaris is not significantly rolled up (Fig. 2B, C).

The pars lateralis of the nasal cavity comprises the frontoturbinal recess (dorsally) and the large maxillary sinus (ventrally) that are separated by the lamina horizontalis but confluent anteriorly (Figs 3C, 4). The frontoturbinal recess houses several turbinals. Both studied specimens have two frontoturbinals and one interturbinal in between, all of which end on the lamina cribrosa (Fig. 2). The frontoturbinals are double scrolls. Frontoturbinal 1 arises anteriorly from the ossified nasal capsule and then moves onto the frontal bone while frontoturbinal 2 arises from the lamina horizontalis (Fig. 3C). The interturbinal between the frontoturbinals is simpler in shape (scrolled dorsally), smaller and shorter than the frontoturbinals and located in the posterior part of the frontoturbinal recess (Figs 2B, C, 3C). It arises from the ossified lateral wall of the nasal capsule (paries nasi) and only its posterior end is attached to the maxillary bone and the most lateral rim of the lamina cribrosa. Specimen M12939 shows
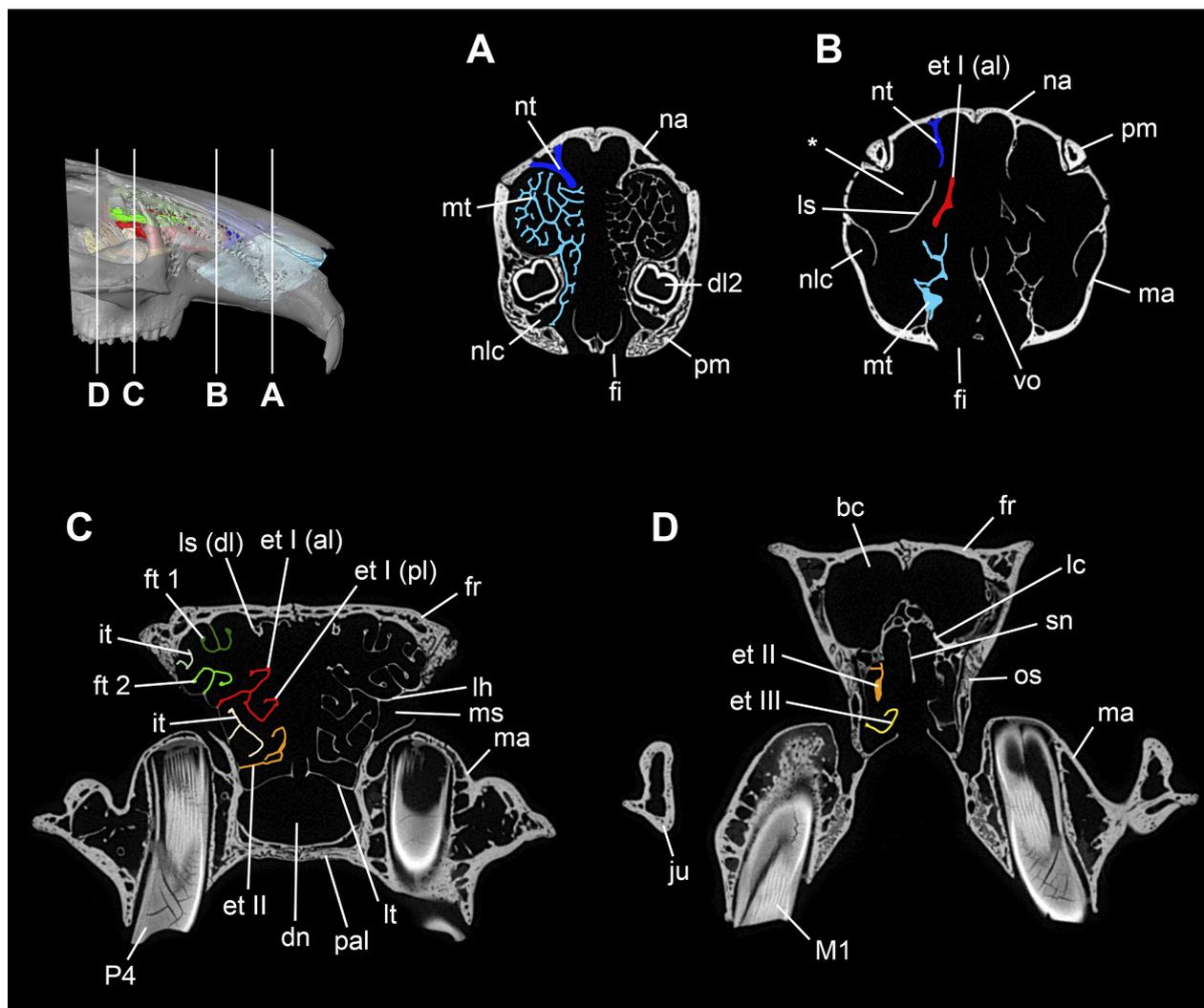
Figure 3. Transversal μCT images through the nasal cavity of *Pentalagus furnessi* (M 12940) from anterior (**A**) to posterior (**D**). Sections are indicated on the 3D model. Colour code of the right turbinal skeleton refers to Fig. 2. The asterisk (*) refers to the cavity formed by the nasoturbinal and lamina semicircularis. Abbreviations: al, anterior lamella; bc, brain cavity; dI2, upper second deciduous incisor; dl, dorsal lamella; dn, ductus nasopharyngeus; et I–III, ethmoturbinal I–III; fi, foramen incisivum; fr, frontal bone; ft1–2, frontoturbinal 1–2; it, interturbinal; ju, jugal bone; lc, lamina cribrosa; lh, lamina horizontalis; ls, lamina semicircularis; lt, lamina terminalis; M1, upper molar 1; ma, maxillary bone; ms, maxillary sinus; mt, maxilloturbinal; na, nasal bone; nlc; nasolacrimal canal; nt, nasoturbinal; os, orbitosphenoid; P4, upper premolar 4; pal, palatinum; pl, posterior lamella; pm, premaxillary bone; sn, septum nasi; vo, vomer. Not to scale.

some variation in that the left interturbinal forms a short straight lamella; the right frontoturbinal 2 is only a single scroll maybe due to constraints in space caused by the single-scrolled right interturbinal (Fig. 4B). In addition, both specimens show an additional small and short interturbinal between frontoturbinal 2 and ethmoturbinal I located in the anterior frontoturbinal recess (Fig. 2B, D). In specimen M 12940 this interturbinal is a straight but low lamella that diverges together with frontoturbinal 2 from the lamina horizontalis, runs posteromedially and merges with ethmoturbinal I (Fig. 4A). Specimen M 12939 shows a somewhat different pattern. Here, on the right side this additional interturbinal is a very short and low lamella arising from the lamina horizontalis, with no contact to frontoturbinal 2 or ethmoturbinal I. On the left side the additional interturbinal is just a very low ridge (Fig. 4B).

The pars posterior of the nasal cavity comprises the ethmoturbinal recess and houses three ethmoturbinals and one interturbinal between ethmoturbinal I and II (Fig. 2); all of these turbinals end on the ventral surface of the lamina cribrosa. Ethmoturbinal I is by far the largest olfactory turbinal. Anteriorly, it is separated into an anterior lamella, whose anterior process projects into the pars anterior of the nasal cavity, and a posterior lamella (Fig. 3B, C). Both lamellae are straight at their front end and arise from the lamina horizontalis. More posteriorly they are attached with a common root to the lamina horizontalis, that partly forms the lateral sidewall of the nasal cavity, and at the very end to the frontal bone. The posterior end of ethmoturbinal I and the lamina cribrosa together form a deep funnel that transmits the olfactory nerves (cranial nerve I) of that area. During their course both lamellae of ethmoturbinal I become single and double scrolls. Inter-
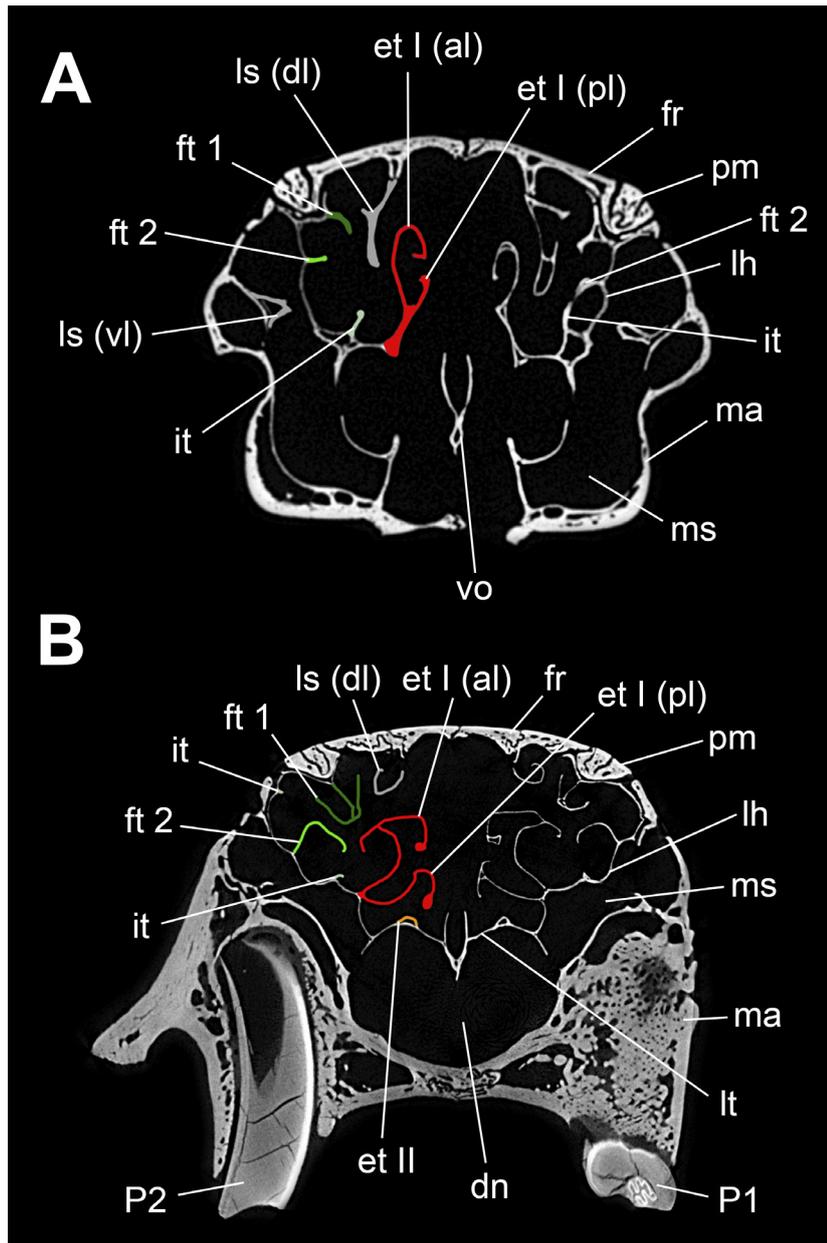
Figure 4. Transversal µCT images through the nasal cavity of *Pentalagus furnessi.* **A** specimen M 12940, **B** specimen M 12939. Note the differences in topography of the additional interturbinal between frontoturbinal 2 and ethmoturbinal I. In specimen M 12940 anteriorly this interturbinal and frontoturbinal 2 have a common origin and the former runs posteromedially to merge with ethmoturbinal I (**A**), whereas in specimen M 12939 the additional interturbinal is a very low ridge on the lamina horizontalis (**B**). Colour code of the right turbinal skeleton refers to Fig. 2. Abbreviations: al, anterior lamella; dl, dorsal lamella; dn, ductus nasopharyngeus; et I–II, ethmoturbinal I–II; fr, frontal bone; ft1–2, frontoturbinal 1–2; it, interturbinal; lh, lamina horizontalis; ls, lamina semicircularis; lt, lamina terminalis; ma, maxillary bone; ms, maxillary sinus; P1–2, upper premolar 1–2; pl, posterior lamella; pm, premaxillary bone; vl, ventral lamella; vo, vomer. Not to scale.

estingly, both studied specimens show different scroll patterns. In M 12940 both lamellae are rolled up inversely, i.e., the anterior lamella ventromedially and the posterior lamella dorsolaterally (Fig. 4A). The anterior lamella becomes a double scroll that shifts to a single scroll (rolled up dorsolaterally), while the posterior lamella remains a single scroll (Fig. 3C); in addition, the posterior lamella of the left ethmoturbinal I has a short lateral epiturbinal. In contrast both lamellae of ethmoturbinal I in M 12393 are rolled up ventromedially in their anterior parts and then both become double scrolls (Fig. 4B); in the poste-

rior lamella the double scroll portion is quite short as this is the transition from a ventromedially to dorsolaterally rolled up single scroll.

The interturbinal is relatively short and situated in the posterior part of the ethmoturbinal recess where it arises entirely from the lamina horizontalis (Figs 2B, D, 3C). The interturbinal is ventrally rolled up (single scroll) but forms a double scroll for a short distance.

Ethmoturbinal II is the second largest ethmoturbinal (Fig. 2A, B, D). Anteriorly it arises from the lamina terminalis and then it runs posterolaterally onto the maxil-
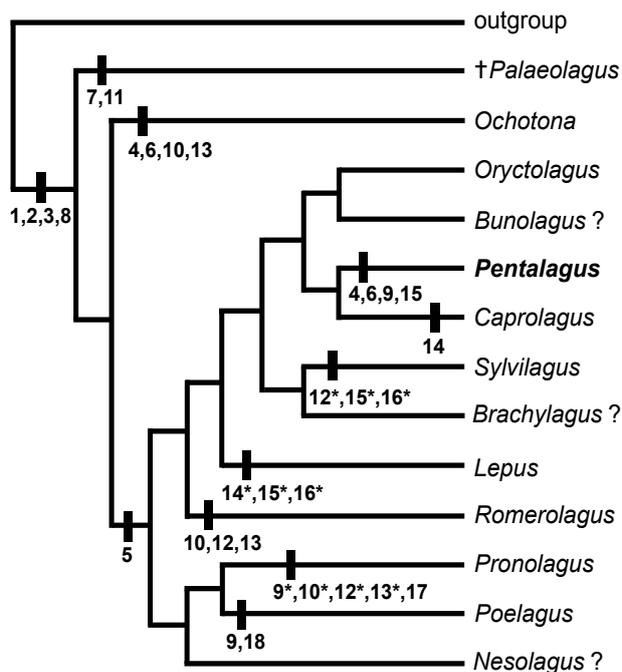
Figure 5. Apomorphic characters of the turbinal skeleton of Lagomorpha mapped on a phylogeny comprising all extant genera based on molecular data (Robinson and Matthee 2005). Position of the early Oligocene lagomorph *Palaeolagus haydeni* according to Fostowicz-Frelik and Meng (2013). Outgroup comprises *Sciurus vulgaris* (Rodentia) and *Tupaia* sp. (Scandentia). Morphological data for previously described species are taken from Ruf (2014) and Ruf et al. (2021). Species for which no data on the turbinal morphology is available are labelled with a question mark. Characters: 1, dendritic maxilloturbinal; 2, excavated nasoturbinal that contacts the lamina semicircularis; 3, rolled up posterior margin of lamina semicircularis; 4, almost straight posterior margin of lamina semicircularis; 5, rolled up ventral lamella of lamina semicircularis; 6, straight ventral lamella of lamina semicircularis; 7, lamina semicircularis with anterolaterally projecting additional process; 8, interturbinal between frontoturbinal 1 and 2; 9, interturbinal between frontoturbinal 1 and 2 reduced in size and complexity; 10, loss of interturbinal between frontoturbinal 1 and 2;11, frontoturbinal 2 reduced in size and complexity; 12, loss of interturbinal between ethmoturbinal I and II; 13, loss of ethmoturbinal III; 14, ethmoturbinal IV; 15, additional interturbinals in frontoturbinal recess; 16, additional interturbinals in ethmoturbinal recess; 17, very slender ethmoturbinal I; 18, slender ethmoturbinal II, III and interturbinal between first two ethmoturbinals. Asterisk (*) indicates characters restricted to certain species.

lary bone (Figs 3C, 4B). The posterior end is an almost straight lamella hanging down from the lamina cribrosa (Fig. 3D). Ethmoturbinal II of M 12940 is mostly a single scroll, whose orientation of rolling up changes from ventrally to laterally. On the right side a short lateral epiturbinal is evident in the area where the orientation of rolling up changes. In specimen M 12939, the anterior part of ethmoturbinal II is almost straight and thus this turbinal is a single scroll (rolled up dorsolaterally). However, the left ethmoturbinal II shows a ventral epiturbinal that forms a short double scroll.

Ethmoturbinal III is the most posterior olfactory turbinal and its size is comparable to the interturbinal inside the ethmoturbinal recess (Fig. 2A, B, D). The anterior part of ethmoturbinal III is attached to the maxillary bone but the rest arises from the partly ossified lateral wall of the posterior nasal cavity (paries nasi) (Fig. 3D). Like ethmoturbinal II ethmoturbinal III shows a changing orientation of its single scroll, but in contrast to the former from dorsolaterally to ventrolaterally; in the transition area a short double scroll is present.

Discussion

Generally, the turbinal skeleton of *Pentalagus furnessi* resembles the pattern and characters observed in other Leporidae (Ruf 2014). *Pentalagus furnessi* resembles the lagomorph grundplan in showing a dendritic maxilloturbinal and an excavated nasoturbinal that contacts the lamina semicircularis, and the leporid grundplan in having an interturbinal between frontoturbinal 1 and 2 (Ruf 2014) (Fig. 5). All these characters are also present in the stem-lagomorph *Palaeolagus haydeni* (Ruf et al. 2021). A nasoturbinal that contacts or is continuous with the lamina semicircularis has also been observed in *Potamogale velox* and in marsupials (Macrini 2012; Ruf et al. 2020) but is not present in *Sciurus vulgaris*, muroid rodents and Scandentia (Ruf 2014; Ruf et al. 2015). Concerning the turbinal pattern in the pars posterior of the nasal cavity (three ethmoturbinals, one interturbinal between ethmoturbinal I and II, ethmoturbinal I with two major lamellae) *Pentalagus furnessi* represents a common mammalian pattern. This has been also observed in *Palaeolagus haydeni*, many leporids (*Poelagus marjorita*, *Pronolagus* cf. *saundersiae*, *Oryctolagus cuniculus*, *Sylvilagus* spp., *Lepus* spp.), many rodents (e.g., *Sciurus vulgaris*, *Mus musculus*, *Mesocricetus auratus*), and Scandentia (Ruf 2014, 2020; Ruf et al. 2015, 2021).

In addition, *Pentalagus furnessi* shows some apomorphic characters in the turbinal skeleton (Fig. 5). A derived feature that unites Lagomorpha and *Palaeolagus haydeni* is a significantly rolled up posterior margin of the lamina semicircularis (Ruf 2014; Ruf et al. 2021), which is not the case in *Pentalagus furnessi* (Fig. 6A). The latter is derived from the leporid grundplan in that the ventral lamella of the lamina semicircularis is straight. Due to the thickened free margin it differs from the straight lamina semicircularis in Ochotonidae (Ruf 2014). A further apomorphic character of *Pentalagus furnessi* is the reduced (proportionally short and single-scrolled) interturbinal between frontoturbinal 1 and 2 (Fig. 6B). It should be mentioned that reduction and especially loss of this interturbinal evolved several times independently within Lagomorpha, e.g., in Ochotonidae, *Romerolagus diazi*, and *Pronolagus* spp. (Ruf 2014).

The two studied specimens of *Pentalagus furnessi* show some variation in the detailed morphology of certain olfactory turbinals including left-right asymmetry,
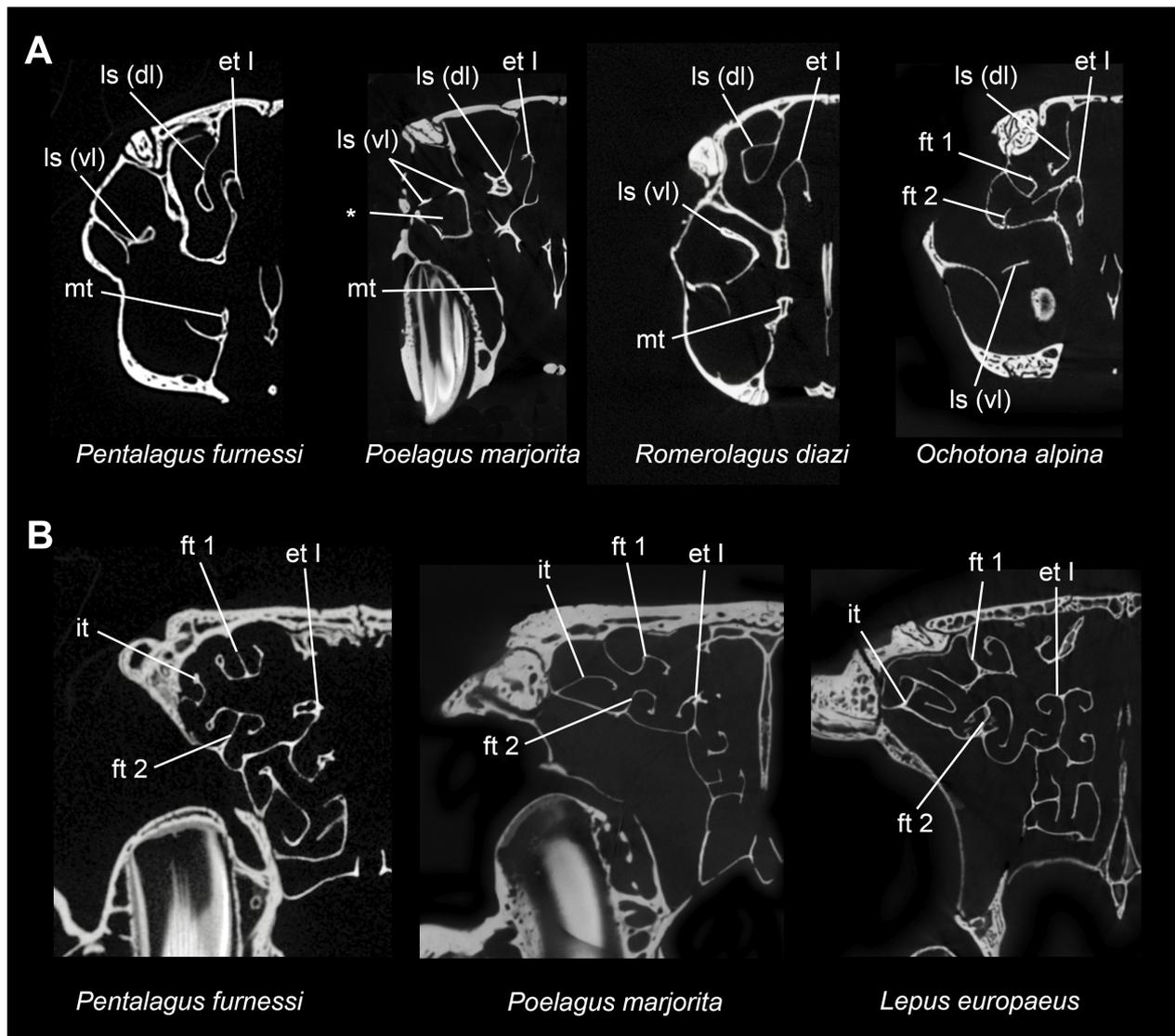
Figure 6. Comparison of *Pentalagus furnessi* (M 12940), *Poelagus marjorita* (28732), *Romerolagus diazi* (10977), *Lepus euro-paeus* (M6335), and *Ochotona alpina* (100485) based on transversal μCT images through the nasal cavity. **A** different patterns of the lamina semicircularis; the ventral lamella can be significantly rolled up like in *Poleagus* and *Romerolagus*, or straight like in *Pentalagus* and *Ochotona*; note the cavity formed by the ventral lamella of *Poelagus* as indicated by the asterisk (*). **B** turbinal shape patterns in the frontoturbinal recess; note the different orientation of scrolling of the interturbinal in *Pentalagus* and *Poelagus*. Abbreviations: dl, dorsal lamella; et I, ethmoturbinal I; ft1–2, frontoturbinal 1–2; it, interturbinal; ls, lamina semicircularis; mt, maxilloturbinal; vl, ventral lamella. Not to scale.

e.g., the additional interturbinal between frontoturbinal 2 and ethmoturbinal I. Intraspecific variation of smaller interturbinals has already been described in *Oryctolagus cuniculus*, some *Sylvilagus* and *Lepus* species, and in *Canis lupus familiaris* (Ruf 2014; Wagner and Ruf 2019, 2021). The general morphology and number of the major olfactory turbinals (frontoturbinals, ethmoturbinals, interturbinal between ethmoturbinal I and II, lagomorph interturbinal between frontoturbinals) used for comparative and systematic purposes is normally not affected. However, there are very few observations on variation in these major turbinals: *Myocastor coypus* is generally lacking frontoturbinals but some studied specimens have one (Martinez et al. 2020; pers. obs. of QM and IR), *Notoryctes typhlops* shows some intraindividual variation in having two frontoturbinals on the left side and three

ones on the right side (Macrini 2012) and a fetal stage of *Daubentonia madagascariensis* has four ethmoturbinals in contrast to an adult stage with only three ethmoturbinals (Maier and Ruf 2014). As the virtual reconstruction of the turbinal skeleton is quite time consuming most studies rely only on a single specimen per species and thus intraspecific variation has not been detected very often. Intraspecific variation can only be elucidated by larger sample sizes in future studies.

The sister-group relationship of *Pentalagus furnessi* is still debated and several hypotheses exist. Possible candidates are *Pronolagus* spp. (eastern and southern Africa), *Bunolagus monticularis* (South Africa), *Poelagus marjorita* (The Democratic Republic of the Congo, South Sudan, Sudan, Uganda) and *Caprolagus hispidus* (Himalayan region of India, Bhutan, Nepal) although morpho-

logical similarities with the former may be due to convergent evolution (Dawson 1981; Yamada et al. 2002; Stoner et al. 2003; Matthee et al. 2004; Robinson and Matthee 2005; Ge et al. 2013; Cano-Sánchez et al. 2022). The turbinal skeleton does not elucidate the sister-group relationship of *Pentalagus furnessi* as much as expected because a puzzling pattern becomes evident. Among the studied *Pronolagus* specimens only *Pronolagus* cf. *saundersiae* shows the same turbinal count as *Pentalagus furnessis* (except for the additional small interturbinal in the frontoturbinal recess) as well as a very reduced interturbinal between the frontoturbinals. However, ethmoturbinal I of *Pronolagus* cf. *saundersiae* is very different from that in *Pentalagus furnessi* in being slender with a short posterior lamella. *Pronolagus rupestris* and *Pronolagus randensis* lack certain turbinals and thus are highly derived from the lagomorph grundplan (Ruf 2014). However, as long as the turbinal skeleton of *Pronolagus crassicaudatus* remains undescribed the polarization within that genus remains ambiguous and thus, comparison with the Amami rabbit is limited. *Pentalagus furnessi* and *Poelagus marjorita* show the same number of major olfactory turbinals but they differ significantly in their proportions. While the turbinals of the ethmoturbinal recess of *Poelagus marjorita* are more slender, the interturbinal between the frontoturbinals is proportionally longer than in *Pentalagus furnessi*. However, all turbinals of the frontoturbinal recess of *Poelagus marjorita* are reduced in that they form single scrolls but in contrast to *Pentalagus furnessi* the interturbinal is scrolled ventrally (Fig. 6B); this indicates a convergently evolved pattern (Fig. 5). Furthermore, in *Poelagus marjorita* the lamina semicircularis is proportionally much larger and resembles the leporid grundplan; the ventral lamella of *Poelagus marjorita* differs from other lagomorphs in forming a large cavity (Fig. 6A). In contrast, the maxilloturbinal of *Poelagus marjorita* appears to be shorter and lower with less ridges, although this could be an artefact due to poor preservation (Ruf 2014). However, one should bear in mind that differences in turbinal number, complexity, proportion and relative size may be related to ecology and reflect potential adaptations (e.g., Martinez et al. 2018, 2020). In terms of overall proportions and pattern of the turbinal skeleton *Pentalagus furnessi* also compares to *Caprolagus hispidus*, although the latter has four ethmoturbinals and a larger interturbinal between the frontoturbinals. Furthermore, *Pronolagus* cf. *saundersiae*, *Poelagus marjorita* and *Caprolagus hispidus*, are all lacking further small interturbinals (Ruf 2014). Unfortunately, the turbinal skeleton of *Bunolagus monticularis* has not been studied to date.

Conclusion

The first anatomical description of the turbinal skeleton in *Pentalagus furnessi* sheds new light on intracranial diversity and cranial variation in Leporidae. The Amami rabbit shows a combination of typical leporid and auta-

pomorphic characters. The latter comprise the relatively short and single-scrolled interturbinal between frontoturbinal 1 and 2 and a straight ventral lamella of the lamina semicircularis. *Pentalagus furnessi* differs from the turbinal skeleton of possible sister-group species in several respects. This underpins the great variation observed in the lagomorph skull that contradicts the generally assumed conservative morphology of Lagomorpha (e.g., Fostowicz-Frelik and Meng 2013; Kraatz et al. 2021). For instance, variation in skull shape changes might reflect some loss of phylogenetic signal at the generic level and a high degree of convergent adaptations due to extensive extinctions especially in Ochotonidae and the radiation of modern Leporidae at the end and after the Miocene (Ge et al. 2013, 2015). However, the present study clearly shows the need for more detailed comparative morphological studies of cranial characters ideally covering all living lagomorph genera and species.

Pentalagus furnessi has a heavier and thicker skull than many other leporid species (Ge et al. 2015), which refers to its smaller eyes and ear regions and implies some primitive pattern; compared to *Lepus europaeus* and *Oryctolagus cuniculus* the rostrum of *Pentalagus furnessi* appears to be proportionally smaller and less robust (Otsuka et al. 1980: figs. 2, 3), which indicates a smaller nasal cavity. Future morphometric studies on surface area and complexity of the respiratory and olfactory turbinal skeleton (according to Martinez et al. 2018 and Wagner and Ruf 2019) may help to elucidate morphofunctional adaptations related to environment, climate, foraging and social behavior in the Amami rabbit as well as in other living lagomorph species.

Acknowledgements

References

Cano-Sánchez E, Rodríguez-Gómez F, Ruedas LA, Oyama K, Leon-Paniagua L, Mastretta-Yanes A, Velazquez A (2022) Using ultraconserved elements to unravel lagomorph phylogenetic relation-

ships. Journal of Mammalian Evolution 29: 395–411. https://doi.org/10.1007/s10914-021-09595-0

Dawson MR (1981) Evolution of modern leporids. In: Myers K, MacInnes CD (Eds) Proceedings of the World Lagomorph Conference, Ontario (Canada), August 1979. University of Guelph Press, Ontario, 1–8.

Frick H, Heckmann U (1955) Ein Beitrag zur Morphogenese des Kaninchenschädels. Acta Anatomica 24: 268–314.

Fostowicz-Frelik Ł, Meng J (2013) Comparative morphology of premolar foramen in lagomorphs (Mammalia: Glires) and its functional and phylogenetic implications. PLoS ONE 8: e79794. https://doi.org/10.1371/journal.pone.0079794

Ge D, Yao L, Xia L, Zhang Z, Yang Q (2015) Geometric morphometric analysis of skull morphology reveals loss of phylogenetic signal at the generic level in extant lagomorphs (Mammalia: Lagomorpha). Contributions to Zoology 84: 267–284. https://doi.org/10.1163/18759866-08404001

Ge D, Wen Z, Xia L, Zhang Z, Erbajeva M, Huang C, Yang Q (2013) Evolutionary history of lagomorphs in response to global environmental change. PLoS One 8: e59668. https://doi.org/10.1371/journal.pone.0059668

Hennig W (1984) Taschenbuch der Speziellen Zoologie Teil 1, Wirbellose I, ausgenommen Gliedertiere. Verlag Harri Deutsch, Thun und Frankfurt/Main.

Kraatz B, Belabbas R, Fostowicz-Frelik Ł, Ge D-Y, Kuznetsov AN, Lang MM, López-Torres S, Mohammadi Z, Racicot RA, Ravosa MJ, Sharp AC, Sherratt E, Silcox MT, Słowiak J, Winkler AJ, Ruf I (2021) Lagomorpha as a model morphological system. Frontiers in Ecology and Evolution 9: 636402. https://doi.org/10.3389/fevo.2021.636402

Macrini TE (2012) Comparative morphology of the internal nasal skeleton of adult marsupials based on X-ray computed tomography. Bulletin of the American Museum of Natural History 365: 1–91. https://doi.org/10.1206/365.1

Maier W (1993) Cranial morphology of the therian common ancestor, as suggested by the adaptations of neonate marsupials. In: Szalay FS, Novacek MJ, McKenna MC (Eds) Mammal Phylogeny – Mesozoic Differentiation, Multituberculates, Monotremes, Early Therians, and Marsupials. Springer, New York, NY, 165–181. https://doi.org/10.1007/978-1-4613-9249-1_12

Maier W (2000) Ontogeny of the nasal capsule in cercopithecoids: a contribution to the comparative and evolutionary morphology of catarrhines. In: Whitehead PF, Jolly CJ (Eds) Old World Monkeys. University Press, Cambridge, UK, 99–132.

Maier W, Ruf I (2014) Morphology of the nasal capsule of Primates—with special reference to *Daubentonia* and *Homo*. The Anatomical Record 297: 1985–2006. https://doi.org/10.1002/ar.23023

Matthee CA, Jansen van Vuren B, Bell D, Robinson TJ (2004) A molecular supermatrix of the rabbits and hares (Leporidae) allows for the identification of five intercontinental exchanges during the Miocene. Systematic Biology 53: 433–447. https://doi.org/10.1080/10635150490445715

Martin T, Koenigswald Wv (2020) Mammalian Teeth – Form and Function. Verlag Dr. Friedrich Pfeil, München, 248 pp.

Martinez Q, Clavel J, Esselstyn JA, Achmadi AS, Grohé C, Pirot N, Fabre PH (2020) Convergent evolution of olfactory and thermoregulatory capacities in small amphibious mammals. Proceedings of the National Academy of Sciences 117: 8958–8965. https://doi.org/10.1073/pnas.1917836117

Martinez Q, Lebrun R, Achmadi AS, Esselstyn JA, Evans AR, Heaney LR, Portela Miguez R, Rowe KC, Fabre PH (2018) Convergent evolution of an extreme dietary specialisation, the olfactory system of worm-eating rodents. Scientific Reports 8: 1–13. https://doi.org/10.1038/s41598-018-35827-0

Otsuka J, Toyomitsu Y, Nishinakagawa H (1980) Linear measurements of the bones of *Lepus brachyurus brachyurus* TEMMINCK, *Pentalagus furnessi* STONE and *Oryctolagus cuniculus* LINNAEUS (JW-NIBS) I. On the cranium and ossa trunci. Experimental Animals 29: 441–455. https://doi.org/10.1538/expanim1978.29.4_441

Paulli S (1900) Über die Pneumaticität des Schädels bei den Säugetieren. Eine morphologische Studie. III. Über die Morphologie des Siebbeins und die der Pneumaticität bei den Insectivoren, Hyracoideen, Chiropteren, Carnivoren, Pinnipedien, Edentaten, Rodentiern, Prosimiern und Primaten, nebst einer zusammenfassenden Übersicht über die Morphologie des Siebbeins und die der Pneumaticität des Schädels bei den Säugetieren. Morphologisches Jahrbuch 28: 483–564.

Robinson TJ, Matthee CA (2005) Phylogeny and evolutionary origins of the Leporidae: a review of cytogenetics, molecular analyses and a supermatrix analysis. Mammal Review 35: 231–247. https://doi.org/10.1111/j.1365-2907.2005.00073.x

Ruf I (2014) Comparative anatomy and systematic implications of the turbinal skeleton in Lagomorpha (Mammalia). The Anatomical Record 297: 2031–2046. https://doi.org/10.1002/ar.23027

Ruf I (2020) Ontogenetic transformations of the ethmoidal region in Muroidea (Rodentia, Mammalia): new insights from perinatal stages. Vertebrate Zoology 70: 383–415. https://doi.org/10.26049/VZ70-3-2020-10

Ruf I, Behrens H, Zeller U (2020) Ontogeny and morphofunctional implications of the ethmoidal region in the semiaquatic *Potamogale velox* (Afrotheria, Mammalia). Vertebrate Zoology 70: 679–697. https://doi.org/10.26049/VZ70-4-2020-09

Ruf I, Janßen S, Zeller U (2015) The ethmoidal region of the skull of *Ptilocercus lowii* (Ptilocercidae, Scandentia, Mammalia) – a contribution to the reconstruction of the cranial morphotype of primates. Primate Biology 2: 89–110. https://doi.org/10.5194/pb-2-89-2015

Ruf I, Meng J, Fostowicz-Frelik Ł (2021) Anatomy of the nasal and auditory regions of the fossil lagomorph *Palaeolagus haydeni*: systematic and evolutionary implications. Frontiers in Ecology and Evolution 9: 636110. https://doi.org/10.3389/fevo.2021.636110

Schai-Braun SC, Hackländer K (2016) Family LEPORIDAE (HARES AND RABBITS). In: Wilson DE, Lacher TE Jr, Mittermeier RA (Eds) Handbook of the Mammals of the World. 6. Lagomorphs and Rodents I. Lynx Edicion, Barcelona, pp.62–148.

Smith TD, Bonar CJ (2022) The nasal cavity in agoutis (*Dasyprocta* spp.): a micro-computed tomographic and histological study. Vertebrate Zoology 72: 95–113. https://doi.org/10.3897/vz.72.e76047

Smith TD, Rossie JB (2008) Nasal fossa of mouse and dwarf lemurs (Primates, Cheirogaleidae). The Anatomical Record 291: 895–915. https://doi.org/10.1002/ar.20724

Smith TD, Eiting TP, Bhatnagar KP (2012) A quantitative study of olfactory, non-olfactory, and vomeronasal epithelia in the nasal fossa of the bat *Megaderma lyra*. Journal of Mammalian Evolution 19: 27–41. https://doi.org/10.1007/s10914-011-9178-6

Spoor F, Garland T, Krovitz G, Ryan TM, Silcox MT, Walker A (2007) The primate semicircular canal system and locomotion. Proceedings of the National Academy of Sciences 104: 10808–10812. https://doi.org/10.1073/pnas.0704250104

Stoner CJ, Bininda-Emonds ORP, Caro T (2003) The adaptive significance of coloration in lagomorphs. Biological Journal of the Linnean Society 79: 309–328. https://doi.org/10.1046/j.1095-8312.2003.00190.x

Tomida Y, Otsuka H (1993) First discovery of fossil Amami rabbit (*Pentalagus furnessi*) from Tokunoshima, southwestern Japan. Bulletin of the National Science Museum 19: 73–79. https://www.kahaku.go.jp/research/publication/geology/download/19_2/BNSM_C190203.pdf

Usui K, Tokita M (2018) Creating diversity in mammalian facial morphology: a review of potential developmental mechanisms. EvoDevo 9: 15. https://doi.org/10.1186/s13227-018-0103-4

Van Valkenburgh B, Curtis A, Samuels JX, Bird D, Fulkerson B, Meachen-Samuels J, Slater GJ (2011) Aquatic adaptations in the nose of carnivorans: evidence from the turbinates. Journal of Anatomy 218: 298–310. https://doi.org/10.1111/j.1469-7580.2010.01329.x

Van Valkenburgh B, Pang B, Bird D, Curtis A, Yee K, Wysocki C, Craven BA (2014) Respiratory and olfactory turbinals in feliform and caniform carnivorans: the influence of snout length. The Anatomical Record 297: 2065–2079. https://doi.org/10.1002/ar.23026S

Voit M (1909) Das Primordialcranium des Kaninchens unter Berücksichtigung der Deckknochen. Anatomische Hefte 38: 425–616.

Wagner F, Ruf I (2019) Who nose the borzoi? Turbinal skeleton in a dolichocephalic dog breed (*Canis lupus familiaris*). Mammalian Biology 94: 106–119. https://doi.org/10.1016/j.mambio.2018.06.005

Wagner F, Ruf I (2021) "Forever young"—Postnatal growth inhibition of the turbinal skeleton in brachycephalic dog breeds (*Canis lupus familiaris*). The Anatomical Record 304: 154–189. https://doi.org/10.1002/ar.24422

Wible JR, Hopson JA (1993) Basicranial evidence for early mammal phylogeny. In: Szalay FS, Novacek MJ, McKenna MC (Eds) Mammal Phylogeny – Mesozoic Differentiation, Multituberculates, Monotremes, Early Therians, and Marsupials. Springer, New York, NY, 45–62. https://doi.org/10.1007/978-1-4613-9249-1_5

Yamada F, Takaki M, Suzuki H (2002) Molecular phylogeny of Japanese Leporidae, the Amami rabbit *Pentalagus furnessi*, the Japanese hare *Lepus brachyurus*, and the mountain hare *Lepus timidus*, inferred from mitochondrial DNA sequences. Genes & Genetic Systems 77: 107–116. https://www.jstage.jst.go.jp/article/ggs/77/2/77_2_107/_article/-char/ja

Yamada F, Cervantes FA (2005) *Pentalagus furnessi*. Mammalian Species 782: 1–5.