

Ossification of the respiratory turbinate in Aves and its implications for non-avian dinosaurs

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Abstract In extant amniotes, the respiratory turbinate is a nasal structure unique to endotherms, birds and mammals. The presence of this structure is supposedly correlated with their high metabolic rates and is accordingly potentially informative in evaluating metabolic conditions of fossil forms such as non-avian dinosaurs. However, data of the position and shape of possible osteological correlates (OCs) of this structure in extant birds, which are necessary for exploring evidence of the respiratory turbinate in non-avian dinosaurs, are mostly lacking. Therefore, in the present study, ossification patterns of the respiratory turbinate among phylogenetically diverse extant birds were examined. We found that the presence or absence and degree of ossification were mostly phylogeny-dependent and that the positions of the OCs could vary irrespective of the identity of bones. The latter result suggests that the OCs of the respiratory turbinate may be recognized as a ridge on the dorsal to dorsolateral walls of the nasal cavity in non-avian dinosaurs if they indeed possessed this structure.

Key words: Aves, Dinosauria, Respiratory turbinate, Osteological Correlate

Introduction

A structure called the respiratory turbinate is present in the nasal cavity of the extant endotherms, i.e., mammals and birds (e.g., Lovegrove, 2017). It is a complex structure protruding into the nasal cavity and generally a scroll-like shape in birds (Bang, 1971). Because the respiratory turbinate increases the surface area of the nasal cavity (Jackson and Schmidt-Nielsen, 1964; Schmidt-Nielsen, 1981), it is considered enabling efficient heat and water exchanges that compensate extra heat and water losses caused by high lung ventilation rates typical of endotherms (Hillenius, 1992; 1994; Ruben *et al.*, 1996; Geist, 2000; Hillenius and Ruben, 2004). In addition, mammals and birds, which have achieved endothermy independently from each other, acquired respiratory turbinate convergently (Witmer, 1995b). Therefore, the correlation between endothermy and the presence of the respiratory turbinate appears fairly tight, making this structure potentially informative in evaluating the metabolic conditions of amni-

ote animals, especially fossil forms. Though functional implications of the presence or absence of the respiratory turbinate in non-avian dinosaurs have been intensively debated (Bakker, 1992; Ruben *et al.*, 1996; Paul, 2002; Hillenius and Ruben, 2004), as is the case with the one in the synapsid lineage (Hillenius, 1992; 1994; Crompton *et al.*, 2015), there still has been no consensus reached on whether non-avian dinosaurs really possessed it or not. Distinct evidence of the respiratory turbinate has not yet been found in specimens of non-avian dinosaurs. However, because the avian respiratory turbinate is cartilaginous in general (Bourke *et al.*, 2014), it is possible that non-avian dinosaurs possessed a similar condition. If this is the case, the lack of a fossilized turbinate does not necessarily indicate that they really lacked one.

In the context of the Extant Phylogenetic Bracket (EPB) approach for soft-tissue reconstructions in extinct species, the causal association between soft tissues and their Osteological Correlates (OCs) in their extant relatives is crucial (Witmer, 1995a). In the case of the respiratory turbinate in the avian lineage, such basic information is mostly lacking (Bourke *et al.*, 2014). In order to rectify this trend,

Table 1. List of the examined species and conditions of OCs or ossification of the respiratory turbine.

Species	Examined specimens/ CT data source	Condition	Species	Examined specimens/ CT data source	Condition	Species	Examined specimens/ CT data source	Condition
PALEOGNATHAE								
Struthioniformes			Phoenicopteriformes			Strigiformes		
<i>Struthio camelus</i>	Private specimen		<i>Phoenicopterus ruber</i>	YIO-65267**		<i>Srix leptogrammica</i>	NSM-PO 278	
Rheiformes			Charadriiformes			<i>Srix leptogrammica</i>	NSM-PO 429	
<i>Rhea americana</i>	Private specimen		<i>Chroicocephalus ridibundus</i>	NSM-PO 422		<i>Srix uralensis</i>	NSM-PO 557	
Apterygiformes			<i>Fratercula cirrhata</i>	NSM-PO 537		Bucerotiformes		
<i>Apteryx australis</i>	CM Birds S-245*	scroll	<i>Fratercula corniculata</i>	NSM-PO 577		<i>Buceros rhinoceros</i>	NSM-PO 481	
Casuariformes			<i>Larus crassirostris</i>	NSM-PO 195		<i>Tockas erythrorhynchus</i>	NSM-PO 539	
<i>Dromaius novaehollandiae</i>	Private specimen		<i>Scolopax mira</i>	NSM-PO		Coraciiformes		
Tinamiformes			<i>Scolopax rusticola</i>	NSM-PO 161		<i>Alcedo atthis</i>	YIO-72024**	
<i>Eudromia elegans</i>	NSM-PO 542		<i>Synthyris thorampus antiquus</i>	NSM-PO 428		<i>Halcyon coromanda</i>	NSM-PO 543	
NEOGNATHAE			<i>Uria aalge</i>	NSM-PO 565		<i>Megaceryle lugubris</i>	NSM-PO 77	
GALLOANSERES			AEQUORNITHES			<i>Megaceryle lugubris</i>	NSM-PO 540	
Galliformes			Gaviiformes			AUSTRALAVES		
<i>Chrysolophus amherstiae</i>	NSM-PO 256		<i>Gavia arctica</i>	NSM-PO 545		Falconiformes		
<i>Chrysolophus pictus</i>	NSM-PO 40		Sphenisciformes			<i>Falco peregrinus</i>	NSM-PO 245	ridge
<i>Coturnix japonica</i>	NSM-PO 147		<i>Pygoscelis adeliae</i>	NSM-PO 702		<i>Falco tinnunculus</i>	NSM-PO 391	
<i>Gallus gallus</i>	NSM-PO 37		Procellariiformes			Pittidiformes		
<i>Numida meleagris</i>	NSM-PO 23		<i>Ardeanna grisea</i>	NSM-PO 601		<i>Amazona oratrix</i>	NSM-PO 7	
<i>Pavo muticus</i>	NSM-PO 538		<i>Ardeanna tenuirostris</i>	NSM-PO 236		<i>Ara macao</i>	NSM-PO 492	ridge
<i>Phasianus colchicus</i>	NSM-PO 255		<i>Calonectris leucomelas</i>	NSM-PO 44		<i>Loriculus galgulus</i>	YIO-65405**	
<i>Phasianus versicolor</i>	NSM-PO 232		<i>Calonectris leucomelas</i>	NSM-PO 209		<i>Melospittacus undulatus</i>	NSM-PO 125	ridge
<i>Phasianus versicolor</i>	NSM-PO 272		<i>Fulmarus glacialis</i>	NSM-PO 330		<i>Melospittacus undulatus</i>	Private specimen	ridge
<i>Symnaticus soemmerringii</i>	NSM-PO		<i>Oceanodroma furcata</i>	NSM-PO 405		<i>Nymphicus hollandicus</i>	NSM-PO 5	ridge
Anseriformes			<i>Phoebastria albatrus</i>	NSM-PO 235		<i>Psittacula alexandri</i>	NSM-PO 52	ridge
<i>Aix galericulata</i>	NSM-PO 259		<i>Phoebastria nigripes</i>	NSM-PO 388		<i>Psittacus erithacus</i>	NSM-PO 490	ridge
<i>Anas acuta</i>	NSM-PO 434		<i>Phoebastria nigripes</i>	NSM-PO 390		Passeriformes		
<i>Anas platyrhynchos</i>	NSM-PO 155		<i>Pterodroma hypoleuca</i>	NSM-PO 291		<i>Corvus corone</i>	NSM-PO 263	
<i>Anser cygnoides</i>	NSM-PO 138		Ciconiiformes			<i>Corvus macrorhynchos</i>	NSM-PO 35	
<i>Aythya marila</i>	NSM-PO 68		<i>Ciconia nigra</i>	NSM-PO 16		<i>Corvus macrorhynchos</i>	NSM-PO 548	
<i>Brania hutchinsii</i>	NSM-PO 270		Suliformes			<i>Corvus macrorhynchos</i>	NSM-PO 604	
<i>Cygnus olor</i>	NSM-PO 98		<i>Phalacrocorax carbo</i>	NSM-PO 536		<i>Cyanopica cyanus</i>	NSM-PO 477	
NEOAVES			Pelecaniformes			<i>Cyanoptila cyanomelana</i>	NSM-PO 198	
Caprimulgiformes			<i>Ardea cinerea</i>	Private specimen	ridge	<i>Eophona personata</i>	NSM-PO 110	
<i>Caprimulgus indicus</i>	NSM-PO 133		<i>Butorides striata</i>	NSM-PO 413		<i>Hypsipetes amaurotis</i>	NSM-PO 33	
Cuculiformes			<i>Gorsachius gossagi</i>	NSM-PO 117		<i>Hypsipetes amaurotis</i>	NSM-PO 34	
<i>Cuculus saturatus</i>	NSM-PO 120		<i>Nycticorax nycticorax</i>	NSM-PO 150	ridge	<i>Hypsipetes amaurotis</i>	NSM-PO 501	
Columbiformes			<i>Nycticorax nycticorax</i>	NSM-PO 276	ridge	<i>Leiothrix lutea</i>	NSM-PO 588	
<i>Columba livia</i>	NSM-PO 148		<i>Nycticorax nycticorax</i>	NSM-PO 607	ridge	<i>Lonchura atricapilla</i>	NSM-PO 71	
Strapiiformes			<i>Threskiornis melanoleuca</i>	NSM-PO 201		<i>Lonchura oryzivora</i>	NSM-PO 82	ridge
<i>Streptopelia orientalis</i>	NSM-PO 504		TELLURAVES			<i>Lonchura striata</i>	NSM-PO 184	
Gruiformes			Accipitriformes			<i>Loxia curvirostra</i>	NSM-PO 595	
<i>Antigone vipio</i>	NSM-PO 534		<i>Accipiter gentilis</i>	NSM-PO 12		<i>Motacilla alba</i>	NSM-PO 594	
<i>Gallinula chloropus</i>	NSM-PO 179		<i>Aegypius monachus</i>	NSM-PO 127	scroll	<i>Motacilla cinerea</i>	NSM-PO 514	
<i>Gruus carunculata</i>	NSM-PO 203		<i>Cathartes aura</i>	NSM-PO 540		<i>Passer montanus</i>	NSM-PO 505	
<i>Gruus grus</i>	NSM-PO 268		<i>Gyps bengalensis</i>	NSM-PO 546	scroll	<i>Stipitarius varius</i>	NSM-PO 118	
<i>Gruus paradisaea</i>	NSM-PO 251		<i>Haliaeetus albicilla</i>	NSM-PO 533	scroll	<i>Spinus spinus</i>	NSM-PO 591	
<i>Rallus aquaticus</i>	NSM-PO 530		<i>Vultur gryphus</i>	NSM-PO 392	scroll	<i>Spondopar cinereus</i>	NSM-PO 47	
						<i>Terpsiphone atrocaudata</i>	NSM-PO 62	ridge
						<i>Terpsiphone atrocaudata</i>	NSM-PO 450	
						<i>Turdus eunomus</i>	NSM-PO 73	
						<i>Zosterops japonicus</i>	NSM-PO 45	

The classification scheme follows Gill *et al.* (2021). Note: *, CT data sets provided by L. M. Witmer; **, CT data sets provided by YIO database.

this study examined OCs of this structure in birds and discussed potential positions of its OCs in the nasal cavity of fossil taxa on the lineage leading to birds. Because the avian turbinate rarely ossifies (Bourke *et al.*, 2014), it is not reasonable to reliably identify its OCs based solely on observations of dry skulls. However, some birds possess an ossified turbinate (Bang, 1971; Zusi, 1993). Skulls of such birds were examined in detail to produce reference data for identifying the positions and form of possible OCs in non-avian dinosaurs.

Institutional Abbreviations

CM, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, U.S.A.; CMNH, Cleveland Museum of Natural History, Cleveland, Ohio, U.S.A.; NSM-PO, National Museum of Nature and Science, Tsukuba, Ibaraki, Japan; OUVC, Ohio University Vertebrate Collections, Athens, Ohio, U.S.A.; YIO, Yamashina Institute for Ornithology, Abiko, Chiba, Japan.

Materials and Methods

99 species of extant birds belonging to 26 order-level clades were examined based on dry skulls or X-ray computed tomographic (CT) scan data sets of the heads of 112 specimens in total (Table 1). For each species, the degree of the ossification and attachment position of the respiratory turbinate were recorded. In addition, in order to infer the phylogenetic timing of turbinate ossification, ancestral state reconstruction on avian phylogeny was performed using the parsimony method by Mesquite version 3.61 (Maddison and Maddison, 2019). The tree topology for the analysis was obtained from the BirdTree.org website (Jetz *et al.*, 2012, 2014).

Results

The results are summarized in Tables 1 and 2. Whereas only cartilaginous turbinate was observed in most major clades, ossified turbinate was present in Accipitriformes and Psittaciformes, as well as in a few species in other clades (Table 2). The degree of ossification of the respiratory turbinate also varied among these clades. In Accipitriformes, turbi-

Table 2. Ratio of the number of species possessing OCs of the respiratory turbinate or ossified turbinate/the number of the examined species in each clade. If a single species contained individuals both with and without an ossified turbinate/ridge, it was counted for possessing the structure.

Species	Ratio
PALEOGNATHAE	1/5
Struthioniformes	0/1
Rheiformes	0/1
Apterygiformes	1/1
Casuariiformes	0/1
Tinamiformes	0/1
NEOGNATHAE	14/94
GALLOANSERES	0/16
Galliformes	0/9
Anseriformes	0/7
NEOAVES	14/78
Caprimulgiformes	0/1
Cuculiformes	0/1
Columbiformes	0/2
Gruiformes	0/6
Phoenicopteriformes	0/1
Charadriiformes	0/8
AEQUORNITHES	2/17
Gaviiformes	0/1
Sphenisciformes	0/1
Procellariiformes	0/8
Ciconiiformes	0/1
Suliformes	0/1
Pelecaniformes	2/5
TELLURAVES	12/42
Accipitriformes	4/6
Strigiformes	0/2
Bucerotiformes	0/2
Coraciiformes	0/3
AUSTRALAVES	8/29
Falconiformes	1/2
Psittaciformes	5/7
Passeriformes	2/20

nate ossified extensively enough to remain as a scroll-like structure in the skull across the clade (Fig. 1A). It protruded from the roof of the bony nasal cavity. In Psittaciformes, the turbinate did not ossify but left a ridge as an OC on the roof of the nasal cavity (Fig. 1B). The examined skull of the falconiform *Falco peregrinus* preserved a bony scroll turbinate projecting into the nasal cavity from the lateral wall. Although the respiratory turbinate did not ossify in Pelecaniformes or Passeriformes in general, *Ardea cinerea*, *Nycticorax nycticorax*, *Lonchura oryzivora* and *Terpsiphone atrocaudata* were exceptions in leaving bony ridges as OCs (Fig. 1C). In Paleognathae, *Apteryx australis* is the exception in possessing a fully ossified turbinate.

In birds having robustly ossified beaks such as accipitriforms and psittaciforms, it is hardly possible to draw clear borders among bones contributing

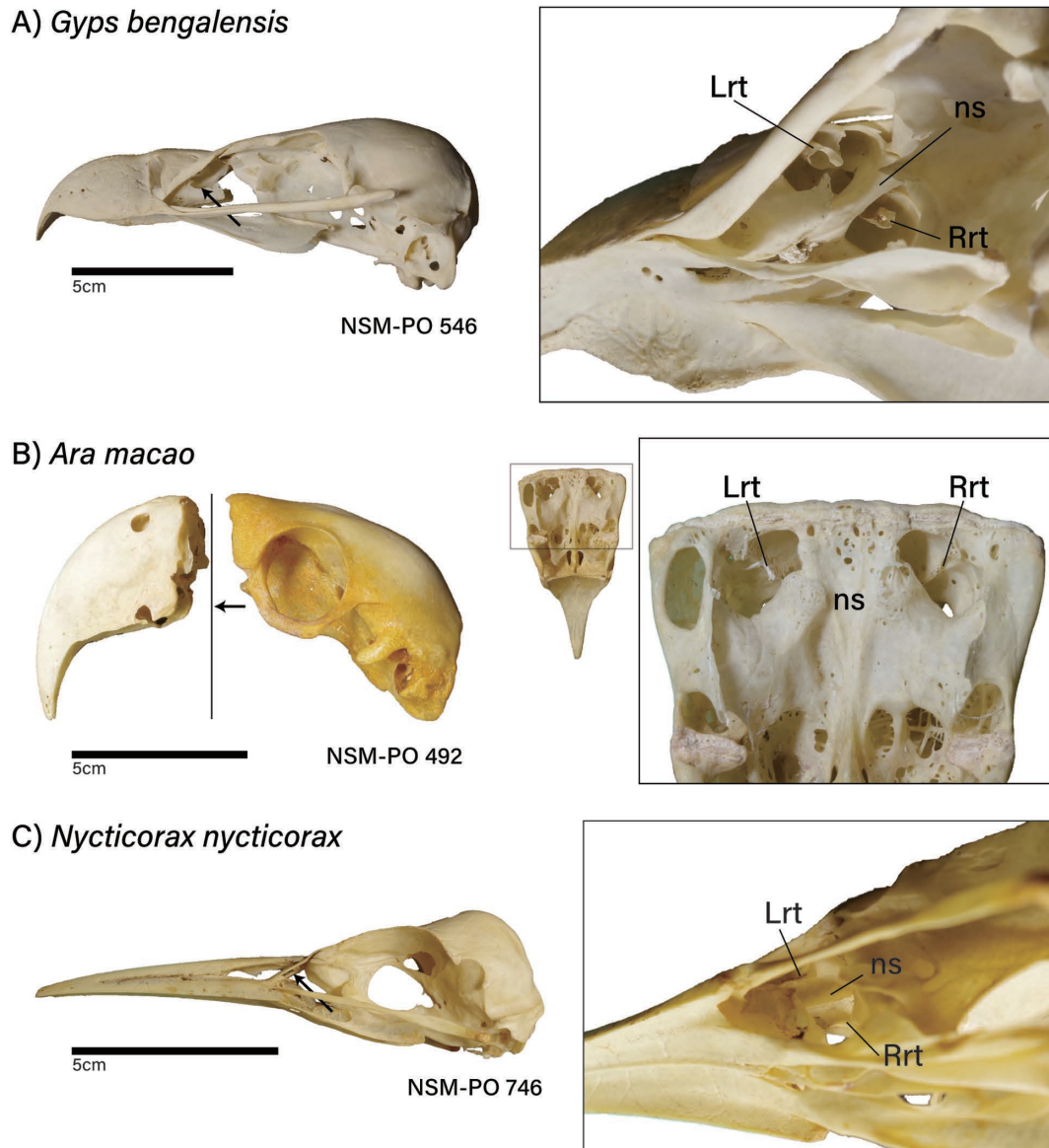


Fig. 1. Ossified ridges or turbinates in the skulls of *Gyps bengalensis* (A), *Ara macao* (B), and *Nycticorax nycticorax* (C). The arrow in each whole skull on left side indicates the direction of the close-up view on right side. Abbreviations: Lrt, left respiratory turbinate; ns, nasal septum; Rrt, right respiratory turbinate.

to the beak, i.e., premaxilla, maxilla, palatine and nasal. However, their respiratory turbinate appears to leave ridges or scrolls on the nasal, maxilla or both among the beak-forming bones (Heilman, 1926; Knutsen, 2007; Jansen, 2008) although the positions of these structures vary among species.

CT-scan images of heads of the species that were either found to have the OCs as described above or belonged to the same order-level clade as such species showed that these OCs were indeed associated with the respiratory turbinate (Fig. 2A). In Paleognathae (*Struthio camelus*, *Rhea americana* and *Dromaius novaehollandiae*) and some species belonging to other clades, dry skulls sometimes maintain ridges on the roof (dp in Fig. 2B). How-

ever, such ridges represent curling edges of the dorsal plate of the mesethmoid (Ali *et al.*, 2008), which support the lateral wall of the olfactory cavity and the olfactory turbinate as described in Bourke *et al.* (2014). These ridges ossifies more often than the OCs for the respiratory turbinate. Similar, paired ridges were present on the roof of the nasal cavity in *Phoebastria nigripes* (pr; Fig. 2C). However, these ridges were not associated with either respiratory or olfactory turbinate and can be distinguished from the ridges in other birds observed in this study in the following aspects. First, the contralateral ridges in *P. nigripes* anteriorly merged with each other as well as with a median septum. This is a condition that is not present in the ridge associated with the

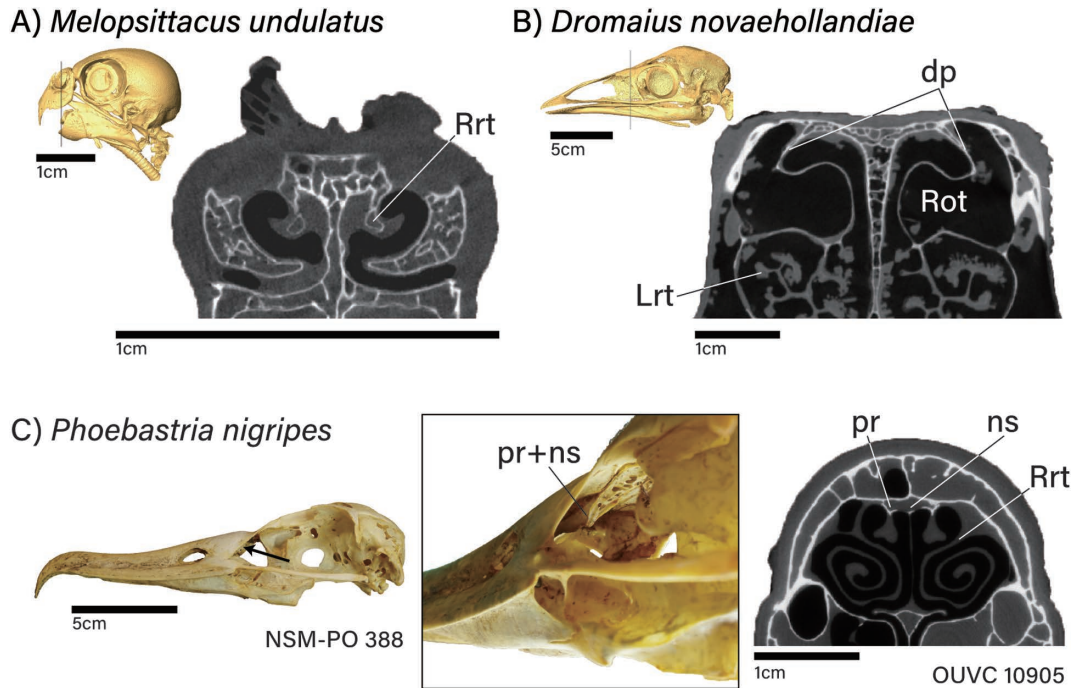


Fig. 2. Cross-sectional CT-scan images showing ossified ridges in the nasal cavity that are either associated with the respiratory turbinate (A, *Melopsittacus undulatus*) or not (B and C, *Dromaius novaehollandiae* and *Phoebeastria nigripes*, respectively). The dorsal plate of the mesethmoid in *D. novaehollandiae* supports the lateral wall of the olfactory cavity and the olfactory turbinate (B) whereas ridges in *P. nigripes* (termed pseudo-ridges herein) is not associated with seither respiratory or olfactory turbinate (C). Abbreviations: dp, dorsal plate; Lrt, left respiratory turbinate; ns, nasal septum; pr, pseudo-ridge; Rot, right olfactory turbinate; Rrt, right respiratory turbinate.

respiratory turbinate. In addition, they were positioned much more medially than the ridge supporting the respiratory turbinate in other birds. The position of the paired protrusions supported by these ridges in *P. nigripes* suggests that they may serve the olfactory function as does the olfactory turbinate (Bang, 1971, fig. 7 [3]).

Discussion

Among extant birds, the degree of ossification of the respiratory turbinate depends on their phylogenetic positions to some extent: it ossifies in most species belonging to Accipitriformes and Psittaciformes. This result may indicate that its ossification is related to the degree of beak ossification because the latter is high in Accipitriformes and Psittaciformes. In addition, the position of the ridge supporting the turbinate varies among species, ranging from the lateral to the dorsal walls of the nasal cavity proper, and is apparently not dependent on the homology of the bones, that is, the ridge may be positioned on the nasal or maxilla. This may be explained by the fact that the nasal capsule is a cartilaginous element developmen-

tally independent of other elements of the chondrocranium or membranous cranial bones (de Beer, 1937). More detailed studies focusing on morphogenesis of the respiratory turbinate are necessary in order to confirm that its attachment is indeed independent of the identity of adult bones and can have variable positions in the main nasal airway.

The result of ancestral state reconstruction of the presence/absence of ossification shows that the most recent common ancestor of Aves lacked an ossified respiratory turbinate whereas ossification occurred independently for several times in this clade (Fig. 3). There is still no consensus regarding the avian phylogeny, especially the relationship among major clades (e.g., Jetz *et al.*, 2012; 2014; Prum *et al.*, 2015). Regardless of which Avian tree topology is adopted, however, the lack of an ossified turbinate ancestrally in Aves and later, independent ossification in several clades found in the present result will hold.

The above observations on robustly-beaked clades indicate that the OC for the respiratory turbinate may be recognized as a ridge positioned on the dorsal to dorsolateral walls of the nasal cavity proper if a fossil species of Avemetatarsalia indeed had the structure. It

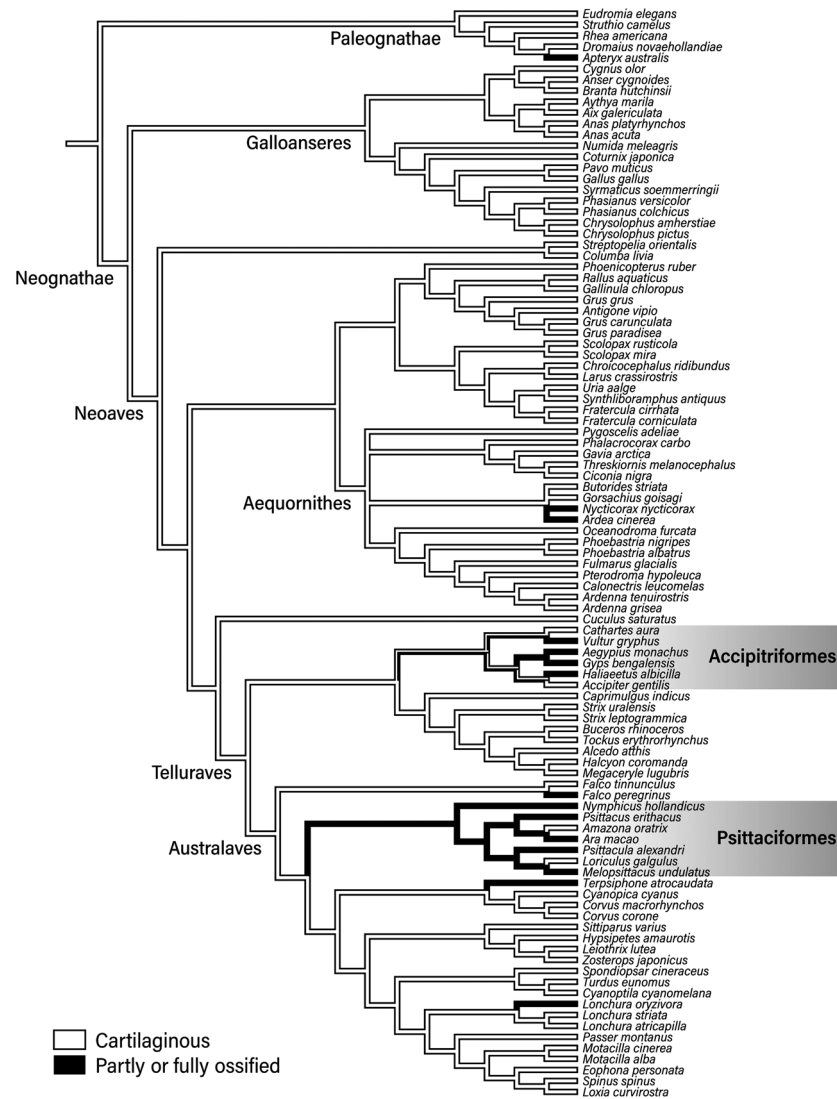


Fig. 3. Ancestral reconstruction of the presence/absence of the ossified turbinate by the parsimony method. The tree topology was obtained from the BirdTree.org website (Jetz *et al.*, 2012, 2014).

is noteworthy that the presence or absence of the OC varied even among several specimens of *Terpsiphone atrocaudata* (Table 1), suggesting that a fossil taxon may also show similar individual variations. Furthermore, the ridge supporting the olfactory turbinate as seen in Paleognathae needs to be distinguished from the one associated with the respiratory turbinate in fossil taxa. In the case of non-avian theropod dinosaurs, both the nasal cavity proper and olfactory region extended rostrocaudally (Witmer and Ridgely, 2009), potentially making the positions of the respiratory and olfactory turbinates rather distant from each other. Such a condition may facilitate identification of a certain OC of the respiratory turbinate and distinction from the olfactory one.

Previously, Witmer and Ridgely (2010) identified a possible respiratory turbinate in CT-scan images

of CMNH 7541 (either *Nanotyrannus* or a juvenile *Tyrannosaurus*) that appears vaguely within matrix associated with both the nasal and the maxilla. Bourke *et al.* (2014) proposed a ridge on the roof of the nasal cavity in Pachycephalosauridae, particularly *Stegoceras validum*, as a putative OC. Whether non-avian dinosaurs really had the respiratory turbinate or not remains uncertain because, in the context of the EPB approach, the second closest bracketing taxon, Crocodylia, lacks the turbinate, making the inference equivocal (Level II inference; Witmer, 1995a), as well as because the structure was so fragile that it would be rarely preserved in the fossil record even if it had really existed (Bourke *et al.*, 2014). However, the possible position of the OC identified in this study is consistent with those of the structures suggested as evidence of

their possessing the respiratory turbinate by Witmer and Ridgely (2010) and Bourke *et al.* (2014), thus providing some support for their arguments.

Acknowledgements

Several CT-scan data sets were obtained from YIO specimen database (decochan.net). The CT-scan data sets of *Apteryx australis* (CM Birds S-245) and *Phoebastria nigripes* (OUVC 10905) were provided by L. M. Witmer (Ohio University, Athens, Ohio, U.S.A.), with the latter being available at MorphoSource (morphosource.org; Media ID 000078054). An anonymous reviewer made constructive suggestions that improve the clarity of the manuscript. S.T. was supported by the Sasakawa Scientific Research Grant 2021–5012 from the Japan Science Society.

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