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On the occurrence of lateral openings and fossae (pleurocoels) in the thoracic vertebrae of neornithine birds and their functional significance

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Abstract

The occurrence of lateral openings and pleurocoels (lateral fossae) in the corpus of the thoracic vertebrae of extant and fossil neornithine birds is reviewed, with both features having been identified as osteological correlates of the avian pulmonary system. Openings mainly occur in larger species with a high overall bone pneumatization but do not seem to serve for the passage of lung or air sac diverticula. Pleurocoels, on the other hand, are not directly related to pneumatic features and constitute a plesiomorphic trait that was widespread in Mesozoic non-neornithine birds. It is noted that an inverse correlation exists between the occurrence of pleurocoels and the pneumatization of the humerus, with pleurocoels being mainly found in extant and fossil taxa, in which the humerus is not pneumatized by diverticula of the clavicular air sac. Here it is hypothesized that pleurocoels primarily serve to increase the structural resistance of the vertebral body and were reduced multiple times in neornithine birds. In some taxa, their reduction may be related to the development of the furcula, which assists ventilation of the clavicular and cervical air sacs and may thereby contribute to the pneumatization of both, the humerus and the thoracic vertebrae. If so, Mesozoic non-neornithine birds, which had a rigid furcula with massive shafts as well as non-pneumatic humeri and pronounced pleurocoels, are likely to have differed in functional aspects of their air sac system from extant birds.

Key words

Introduction

Birds have a unique respiratory system, which is very different from that of all extant non-avian land vertebrates. Unlike in other tetrapods, the lungs of birds are rigid and dorsally fixed to the vertebral column and ribs, and their ventilation is enhanced by a system of air sacs, which regulate a unidirectional air flow through the lungs (Duncker 1971; McLelland 1989). Some of these air sacs form diverticula that invade surrounding bones, with the associ-ated foramina representing osteological correlates of the avian pulmonary system.

Skeletal features related to bone pneumatization are distributed over the entire avian skeleton and involve traits (such as pneumatic foramina, heavily trabeculated bone structures, and hollow bone shafts) associated with the skull, major limb and pectoral girdle bones, as well as the vertebral column (e.g., Gutherz and O'Connor 2021).

In particular, the pneumatization of the vertebrae played an important role in inferences on the occurrence of air sacs in non-avian dinosaurs (e.g., Sereno et al. 2007, 2008; Wedel 2009). Two features are of main interest in this regard: foramina enabling the passage of pneumatic structures and pleurocoels, that is, marked fossae on the lateral surfaces of the bodies of the thoracic vertebrae.

An overview of pneumatic structures associated with the vertebrae of archosaurs was given by O'Connor (2006), who replaced the long-established term pleurocoel with "pulmonary fossa". O'Connor (2006) detailed that these are associated with different anatomical structures in crocodilians and birds, including fat deposits (in the thoracic vertebrae of crocodilians), musculature (in the caudal vertebrae of crocodilians), as well as pulmonary tissue of the lungs (in the thoracic vertebrae of birds). However, this study had a major focus on non-avian dinosaurs and only examined a restricted taxonomic sample of extant birds. In their comprehensive morphological character matrix, Livezey and Zusi (2006) scored the presence of lateral openings ("foramina pneumatica"; character 850) in various taxa, but the occurrence of pleurocoels (character 851) was only assessed for Mesozoic birds and coded as unknown for all extant taxa.

Centrally situated openings in the lateral surfaces of the body of the thoracic vertebrae occur in crocodilians (O'Connor 2006: fig. 9C) and non-avian theropods (e.g., Britt et al. 1998: fig. 3a; Currie et al. 2015: fig. 2A). As yet, however, and to the best of my knowledge, these have not been reported from Mesozoic birds. Well-developed pleurocoels on the thoracic vertebrae, by contrast, are present in a large number of Mesozoic birds outside the avian crown group (Neornithes). Even though they are absent in *Archaeopteryx* (Mayr et al. 2007; Wellnhofer 2009) and restricted to the caudalmost thoracic vertebrae in the Sapeornithiformes (Zhou and Zhang 2003), pronounced pleurocoels occur in the Confuciusornithiformes (Chiappe et al. 1999), Enantiornithes (Chiappe and Walker 2002: fig. 11.4; Atterholt et al. 2018: fig. 2H), and Mesozoic taxa of the Ornithuromorpha, such as *Apsaravis* (Clarke and Norell 2002), *Yixianornis* (Clarke et al. 2006), *Yanornis* (Zhou and Zhang 2001), *Gansus* (You et al. 2006), as well as the Ichthyornithiformes (Clarke 2004: fig. 40) and Hesperornithiformes (Bell and Chiappe 2020). The distribution of this feature suggests that marked pleurocoels are plesiomorphic for the Pygostylia, the clade encompassing the Confuciusornithiformes, Enantiornithes, and Ornithuromorpha, with the latter including extant birds (Neornithes).

As detailed below, pleurocoels were identified in various Cenozoic neornithine birds, the closest extant relatives of which lack these structures. The present study not only aims at providing an overview of lateral openings and pleurocoels in the bodies of the thoracic vertebrae of extant and fossil neornithine birds, but also addresses some functional aspects of these features. For the first time, a correlation between the occurrence of pleurocoels and the absence of a pneumatization of the humerus is noted, which may open a new view on the correlated evolution of some postcranial skeletal features of birds.

Material and methods

Concerning extant birds, this study is based on an examination of skeletons of multiple representatives of all extant higher-level clades in the collection of Senckenberg Research Institute Frankfurt (SMF). In higher-level groups ("families" and "orders"), for which pleurocoels or lateral openings have not been previously reported, only random sampling of a few individuals was performed, whereas taxonomic sampling was dense in the Anseriformes, Procellariiformes, Gruiformes, and Charadriiformes, where multiple representatives of all genus-level taxa in the collection were examined (see http://sesam.senckenberg.de for the holdings of bird skeletons in the ornithological collection of SMF). Furthermore available were the pulmonary injection preparations of Hans-Rainer Duncker (Duncker 1971), which were also consulted by O'Connor (2006) and are now deposited in Senckenberg Research Institute Frankfurt.

Livezey and Zusi (2006) noted that "[t]he term "pleurocoel" is properly restricted to true, essentially circular atria or depressions that *penetrate* the corpus to admit diverticulae pneumaticae [sic], features distinct from mere excavations or depressions" (Livezey and Zusi 2006: p. 140, character 851). Other authors likewise applied the term to openings in the lateral body of the thoracic vertebrae (e.g., Sereno et al. 2007; Novas et al. 2008; Rauhut et al. 2018). Under this definition, however, pleurocoels would be homologous to openings in the vertebral body, and there exists little reason to restrict the use of the term pleurocoel in such way. Etymologically, the word is derived from πλευρά (pleura: side) and κοῖλος (koilos: hollow, concave), denoting mere lateral depressions rather than pneumatic features. In the following, the term pleurocoel is therefore used for pronounced, subovate lateral depressions on the vertebral body, irrespective of whether these are related to pneumatic structures. The term lateral openings, as used in the following, corresponds to the central pneumatic foramen or central vascular foramen, respectively, of O'Connor (2006).

Institutional abbreviations: AMNH – American Museum of Natural History, New York, USA; MGUH – Geological Museum, Copenhagen, Denmark; NHMUK – Natural History Museum, London, UK; SMF – Senckenberg Research Institute Frankfurt, Germany; UM – University of Michigan, Museum of Paleontology, Ann Arbor, USA.

Results

The occurrence of lateral openings

In crocodilians, centrally situated foramina on each of the lateral surfaces of the body of the thoracic (dorsal) vertebrae serve for the passage of blood vessels and nerves (O'Connor 2006: fig. 9C). Similarly sized and shaped
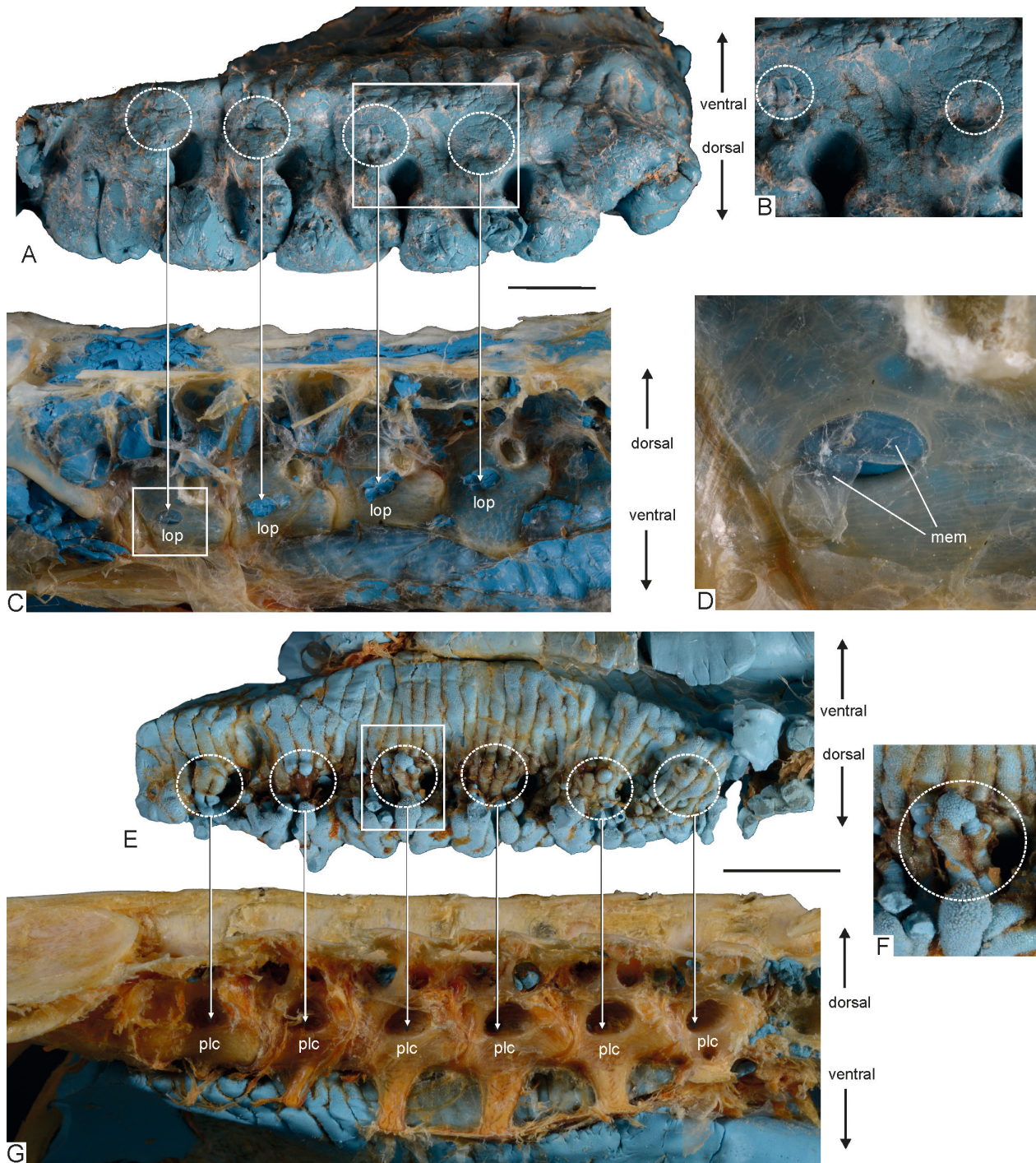
Figure 1. Pulmonary injection preparations from the collection of Hans-Rainer Duncker: **A–D**, *Chauna torquata* (Anseriformes, Anhimidae); **A** depicts the latex cast of the right lung (rotated by 180°), in **C** the corresponding part of the vertebral column (caudalmost thoracic vertebrae, right side) of the same specimen is shown; **B** and **D** are details of the framed areas in **A** and **C**. **E–G**, *Fulmarus glacialis* (Procellariiformes, Procellariidae); **E** depicts the latex cast of the right lung (rotated by 180°), in **G** the corresponding part of the vertebral column (caudalmost thoracic vertebrae, right side) of the same specimen is shown; **F** is a detail of the framed area in **E** showing a "pulmonary protuberance" (encircled) sensu O'Connor (2006). The dotted circles in **A** and **E** denote the latex casts of the lateral openings and pleurocoels, respectively. Abbreviations: lop, lateral opening; mem, membrane covering lateral opening; plc, pleurocoel. The scale bars equal 10 mm.

openings occur in the thoracic vertebrae of some neornithine taxa, but just by an examination of the vertebrae alone, it is not possible to ascertain whether they represent neurovascular or pneumatic features.

　　Lateral openings in the thoracic vertebrae are particularly well developed in the anseriform Anhimidae (Fig.

1A–D, 2A). A pulmonary injection preparation of *Chauna torquata* from the Duncker collection shows them to be filled with the latex injection mass (Fig. 1C). Even though the structures are therefore associated with pneumatic traits, the injection mass within the vertebrae is not conjoined with the latex cast of the lungs (Fig. 1A, B)
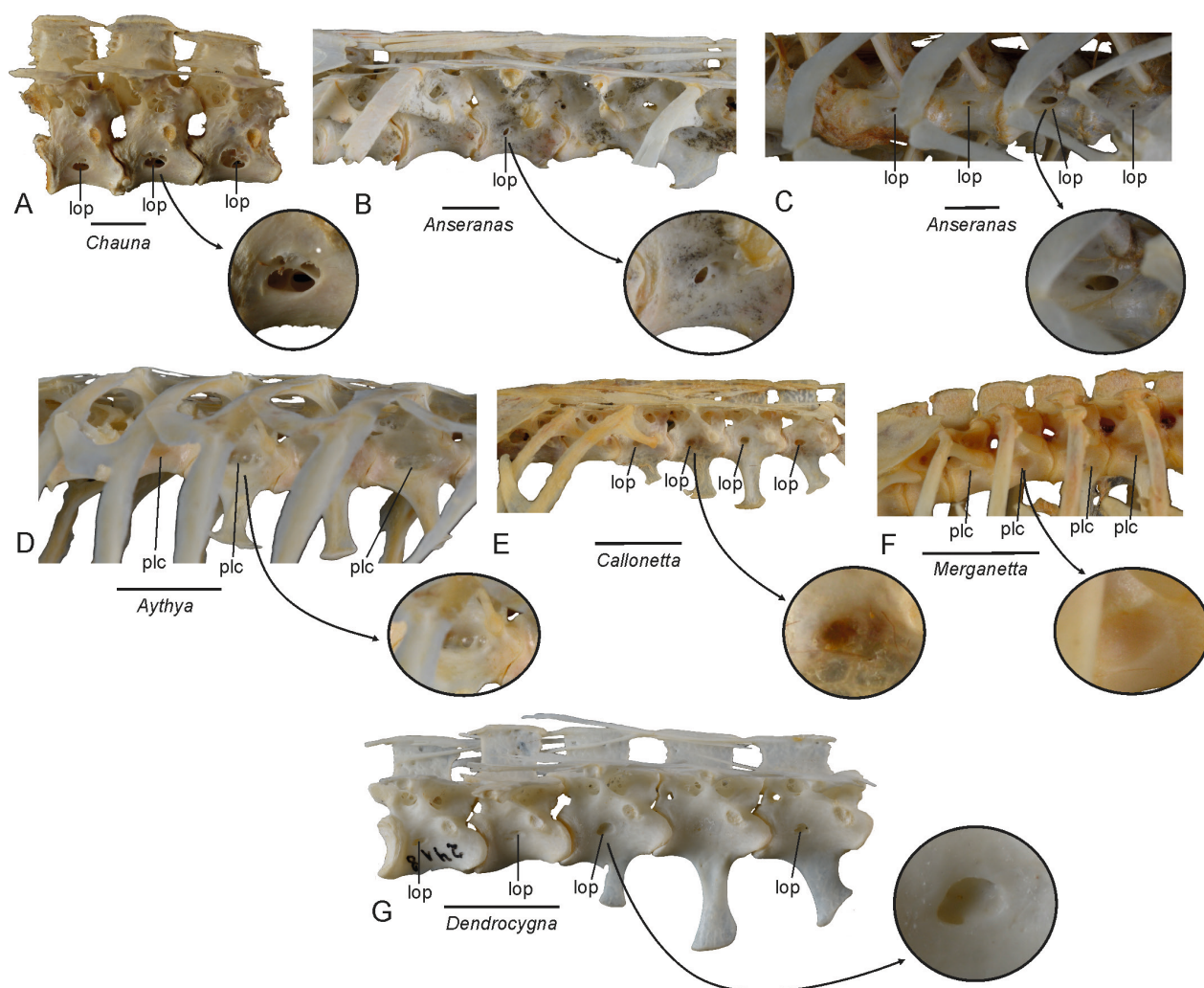
Figure 2. Caudalmost thoracic vertebrae of anseriform birds in right lateral view. **A**, *Chauna torquata* (Anhimidae; SMF 11885).
B, *Anseranas semipalmata* (Anseranatidae; SMF 19902). **C**, *A. semipalmata* (SMF 11276). **D**, *Aythya australis* (Anatidae; SMF
17945). **E**, *Callonetta leucophrys* (Anatidae; SMF 18330). **F**, juvenile *Merganetta armata* (Anatidae; SMF 14859). **G**, *Dendrocygna
viduata* (Anatidae; SMF 2418). Abbreviations: lop, lateral openings; plc, pleurocoel. The scale bars equal 10 mm.

and some of the openings are at least partially closed by
a membrane (Fig. 1D). Therefore, they do not appear to
serve for the passage of lung or air sac diverticula and
may actually represent fenestrae rather than foramina.

   Lateral openings also occur in the thoracic vertebrae of
other anseriform birds, in which their occurrence is, however,
more variable. These openings are present in some
individuals of *Anseranas semipalmata* (Anseranatidae;
Fig. 2B, C), and within the Anatidae they occur in the
Dendrocygninae, most taxa of the Aythyini (*Amazonetta*,
Marmaronetta, *Pteronetta*, *Netta*, *Asarcornis*, *Cairina*,
Aix), the taxa *Callonetta* and *Malacorhynchus*, as well
as a few species of the Anatini (*Anas erythrorhyncha*).
Lateral openings are furthermore found in the cranial
thoracic vertebrae of some Anserini (e.g., *Branta sandvicensis*;
O'Connor 2006: fig. 2B), whereas they are absent
in the Oxyurini, Mergini, Tadornini, and most Anatini.
Openings are also absent in *Chenonetta* and *Sarkidiornis*,
which resulted as sister taxa of other Aythyini in an analysis
by Gonzalez et al. (2009).

   Centrally located lateral openings in the corpus of all
or most thoracic vertebrae are likewise present in the
gruiform Gruoidea (Gruidae, Aramidae, and Psophiidae;
Fig. 3D–F), the procellariiform Diomedeidae (Fig. 4A),
and in the Opisthocomiformes (Fig. 3M). Among taxa
of the Aequornithes (the clade including most aquatic
and semi-aquatic neornithine birds), lateral openings are
found in the Phaethontiformes (Fig. 3B), Sulidae (Fig.
3A), Balaenicipitidae (Fig. 3C), and Scopidae. Small and
irregularly distributed openings in the lateral surfaces
of the thoracic vertebrae are also found in some Otidiformes
(e.g., *Ardeotis kori*; Fig. 3G, H), Musophagiformes
(*Corythaeola cristata*; Fig. 3L); some Accipitriformes
(Cathartidae, Sagittariidae, and a few large-sized
Accipitridae, such as *Haliaeetus*; Fig. 3I, J) and some
Strigiformes (*Bubo*; Fig. 3K). A few Procellariiformes
(e.g., *Macronectes halli*, *Calonectris diomedea*), some
Laridae (e.g., *Larus audouinii*), and *Anous stolidus* (Fig.
4I) furthermore exhibit multiple openings within pleurocoels.

   Concerning fossil neognathous taxa, centrally positioned
lateral openings in the bodies of the thoracic vertebrae
occur in the early Paleogene Lithornithidae (Fig. 5A;
Houde 1988: 21; Bourdon and Lindow 2015), whereas
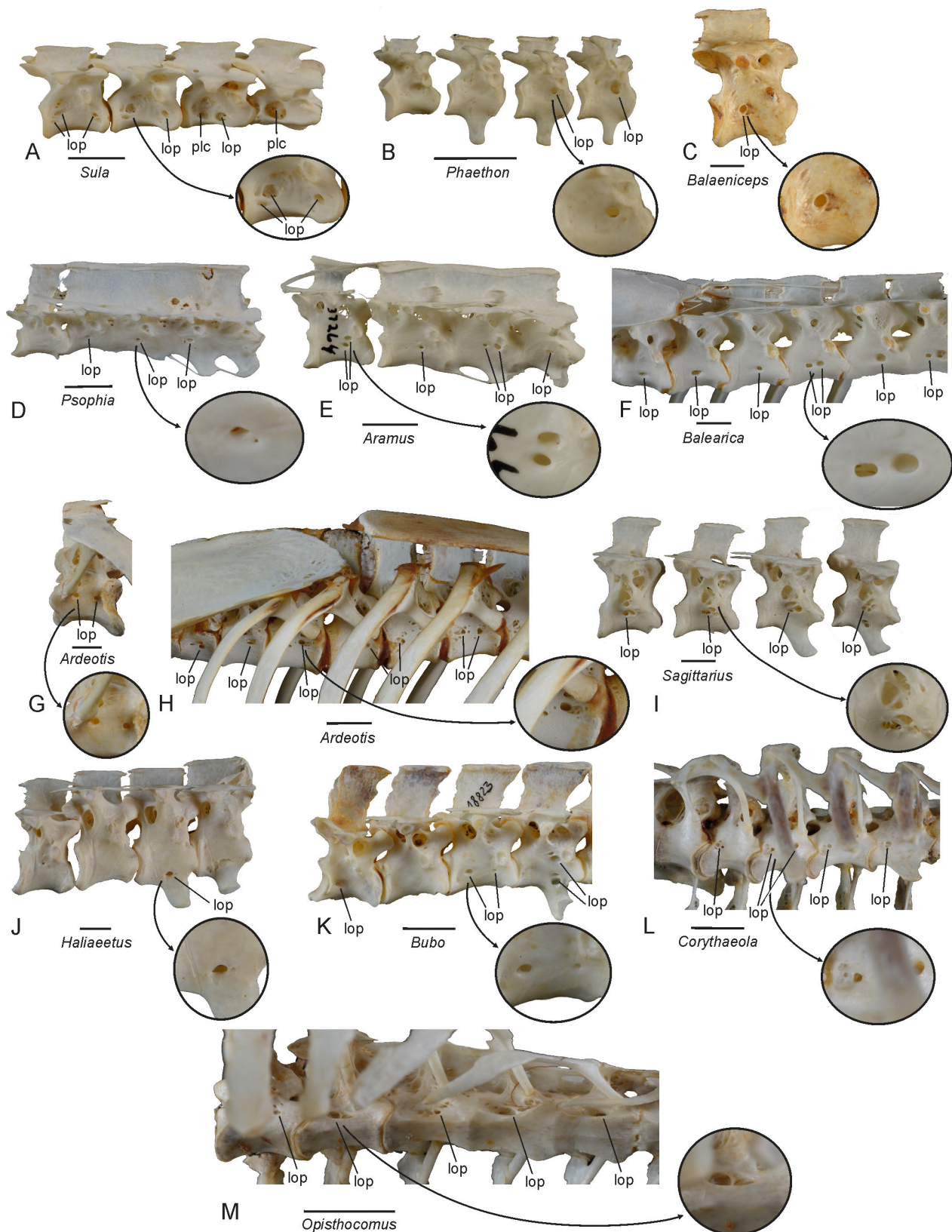
Figure 3. Caudalmost section of thoracic spine and isolated thoracic vertebrae of various neornithine birds with lateral openings (lop) and pleurocoels (plc) in the vertebral corpus (lateral or lateroventral view). **A**, *Sula leucogaster* (Sulidae; SMF 9574). **B**, *Phaethon lepturus* (Phaethontidae; SMF 9969). **C**, *Balaeniceps rex* (Balaenicipitidae; SMF 6293; last but two thoracic vertebra). **D**, *Psophia leucoptera* (Psophiidae; SMF 9576). **E**, *Aramus guarauna* (Aramidae; SMF 9970). **F**, *Balearica regulorum* (Gruidae; SMF 19959). **G**, *Ardeotis kori* (Otididae; SMF 11797 last but one thoracic vertebra). **H**, juvenile *A. kori* (SMF 19961). **I**, *Sagittarius serpentarius* (Sagittariidae; SMF 445). **J**, *Haliaeetus albicilla* (Accipitridae; SMF 1522). **K**, *Bubo bubo sibiricus* (Strigidae; SMF 18823). **L**, *Corythaeola cristata* (Musophagidae; SMF 15047). **M**, *Opisthocomus hoazin* (Opisthocomiformes; SMF 1546). The scale bars equal 10 mm.
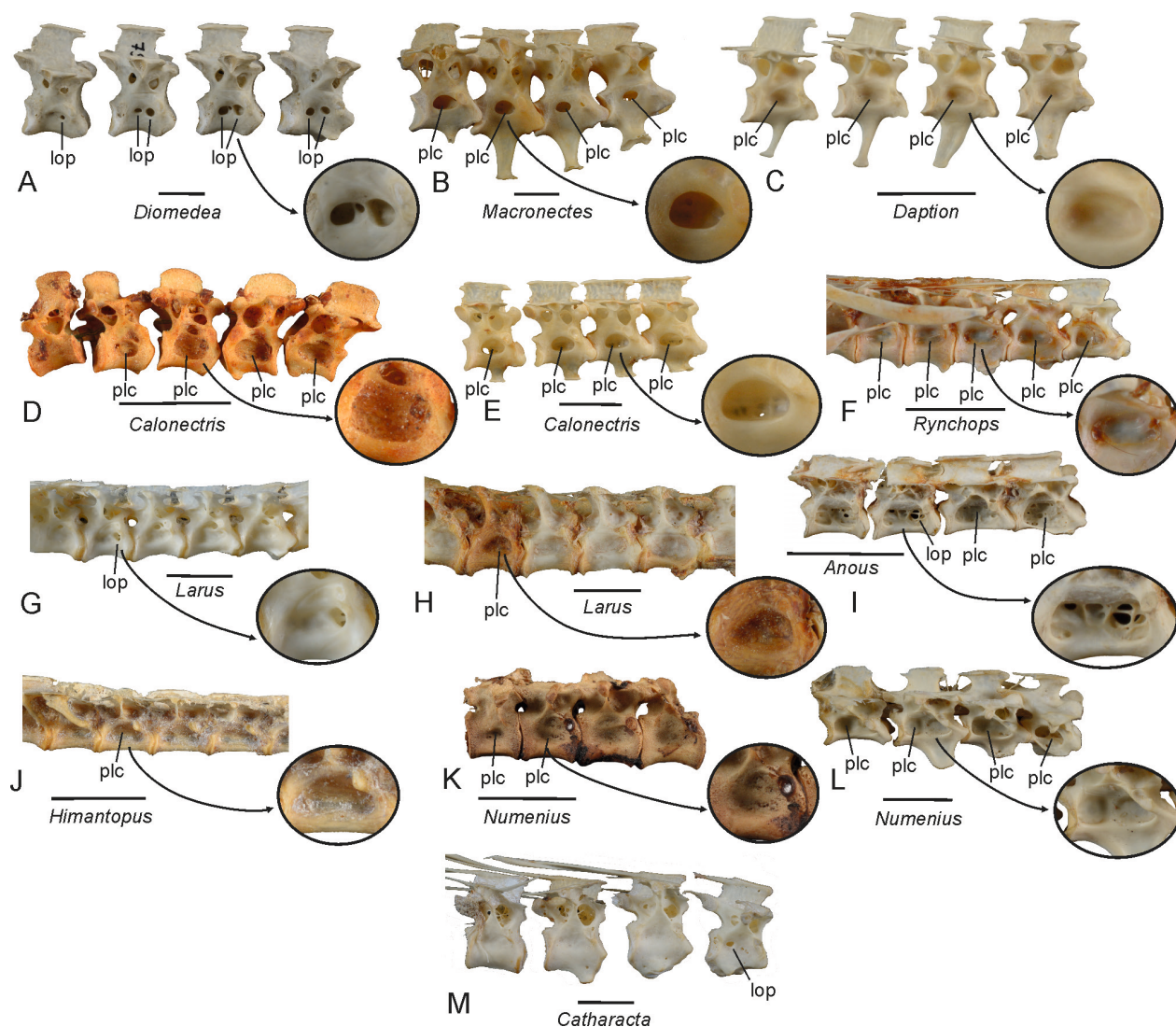
Figure 4. Caudalmost thoracic vertebrae of procellariiform (**A–E**) and charadriiform (**F–M**) birds in right lateral view. **A**, *Diomedea melanophris* (Diomedeidae; SMF 7570). **B**, *Macronectes halli* (Procellariidae; SMF 8949). **C**, *Daption capense* (Procellariidae; SMF 3728). **D**, juvenile *Calonectris diomedea edwardsii* (Procellariidae; SMF 932). **E**, *Calonectris diomedea borealis* (Procellariidae; SMF 8486). **F**, *Rynchops niger* (SMF 4756). **G**, *Larus audouinii* (Laridae; SMF 2444). **H**, *Larus fuscus* (Laridae; SMF 2390). **I**, *Anous stolidus* (Lari; SMF 10146). **J**, *Himantopus himantopus* (Recurvirostridae; SMF 1705). **K**, juvenile *Numenius arquata* (Scolopacidae; SMF 9901). **L**, *Numenius arquata* (Scolopacidae; SMF 20378). **M**, *Catharacta antarctica* (Stercorariidae; SMF 19187). Abbreviations: lop, lateral openings; plc, pleurocoel. The scale bars equal 10 mm.

they are absent in all extant Palaeognathae. Pronounced lateral openings are furthermore present in the thoracic vertebrae of the anseriform *Telmabates antiquus* (Fig. 5D; Presbyornithidae, Howard 1955), the early Eocene stem group strigiform *Primoptynx poliotauros* (Fig. 5B; Mayr et al. 2020), as well as in two taxa of uncertain phylogenetic affinities, that is, the early Eocene *Perplexicervix microcephalon* (Fig. 5C; Mayr 2010) and the late Paleocene *Calcardea junnei* (Fig. 5E; Mayr et al. 2019).

Livezey and Zusi (2006: character 850) also scored lateral openings for the anseriform Dromornithidae and the gruiform taxon *Aptornis* (Aptornithidae). Material of these taxa was not available for study, but at least in some specimens of *Aptornis* pneumatic openings are only present in the dorsal portion of the vertebra but absent on the lateral surfaces on the vertebral body (see Worthy et al. 2011: fig. 2a).

Little is known on the ontogenetic development of lateral openings and there appear to be taxon-specific differences in their development. The thoracic vertebrae of a juvenile individual of *Phoebastria irrorata* (Diomedeidae) do not exhibit lateral openings, whereas numerous openings are present in a juvenile individual of *Ardeotis kori* (Otididae; Fig. 3H).

The distribution of pleurocoels

Pleurocoels on the thoracic vertebrae adjoin the lungs and encompass protuberances of the mediodorsal bronchi ("pulmonary protuberances" of O'Connor 2006). Pleurocoels are therefore not directly associated with diverticula of the air sacs (contra Livezey and Zusi 2006: p. 140) and their functional significance is elusive (see discussion).
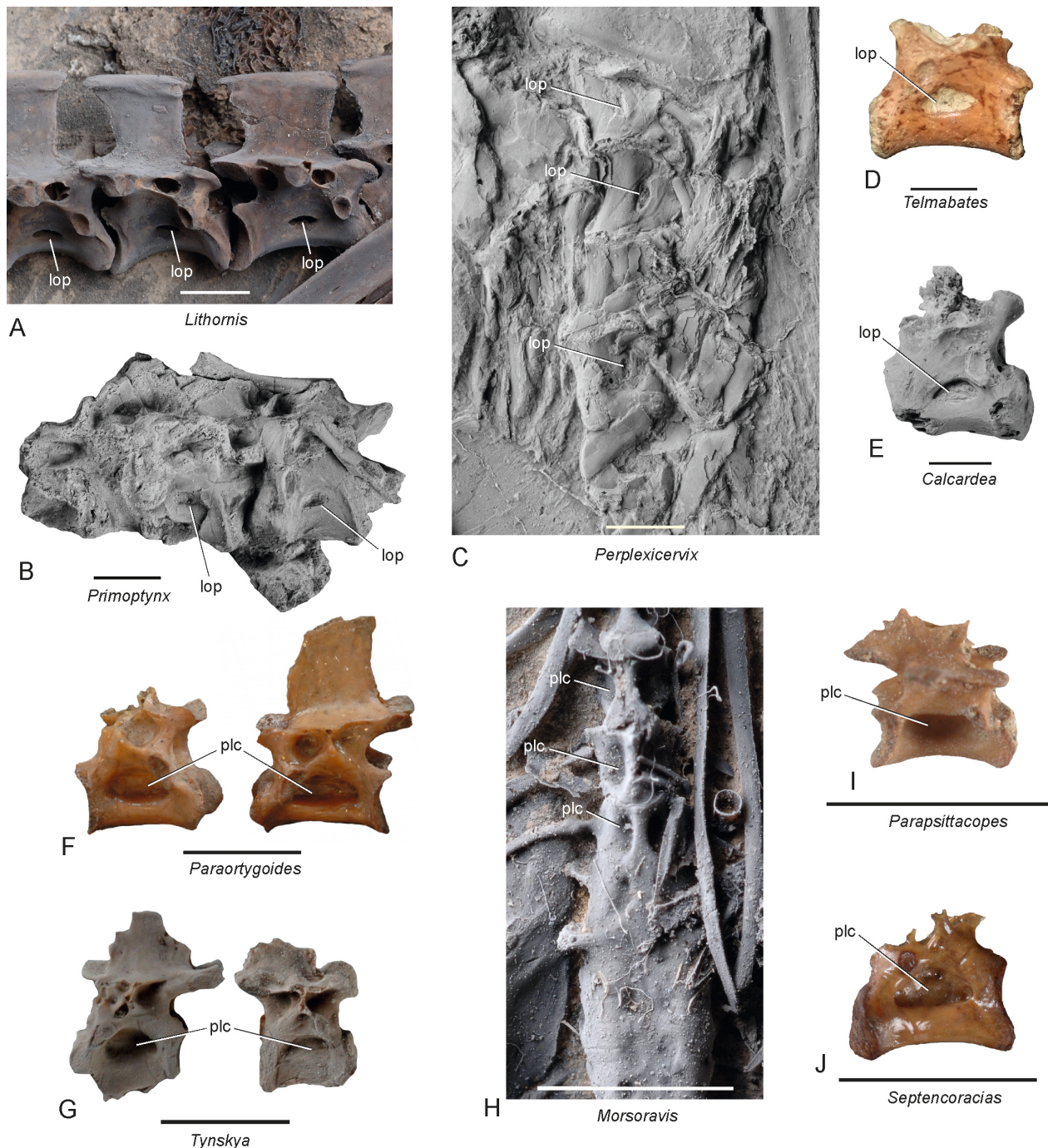
Figure 5. Thoracic vertebrae of fossil taxa with lateral openings (lop) or pleurocoels (plc). **A**, *Lithornis vulturinus* from the early Eocene Fur Formation in Denmark (Lithornithidae; MGUH 26770). **B**, *Primoptynx poliotauros* from the early Eocene of the Willwood Formation, Wyoming, USA (Strigiformes; UMMP 96195). **C**, *Perplexicervix microcephalon* from the latest early or earliest middle Eocene of Messel, Germany (SMF-ME 2559a). **D**, *Telmabates antiquus* from the early Eocene of Argentina (Presbyornithidae; AMNH 3170). **E**, *Calcardea junnei* from the late Paleocene of the Willwood Formation (UM 76882). **F**, *Paraortygoides radagasti* from the early Eocene London Clay of Walton-on-the-Naze, Essex, UK (Gallinuloididae; NHMUK A 6217). **G**, *Tynskya waltonensis* from Walton-on-the-Naze (Messelasturidae; SMF Av 652). **H**, *Morsoravis sedilis* from the Fur Formation (MGUH 28930). **I**, *Parapsittacopes bergdahli* from Walton-on-the-Naze (Psittacopedidae; SMF Av 653). **J**, *Septencoracias* cf. *morsensis* from Walton-on-the-Naze (Coraciiformes; SMF Av 655). The scale bars equal 5 mm.

Among extant birds, pronounced pleurocoels mainly occur in taxa of the Procellariiformes and Charadriiformes. In the Procellariiformes, they are present in most Procellariidae (Fig. 4B–E) except for the species of the taxon *Pelecanoides*. By contrast, pleurocoels are absent in the Diomedeidae and are very shallow in the Oceanitidae and Hydrobatidae. The presence of pleurocoels in a juvenile individual of *Calonectris diomedea edwardsii* (Fig. 4D) suggests that these structures develop early in ontogeny.

In the Charadriiformes, pleurocoels occur in all taxa of the Charadrii (Fig. 4J) and in all Lari (Fig. 4F–H) except for the Turnicidae, Stercorariidae (Fig. 4M), and Alcidae.

Within the charadriiform Scolopaci, pleurocoels are present in the Scolopacidae (Fig. 4K, L) and Rostratulidae, whereas their occurrence is variable in the Thinocoridae (present in *Thinocorus*, absent in *Attagis*) and Jacanidae (present in *Hydrophasianus* and *Jacana*, weakly developed in *Actophilornis*, absent in *Microparra*).

As yet, pleurocoels have not been reported for species outside the Procellariiformes and Charadriiformes, but here their presence is noted for a few species of the Anatidae (*Aythya australis*, *Merganetta armata*; Fig. 2F) as well as some Sulidae (*Sula sula*; Fig. 3A). In the latter two taxa, they exhibit multiple openings (pneumatic pores).

Thoracic vertebrae with well-developed pleurocoels were reported for various stem group representatives of higher-level taxa, the extant members of which lack such fossae. This is true for the stem group galliform *Paraortygoides radagasti*, which belongs to the Gallinuloididae (Fig. 5F; Dyke and Gulas 2002). Pronounced pleurocoels also occur in *Morsoravis sedilis* from the early Eocene Fur Formation in Denmark (Fig. 5H; Bertelli et al. 2010; Mayr 2011a), *Pumiliornis tessellatus* from the latest early or earliest middle Eocene of Messel in Germany (Mayr 2011a), the early Eocene Halcyornithidae and Messelasturidae (Fig. 5G; Mayr 2021), the zygodactyl stem group passeriform *Parapsittacopes bergdahli* (Fig. 5I; Mayr 2020), as well as the stem group coraciiform *Septencoracias* cf. *morsensis* (Fig. 5J; Mayr in press). In *Morsoravis*, the pleurocoels extend onto the cranialmost synsacral vertebrae.

Discussion

Owing to their absence in all Mesozoic birds outside Neornithes, large openings in the lateral surfaces of the vertebral body probably represent a derived neornithine trait and evolved multiple times independently in only distantly related lineages. Even though such openings also occur in small species (e.g., some representatives of the anseriform Aythyini), they are mainly found in large-sized birds and appear to be due to an increased skeletal pneumatization. Lateral openings in the bodies of the thoracic vertebrae are often correlated with pneumatic foramina in the sternal extremity of the coracoid, which are present in the Anhimidae, Anseranatidae, Psophiidae, Gruidae, and Opisthocomiformes. Such coracoideal foramina are, however, absent in other taxa that exhibit openings in the bodies of the thoracic vertebrae, so that their presence in the above taxa is likely to be due to a higher overall degree of pneumatization in different parts of the skeleton and not due to an immediate functional correlation.

As detailed in the introduction, and in contrast to lateral openings, pleurocoelous thoracic vertebrae occur in virtually all Mesozoic non-neornithine birds except for the Archaeopterygiformes. Pleurocoels are therefore probably plesiomorphic for the Pygostylia, the clade in-

cluding the Confuciusornithiformes, Enantiornithes, and Ornithuromorpha. They are found in the closest Mesozoic relatives of neornithine birds (Ichthyornithiformes, Hesperornithiformes), but it is not straightforward to determine whether pleurocoels were also present in the stem species of the Neornithes. If only the extant species are considered, it is most parsimonious to assume that the pronounced pleurocoels of the Procellariiformes and Charadriiformes are autapomorphic for these two taxa. However, the occurrence of pleurocoels in phylogenetically early diverging and geologically old stem group representatives of taxa whose extant representatives lack these structures, such as the Galliformes (*Paraortygoides*), Passeriformes (*Parapsittacopes*), and the coraciiform Coracii (*Septencoracias*), suggests that they were independently reduced in only distantly related neornithine clades. Accordingly, it is here hypothesized that pleurocoels were present in the last common ancestor of at least neognathous birds and possibly also in that of Neornithes as a whole.

O'Connor (2006: 1218) concluded that pleurocoels ("pulmonary fossae") "are causally associated with medially directed para-bronchial protuberances, and hence, provide robust osteological correlates for both lung position and composition. (…). The identification of similar vertebral modifications in fossil archosaurs helps constrain inferences related not only to lung position, but to aspects of the intrapulmonary structure (…) of the exchanger itself. Pulmonary fossae, combined with the wealth of data on postcranial pneumaticity, support not just the presence of air sacs, but also of a level of pulmonary heterogeneity". However, a primary correlation between the presence of pleurocoels and the structure of the avian pulmonary system conflicts with the presence of pleurocoels in only a few extant avian groups and with their absence in *Archaeopteryx* (pleurocoels occur in various sauropod dinosaurs [e.g., Carpenter and Tidwell 2005] and it is not a likely assumption that the pulmonary system of non-avian dinosaurs was more bird-like than that of *Archaeopteryx*).

Instead, there actually exists a negative correlation between pleurocoels and pneumatic features, with pleurocoels being present in taxa that lack pneumatic foramina in the fossa pneumotricipitalis of the humerus. Such is the case in the Procellariiformes, in which all taxa except for the Diomedeidae have non-pneumatic humeri. The Diomedeidae, by contrast, lack pleurocoels on the thoracic vertebrae but are the only procellariiform birds that exhibit pneumatic foramina in the fossa pneumotricipitalis. The thoracic vertebrae of the Oceanitidae, Hydrobatidae, and the procellariid taxon *Pelecanoides* are mediolaterally compressed, which may account for the absence of pleurocoels in these taxa. In the Charadriiformes, pneumatic foramina in the fossa pneumotricipitalis of the humerus are absent in all taxa except for the Stercorariidae, Rynchopidae, and *Anous* (Lari) (Mayr 2011b). Again, the Stercorariidae are among the few charadriiform taxa that lack pleurocoels, whereas these are present in *Anous* and *Rynchops* (Rynchopidae). Unlike in most other charadriiforms, however, the pleurocoels of

Anous exhibit multiple openings (pneumatic pori). This is also true for *Sula sula*, in which the humerus is pneumatized and the pleurocoels exhibit multiple openings. In the Anseriformes, pneumatic foramina in the fossa pneumotricipitalis are absent in *Aythya*, *Merganetta*, and other diving ducks, with *Aythya australis* and *Merganetta armata* being among the few anseriform taxa that exhibit pleurocoels.

All Mesozoic non-neornithine birds with pleurocoels likewise have a non-pneumatic humerus, and pneumatic foramina in the humerus are also absent in all fossil neornithine taxa, for which pleurocoels have been reported. Such is true for the Halcyornithidae and Messelasturidae (Mayr 2021) as well as the stem group passeriform *Parapsittacopes* (Mayr 2020). The proximal end of the humerus of *Morsoravis* is unknown and the specimens of *Pumiliornis* do not allow the recognition of close details of the pneumotricpital fossa. Details pertaining to the fossa pneumotricipitalis are also unknown for the stem group galliform *Paraortygoides*, but in other early Eocene stem group Galliformes, the humerus appears to have been non-pneumatic (see Hwang et al. 2010: fig. 1).

There are a few extant taxa with non-pneumatic humeri that lack pleurocoels (Mayr and Clarke 2003). These include the Rallidae, Sarothruridae, and Heliornithidae as well as the Gaviiformes, Sphenisciformes, and Podicipediformes. The bodies of the thoracic vertebrae of the former three taxa of the Ralloidea are unusually low dorsoventrally, whereas the latter three taxa are specialized divers and their thoracic vertebrae have mediolaterally compressed bodies, which conflicts with the development of pleurocoels.

The fact that most taxa with distinct pleurocoels have non-pneumatic humeri raises the question about a possible functional correlation between the pneumatization of the humerus and the morphology of the thoracic vertebrae. Most extant birds have nine air sacs. The humerus is pneumatized by diverticula of the clavicular air sac (McLelland 1989), which also sends out diverticula into bones of the pectoral girdle. The thoracic vertebrae, by contrast, are pneumatized by the cervical air sacs, which extend caudally within the vertebral column (McLelland 1989). Here, it is hypothesized that there exists a correlation between the formation of pleurocoels and the development of these air sacs, which in turn may be functionally dependent on the morphology of the furcula.

In birds that have a furcula with narrow shafts, the bone acts as a spring during flight, and "the coupled actions of the sternum and furcula appear to be part of a respiratory cycling mechanism between the lungs and air sacs" (Jenkins et al. 1988: 1495). Based on their cranial locations in the thorax, the cervical and clavicular air sacs would be immediately affected by these movements of the furcula. In this regard, it is notable that the furcula of Mesozoic non-neornithine birds is very massive (Mayr 2017, 2021) and could not assume a function in the ventilation of the clavicular and cervical air sacs. Possibly, therefore, these air sacs were less developed in Mesozoic non-neornithine birds and did not send out diverticula into the surrounding bones.

The contribution of furcula movements to the ventilation of the clavicular and cervical air sacs suggests that Mesozoic non-neornithine birds, which had a rigid furcula with massive shafts, differed in some functional aspects of their air sac system from extant birds. Here it is hypothesized that well-developed diverticula of the clavicular and cervical air sacs evolved late in avian evolution and characterize neornithine subclades.

Pleurocoels appear to have been reduced in taxa, in which the thoracic vertebrae are pneumatized (e.g., Anhimidae, Gruoidea), and in those, in which these vertebrae are mediolaterally compressed (e.g., diving birds, taxa of the charadriiform Scolopaci) or are co-ossified to form a notarium (e.g., crown group Galliformes). This suggests a correlation with structural properties of the vertebral column. The cross section of the body of a pleurocoelous thoracic vertebra recalls that of an I-beam, and pleurocoels may increase the dorsoventral bending strength of the corpus of the thoracic vertebrae in taxa, in which the vertebral column of the thorax is subjected to little mediolateral flexion load (see, e.g., Hayes and Gerhart 1985 for general biomechanical considerations on bone strength). Pleurocoels therefore may have evolved to ensure a balanced relationship between the mineral requirements for bone formation and the structural load-bearing capacity of the vertebral body. Pneumatization of a bone adds to its structural resistance (McLelland 1989: 273), and in the case of the thoracic vertebrae it may strengthen the corpus against mediolateral strain. If so, it would have been the structural significance for the stability of the vertebral body, which led to the development of pleurocoels, rather than their function to encompass certain structures (be them muscles, lung tissue, or fat). However, to fully assess this hypothesis, more data need to be gathered on the actual loads that act on the thoracic vertebrae of taxa like gulls, which exhibit pleurocoels, and skuas, which lack them.

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