The coracoscapular joint of neornithine birds—extensive homoplasy in a widely neglected articular surface of the avian pectoral girdle and its possible functional correlates

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Abstract

A survey is given of the morphological variation of the coracoscapular joint of neornithine birds. In Mesozoic stem group representatives, the coracoid exhibits a deeply concave cotyla scapularis, which articulates with a globose tuberculum coracoideum of the scapula. This morphology is likely to be functionally related to the development of a powerful supracoracoideus muscle and the formation of a triosseal canal as a pulley for the tendon of this muscle. In neornithine birds, the coracoid articulates with the scapula either via a concave cotyla or a flat facies articularis, with the latter largely restricting movements of the coracoid to the paramedian plane. Ancestral state reconstruction suggests that a cotyla scapularis is plesiomorphic for Neornithes and that a flat facies articularis scapularis evolved at least 13 times independently within the clade. For several lineages, the transition to a flat facies articularis scapularis can be traced in the fossil record, and the replacement of a cup-shaped cotyla by a flat articular facet seems to have been due to various functional demands. Often, a flat facies articularis scapularis is associated with reduced shafts of the furcula. A weakly developed furcula enables transverse movements of the coracoid and therefore enables a restriction of the mobility of the coracoscapular joint to the paramedian plane. In taxa with a large crop, a flat facies articularis scapularis is likely to be associated with a reorganization of the pectoral musculature, whereas in procellariiform birds, the transition from a cotyla to a facies articularis appears to have been correlated with the capacity for sustained soaring without wing flapping.

Keywords Aves · Coracoid · Evolution · Functional morphology · Locomotion

Introduction

In non-avian theropods, coracoid and scapula are either co-ossified into a scapulocoracoid or articulate via a straight suture (e.g., Jasinoski et al. 2006; Senter 2006). This plesiomorphic condition also occurs in early diverging taxa of the avian stem lineage (Wang et al. 2018).

Well-defined and more localized articular facets characterize Ornithothoraces, the clade including the Cretaceous Enantiornithes and the Ornithuromorpha. These latter two taxa distinctly differ in the morphology of the coracoscapular joint, with the coracoid of the Enantiornithes having a

convex articular facies for the scapula (Chiappe and Walker 2002), whereas the coracoid of early representatives of the Ornithuromorpha—the taxon comprising the avian crown group (Neornithes)—is characterized by a deeply concave cotyla scapularis, which articulates with a globose tuberculum coracoideum of the scapula.

The formation of a deeply concave, cup-shaped cotyla scapularis is likely to have been functionally correlated with the evolution of a modern-type triosseal canal. This canal forms a pulley for the tendon of musculus supracoracoideus, which elevates the wing, and is one of the derived characteristic of the Ornithuromorpha (Fig. 1a–c; Mayr 2017b). Mesozoic species of the Ornithuromorpha were predominantly terrestrial birds, which therefore had to initiate their takeoffs from the ground, and—as indicated by the development of a large sternal keel and a functional triosseal canal—musculus supracoracoideus underwent a strong development in these birds (Mayr 2017b). Their cup-like coracoscapular joint enabled multidirectional mobility of the coracoid relative to the

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Fig. 1 **a** Wing and pectoral girdle bones of a pigeon (*Columba* sp.), with the dotted area indicating the surfaces of the coracoid and sternum occupied by musculus supracoracoideus (after George and Berger 1966: Fig. III.1). **b**, **c** Coracoscaphoid joint of **b** the Common Woodpigeon, *Columba palumbus* (Columbidae; left side, cranio-lateral view), and **c** the Ring-necked Pheasant, *Phasianus colchicus* (Phasianidae; right side, caudodorsal view). **d–f** Omal extremity of the left coracoid (dorsal view) of **d** the Early Cretaceous *Yixianornis grabaui* with a deeply cup-shaped cotyla scapularis (IVPP V 1363; right coracoid, mirrored; surrounding matrix digitally removed), **e** *Sagittarius serpentarius* (Accipitriformes, Sagittariidae) with a deeply cup-shaped cotyla scapularis, and **f** *Rhynchotus rufescens* (Tinamiformes, Tinamidae) with a flat facies articularis scapularis.

The arrows in **a–c** indicate the course of the tendon of the supracoracoideus muscle, which passes through the triosseal canal formed by the processus acrocoracoideus of the coracoid, the extremitas omalis of the furcula, and the acromion of the scapula. *acr* acromion of scapula, *car* carina sterni, *cdp* crista deltopectoralis of humerus, *csc* cotyla scapularis, *csj* coracoscaphoid joint, *exo* extremitas omalis of furcula, *fah* facies articularis humeralis of scapula, *fas* facies articularis scapularis, *fur* furcula, *lco* left coracoid, *lhu* left humerus, *lsc* left scapula, *pac* processus acrocoracoideus of coracoid, *ppc* processus procoracoideus of coracoid, *rco* right coracoid, *ste* sternum, *sup* musculus supracoracoideus, *tbd* tuberculum dorsale of humerus. Not to scale

scapula and may have been critical to absorb mechanical strain on the pectoral girdle elements resulting from contractions of a powerful supracoracoideus muscle.

All volant and some flightless Mesozoic birds of which the coracoid is known have a cup-shaped cotyla scapularis (Fig. 1d; Clarke 2004; Clarke et al. 2006; Longrich 2009; Wang et al. 2015, 2016; Bell and Chiappe 2020), which is likely to be plesiomorphic for Neornithes. However, the coracoscaphoid joint of extant birds shows much variation, and a cup-shaped cotyla scapularis is replaced by a flat articular facet in many taxa (Fig. 1f).

In birds with a deep, cup-shaped cotyla scapularis, the articulation between the coracoid and scapula resembles a ball-and-socket joint, but a true synovial joint is not formed (Fürbringer 1888). Moreover, the mobility of the coracoscaphoid joint is constrained by the ligamentum coracoscaphare interosseum, which is formed by elastic

cartilage and fully envelops the coracoscaphoid joint, thereby firmly connecting the coracoid to the scapula (Baumel and Raikow 1993: 161). This ligament also forms the glenoid cavity for the articulation with the humerus. A cup-shaped cotyla scapularis in general facilitates a multidirectional mobility of the coracoid and scapula relative to each other, but the ligamentous connection of the two bones does not enable true rotational movements.

Although Fürbringer (1888) already addressed the morphology of the coracoscaphoid joint of extant birds in some detail, no comprehensive survey of the morphological variation has been published, nor has the comparative morphology of the joint been considered in otherwise detailed accounts of the functional morphology of the avian wing and pectoral girdle (see, e.g., Sy 1936; Stegmann 1964).

However, the paleornithological literature includes descriptions of a fair number of fossil taxa that document

a transition from a cup-like cotyla scapularis to a flat facies articularis scapularis. In the present study, these data are for the first time compiled and the variation of the coracoscapular articulation of extant birds is examined across a comprehensive taxonomic sampling. Although the main objective of this study was to gather the available morphological data, some possible functional correlates of the observed variation in the coracoscapular joint of fossil and extant neornithine birds are also discussed. An in-depth functional interpretation will, however, have to await future studies of the soft tissue anatomy, which was beyond the scope of the present analysis.

Material and methods

Institutional abbreviations: CM—Canterbury Museum, Christchurch, New Zealand; GMH—Geiseltalsammlung, Martin-Luther Universität of Halle-Wittenberg, Germany; IRSNB—Institut royal des Sciences naturelles de Belgique, Belgium; IVPP—Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; LACM—Los Angeles County Museum, Los Angeles, California, USA; MNHN—Museo Nacional de Historia Natural, Santiago, Chile; SMF—Senckenberg Research Institute Frankfurt, Frankfurt Germany; UCBL—Université Claude Bernard, Lyon, France; UMMP—University of Michigan, Museum of Paleontology, Ann Arbor, Michigan, USA; WDC—The Wyoming Dinosaur Center, Thermopolis, Wyoming, USA.

The nomenclature of the extant species follows the IOC World Bird List (<https://www.worldbirdnames.org>). To describe the direction of movements relative to the body axes, the term paramedian and transverse are used, with the former describing movements in the dorsoventral plane (parasagittal in human anatomy), whereas the latter pertains to mediolateral movements in a plane at a right angle to the rostrocaudal body axis. Skeletons of extant birds were examined in the ornithological collection of Senckenberg Research Institute Frankfurt.

Ancestral character states were reconstructed under the parsimony criterion with Mesquite 2.71 (Maddison and Maddison 2009) based on a recent tree topology resulting from analysis of transcriptome data (Kuhl et al. 2021).

Results

The coracoid and scapula are co-ossified and form a scapulocoracoid in all flightless palaeognathous birds. The different morphologies of the coracoscapular joint of volant Neornithes are summarized in Table 1.

A deeply concave, cup-shaped cotyla scapularis with a circular outline is found in the anseriform Anhimidae and

Anseranatidae, in the Opisthocomidae, Otididae, Ciconiidae, in the pelecaniform Pelecanidae and Balaenicipitidae, and in the accipitriform Sagittariidae. It also occurs in gruiform birds (Gruidae, Aramidae, Psophiidae, Rallidae, and Helionithidae), in all Charadriiformes, in the Pterocliiformes, and in the Ardeidae. A cotyla scapularis is also present though less deeply concave in the Eurypygidae, Rhynochetidae, Scopidae, Oceanitidae, Threskiornithidae, Accipitridae, and some representatives of the Strisores (Nyctibiidae, Steatornithidae, and apodiform birds).

A flat facies articularis scapularis is present in the palaeognathous Tinamidae, and in the Galliformes, Suliformes, Sphenisciformes, all Procellariiformes except the Oceanitidae, Phaethontiformes, Columbiformes, Cuculiformes, Mesitornithiformes, Musophagiformes, Caprimulgidae, Podargidae, Aegothelidae, Cathartidae, Falconidae, Psittaciformes, Passeriformes, Coliiformes, Strigiformes, as well as all members of Eucavitaves (the clade including Trogoniformes, Coraciiformes, and Piciformes; Yuri et al. 2013). Of at least seven of these latter taxa, stem group representatives are known, which have a deep cotyla scapularis:

(1) Galliformes: a cup-like cotyla scapularis occurs in all early Paleogene stem group Galliformes, that is, the Gallinuloididae (Fig. 2a; Mayr and Weidig 2004; Mayr 2006), Quercymegapodiidae (Mourer-Chauviré 1992a, 2000), and Paraortygidae (Mourer-Chauviré 1992a; Mourer-Chauviré et al. 2017; Mayr and Smith 2013). The exact interrelationships between the Paraortygidae, Quercymegapodiidae, and crown Galliformes are uncertain, but the Gallinuloididae are the earliest diverging clade and a cup-like cotyla scapularis is clearly plesiomorphic for Galliformes as a total group (Mayr 2017a).

(2) Procellariiformes: coracoids are known from only a few Paleogene Procellariiformes, but the coracoid of the early Oligocene Diomedoididae has a cup-shaped cotyla scapularis (Fig. 2f; De Pietri et al. 2009; Mayr and Smith 2012). The exact affinities of the Diomedoididae are unresolved and these birds resulted as the sister taxon of either all crown group Procellariiformes or of the Diomedidae (Mayr and Smith 2012). Among extant Procellariiformes, the Diomedidae, Hydrobatidae, and Procellariidae have a flat facies articularis scapularis, whereas there is a cotyla scapularis of varying depth in the Oceanitidae. Current phylogenetic reconstructions suggest a sister group relationship between the Diomedidae and all other crown group Procellariiformes (Kuhl et al. 2021), so that a flat facies articularis scapularis evolved at least two times independently within Procellariiformes, in the Diomedidae and in the clade formed by Hydrobatidae and Procellariidae. A cup-shaped cotyla scapularis is also present in a procellariiform coracoid from the late Eocene of Antarctica, which was referred to the Gaviiformes by

Hospitaleche and Gelfo (2015). As noted by Mayr and Goedert (2017), this coracoid is from a procellariiform bird and may belong to the stem group albatross *Notoleptos*, which was found in coeval strata (Hospitaleche and Gelfo 2017).

(3) Sphenisciformes: all early Paleogene stem group Sphenisciformes of which the coracoid is known exhibit a deeply excavated cotyla scapularis, which is particularly well-developed in the Paleocene taxa *Kupoupou*, *Muriwaimanu*, *Sequiwaimanu*, and *Kumimanu* (Fig. 2h; Blokland et al. 2019; Mayr and Goedert 2017; Mayr et al. 2018). A somewhat shallower cotyla is also present in the late Eocene taxa *Anthropornis* and *Palaeudyptes* (Jadwiszczak 2006; Hospitaleche 2016) and in the late Oligo-

cene *Kairuku* (Ksepka et al. 2012). In crown group Sphenisciformes, the cotyla scapularis is only weakly concave or there is a flat facies articularis scapularis (Fig. 2i).

(4) Suliformes: a slightly concave articular facet is present in the early Eocene stem group frigatebird *Limnofregata* (Olson 1977) and in the late Oligocene *Borvocarbo*, which is considered to be a stem group representative of the Phalacrocoracidae (Mourer-Chauviré et al. 2004). A deeply concave cotyla scapularis characterizes the coracoid of many Plotopteridae, which are extinct wing-propelled diving seabirds from the North Pacific and are hypothesized to be part of the Suliformes (Fig. 2j, k; Mayr 2017a; Mayr et al. 2021a).

Table 1 Overview of different configurations of the coracoscapular joint of extant neornithine taxa and possibly correlated traits involving the morphology of the pectoral girdle and wing bones, as well as major ontogenetic categories. Taxa with a flat facies articularis scapularis are highlighted in gray. *CSJ* morphology of the coracoscapular joint (0: cotyla scapularis; 1: facies articularis scapularis), *EXS* furcula, width of extremitas sternalis (0: similar to furcular scapus or wider; 1: narrow or completely reduced), *EXO* furcula, extremitas

omalis with articular facet for coracoid (0: no; 1: yes), *FNS* coracoid, foramen nervi supracoracoidei (0: present; 1: absent), *TBD* humerus, tuberculum dorsale strongly developed (0: no; 1: yes), *HUL* humerus length relative to coracoid (0: humerus twice as long as coracoid or shorter than twofold length of coracoid; 1: humerus more than twice as long as coracoid), *ONT* ontogeny (0: precocial, 1: altricial; after Temrin and Tullberg 1995)

	CSJ	EXS	EXO	FNS	TBD	HUL	ONT
Tinamiformes	1	0	0	1	1	0	0
Galliformes	1	0	0	1	1	0	0
Anseriformes: Anhimidae	0	0	0	0	0	1	0
Anseriformes: Anseranatidae	0	0	0	0	0	1	0
Anseriformes: Anatidae	0	0	0	01	1	01	0
Phoenicopteriformes	0	0	0	0	0	1	0
Podicipediformes	1	1	0	1	0	1	0
Opisthocomiformes	0	0	1	1	0	0	0
Gaviiformes	0	1	0	0	0	1	0
Sphenisciformes	1	1	0	1	1	0	1
Procellariiformes	01	0	0	0	0	1	1
Ciconiidae	0	0	0	01	01	1	1
Suliformes	1	01	1	1	01	1	1
Ardeidae	0	0	0	1	1	1	1
Threskiornithidae	0	0	0	1	0	1	1
Pelecanidae	0	0	1	0	0	1	1
Scopidae	0	0	1	1	0	1	1
Balaenicipitidae	0	0	1	0	0	1	1
Phaethontiformes	1	0	0	0	0	0	1
Eurypygiformes: Eurypygidae	0	0	0	1	0	0	0
Eurypygiformes: Rhynochetidae	0	0	0	1	1	1	0
Otidiformes	0	0	0	01	0	1	0
Gruiformes: Gruidae	0	0	0	0	0	1	0
Gruiformes: Aramidae	0	0	0	0	0	1	0
Gruiformes: Psophiidae	0	0	0	0	0	0	0

Table 1 (continued)

Gruiformes: Rallidae	0	1	0	0	0	0	0
Gruiformes: Heliornithidae	0	0	0	0	0	0	1
Charadriiformes: Charadrii	0	0	0	0	1	0	0
Charadriiformes: Scolopaci	0	0	1	1	1	0	0
Charadriiformes: Lari	0	0	1	0	1	1	0
Charadriiformes: Turnicidae	0	0	0	1	1	0	0
Cuculiformes	1	0	0	1	0	0	1
Musophagiformes	1	1	1	0	0	0	1
Columbiformes	1	1	0	1	1	0	1
Pterocliiformes	0	1	0	1	1	0	0
Mesitornithiformes	1	1	0	1	1	0	0
Strisores: Caprimulgidae	1	0	1	1	1	0	0
Strisores: Steatornithidae	0	0	0	1	0	0	1
Strisores: Nyctibiidae	0	0	1	1	0	1	1
Strisores: Podargidae	1	1	0	1	0	1	1
Strisores: Aegothelidae	1	0	0	0	0	0	1
Strisores: Apodidae	0	0	1	0	1	0	1
Strisores: Hemiprocnidae	0	0	1	0	1	0	1
Strisores: Trochilidae	0	0	1	0	0	0	1
Cariamiformes	0	1	1	1	0	1	1
Accipitriformes: Cathartidae	1	0	1	0	0	1	1
Accipitriformes: Sagittariidae	0	0	0	0	0	1	1
Accipitriformes: Accipitridae	0	0	1	0	0	1	1
Falconiformes	1	0	1	0	0	0	1
Psittaciformes	1	1	0	1	1	0	1
Strigiformes	1	1	0	0	0	1	1
Coliiformes	1	0	0	1	0	0	1
Leptosomiformes	1	1	1	0	0	1	1
Bucerotiformes	1	1	0	1	0	0	1
Upupiformes	1	0	0	1	0	0	1
Trogoniformes	1	1	0	1	1	0	1
Coraciiformes	1	1	0	1	0	0	1
Meropidae	1	1	0	1	0	0	1
Alcedinidae	1	1	0	1	0	0	1
Momotidae	1	1	0	1	0	0	1
Piciformes	1	1	0	1	0	0	1
Passeriformes	1	1	0	1	0	0	1

(5) Psittaciformes: a concave cotyla scapularis is present in the middle Eocene Namapsittidae (Mourer-Chauviré et al. 2017) and in the late Eocene Quercy-psittidae (Fig. 2l; Mourer-Chauviré 1992b), both of

which are considered to be stem group representatives of the Psittaciformes.

(6) Coliiformes: a moderately concave cotyla scapularis is also found in the Eocene Sandcoleidae, which are

stem group representatives of the Coliiformes (Fig. 2n; Houde and Olson 1992; Mayr 2017a).

(7) Strigiformes: the coracoid of most early Paleogene stem group Strigiformes is unknown. However, a cotyla scapularis is present in the early Eocene *Primoptynx* (Fig. 2p; Mayr et al. 2020).

Ancestral state reconstruction based on the morphology of the extant species did not allow a conclusive reconstruction of the ancestral state for many taxa (Fig. 3a). However, an analysis, in which Galliformes, Sphenisciformes, Procellariiformes, Suliformes, Strigiformes, Coliiformes, and Psittaciformes were scored as having a cotyla scapularis (the presumed ancestral state for these clades), shows that a cotyla scapularis is plesiomorphic for neornithine birds (Fig. 3b). If reversals into the plesiomorphic state are allowed for, a flat facies articularis scapularis evolved at least 13 times independently, in the stem lineages of the (1) Tinamidae, (2) Galliformes, (3) Podicipediformes, and (4) the clade including Columbiformes, Cuculiformes, Mesitornithiformes, Musophagiformes, Caprimulgidae, Podargidae, and Aegothelidae, as well as in the stem lineages of the (5) Suliformes, (6) Phaethontiformes, (7) Sphenisciformes, (8) Procellariiformes, (9) the clade (Falconidae + Psittaciformes + Passeriformes), the (10) Cathartidae, (11) Coliiformes, (12) Strigiformes, and the (13) Eucavitaves (Fig. 3b). Here, it is considered more likely that the evolutionary transformations of the coracoscapular articulation were unidirectional, from a cup-like cotyla scapularis to a flat facies articularis scapularis. This assumption would raise the number of an independent origin of a flat facies articularis scapularis to 20 and is supported by the fact that flattening of the cotyla scapularis is a recurrent theme in the evolution of many only distantly related lineages, whereas no example of the reverse transition (from a flat facies to a deep cotyla) exists.

Discussion

As detailed in the introduction, a cup-like coracoscapular joint is an apomorphy of the Ornithuromorpha and enables multidirectional mobility of the coracoid relative to the scapula, which in birds is fixed in a relatively immobile position to the ribcage. A shallow facies articularis scapularis, by contrast, restricts motion mainly to a paramedian plane, which raises the question, why a cup-shaped cotyla was replaced by a flat articular facet in many different lineages of neornithine birds.

The fact that stem group representatives of various extant taxa with a flat facies articularis scapularis have a concave cotyla scapularis is indicative of a rapid diversification of

neornithine birds at a time, where the stem species of most major clades still had a plesiomorphic, cup-shaped cotyla scapularis. Ontogenetically, a cup-like cotyla scapularis develops from a flat articulation surface (Fig. 4c, d), so that a flat facies articularis may be a paedomorphic trait. Indeed, most birds with a flat facies are altricial (Table 1), and a delay in skeletal maturation may have favored retention of a flat facies in adulthood. Still, there are notable exceptions, with precocial taxa with a flat facies articularis scapularis including Tinamiformes, crown group Galliformes, Podicipediformes, and Mesitornithiformes, whereas the Pelecanidae, Ciconiidae, Apodiformes and Cariamiformes are altricial and have a cup-like cotyla.

The transition from a cup-like cotyla scapularis to a flat facies articularis scapularis does not involve major changes in other aspects of coracoid morphology (Fig. 2), but many taxa with a deeply concave cotyla scapularis, such as the Anhimidae and Pelecanidae, have an unusually robust, U-shaped furcula. In taxa with a flat facies articularis scapularis, by contrast, the furcula often has very narrow shafts, especially at its sternal extremity (Table 1; Fig. 4). In Mesozoic Ornithuromorpha with a deeply concave cotyla scapularis, the furcula was also much more robust than it is in most extant birds and formed a rigid unit that appears to have been resistant to transversal bending.

To some degree, the shape of the furcula of birds correlates with flight style (Hui 2002; Close and Rayfield 2012), and the different morphologies of the coracoscapular joint may also reflect disparate flight techniques. In this regard, it is notable that a flat facies articularis scapularis is found in some species-rich clades of arboreal birds, such as Eucavitaves (the clade including Trogoniformes, Coraciiformes, and Piciformes), Cuculiformes, Columbiformes, Psittaciformes, and Passeriformes. At least in passerines, the furcula acts as a spring, but this function is not assumed by the furcula of, e.g., many Piciformes, in which both clavicles are not fused at their sternal extremities (Jenkins et al. 1988).

A weakly developed furcula may be related to agile locomotion in dense vegetation, which conforms to the presence of a flat facies in the Enantiornithes (see “Introduction”), the predominant clade of arboreal Mesozoic birds. However, the assumption that a flat facies improves wing flapping capabilities or enables hovering flight does not seem to apply, and in some taxa, the opposite seems to be true. In the Procellariiformes, for example, a cotyla scapularis occurs in the broad-winged Oceanitidae, which employ flapping flight to a greater degree than the Diomededidae, Hydrobatidae, and Procellariidae, with the latter three taxa being adapted to dynamic soaring (flapping flight was also assumed for the extinct Diomededidae, which like the Oceanitinae have a cup-like cotyla scapularis; Mayr 2017a). Hummingbirds also employ powerful wing flapping and have a cup-like cotyla

Fig. 2 Left coracoids in dorsal view to illustrate the transition from a cotyla scapularis (csc) to a facies articularis scapularis (fas) in the stem lineages of several neornithine taxa. **a–c** Galliformes, with **a** the early Eocene stem group galliform *Gallinuloides wyomingensis* (WDC CGR–012; the surrounding matrix was digitally removed, the gray area indicates a digitally removed overlying bone), **b** the early Oligocene paraortygid cf. *Pirortyx major* (IRSNB Av 117), and **c** the extant *Pavo cristatus* (Phasianidae). **d, e** Pelagornithidae, with **d** the Paleocene *Protodontopteryx ruthae* (CM 2018.124.8) and **e** the Miocene *Pelagornis chilensis* (MNHN SGO.PV 1061; right coracoid, reversed). **f, g** Procellariiformes, with **f** the early Oligocene diomedoid *Rupelornis definitus* (IRSNB Av 112a) and **g** the extant *Thalassarche melanophris* (Diomedidae). **h, i** Sphenisciformes, with

h the Paleocene stem group sphenisciform *Sequiawaimanu rosieae* (CM 2016.6.1) and **i** the extant *Eudyptes chrysocome* (Spheniscidae). **j, k** Plotopteridae, with **j** a late Eocene/early Oligocene species identified as *?Tonsala* sp. (SMF Av 614; right side, mirrored, surrounding matrix digitally removed) and **k** the late Oligocene *Plotopterum joaquinensis* (LACM 8927). **l, m** Psittaciformes, with **l** the late Eocene stem group psittaciform *Quercypsitta ivani* (UCBL FSL 367080) and **m** the extant *Psittacus erithacus* (Psittacidae). **n, o** Coliiformes, with **n** the middle Eocene sandcoleid *Eoglaucidium pallas* (GMH XXXV-576) and **o** the extant *Colius striatus* (Coliidae). **p, q** Strigiformes, with **p** the early Eocene *Primoptynx poliotauros* (UMMP 96195) and **q** the extant *Bubo scandiacus* (Strigidae). Scale bars equal 10 mm

Fig. 3 **a** Ancestral state reconstruction for the distribution of the different morphologies of the coracoscaphular joint in extant birds, based on the phylogeny of Kuhl et al. (2021) and the data in Table 1; taxa with a cotyla scapularis are shown in blue, those with a facies articularis scapularis in yellow. **b** A second analysis, in which extant taxa with a flat facies articularis scapularis that have fossil stem lineage representatives with a cotyla scapularis were scored as having a cotyla; for these taxa, which are denoted with a red asterisk, the short yellow terminal branches were added to the figure after the analysis. *Ichthyornis*, *Yixianornis*, and *Archaeornithura* are Cretaceous stem group representatives of the Ornithuromorpha

scapularis, even though they “have kinematically ‘rigid’ wings compared with other avian species” (Tobalske et al. 2007: 2368).

As detailed in the introduction, a cup-like cotyla scapularis evolved in the stem lineage of the Ornithuromorpha and allows multidirectional movements of the coracoid relative to the scapula. Because early ornithuromorph birds had a very rigid furcula, this cup-shaped articulation was the major mobile joint of the pectoral girdle and is likely to have absorbed mechanical strain on the pectoral girdle elements resulting from contractions of a powerful supracoracoideus muscle. Here it is hypothesized that in taxa that have a bendable furcula with weakly developed shafts, transverse mobility of the coracoscaphular joint is no longer functionally necessary and was abandoned with the formation of a flat facies articularis scapularis that constrained the relative movements between the coracoid and scapula to the paramedian plane.

In addition, a cup-like cotyla scapularis was reduced in some soaring birds, in which wing flapping plays a subordinate role. As detailed above, this is exemplified by the coracoscaphular joint of procellariiform birds, in which species that are adapted to dynamic soaring have a flat facies articularis scapularis. Similar considerations may pertain to the Pelagornithidae, in which the Paleocene *Protodontopteryx*, which is considered to have retained flapping flight capabilities (Mayr et al. 2021b), had a larger and more deeply concave cotyla scapularis than the giant Neogene species, which were highly specialized soaring birds (Fig. 2d, e).

A correlation between the robustness of the furcula and the morphology of the coracoscaphular joint is particularly evident in the Galliformes, where Paleogene stem group representatives have a much more robust furcula than the extant taxa (Fig. 4g, h). Stegmann (1964) showed that reduction of

the furcula in galliform birds is related to the development of a large crop. The furcula serves as an insertion site for the cranial portion of musculus pectoralis, and the curvature of the bone results in a cranial position of a portion of this muscle relative to the humerus, which enables the bird to draw the wings forward (see also Bock 2013). In extant Galliformes and other birds with a large crop (e.g., Psittacidae and Columbidae), the furcula is only weakly developed and lacks a cranial curvature. Musculus pectoralis therefore cannot assume the above function, which is adopted by an unusually well-developed musculus coracobrachialis cranialis (Stegmann 1964). This latter muscle originates on the processus acrocoracoideus of the coracoid, and a flat facies articularis scapularis may counteract transverse movements of the coracoid during the contraction of musculus coracobrachialis cranialis and thereby increase the efficiency of this muscle. Similar considerations may apply to psittaciform, and columbiform birds, which likewise have a large crop, a reduced furcula, and a flat facies articularis scapularis.

For some taxa, correlations between the morphology of the coracoscaphular joint and the development of the furcula shafts or wing movements are not obvious, and more research is needed for a full understanding of the functional significance of the variation found in neornithine birds. The Cathartidae, for example, have a flat facies articularis scapularis and a robust furcula with a wide sternal extremity. These birds are adapted to thermal soaring, so that wing flapping plays a role mainly during take-off and landing. This is, however, also true for various taxa with a deep cotyla scapularis, such as the Ciconiidae, Pelecanidae, and Sagittariidae, and even though the functional considerations proposed in the present study explain some of the observed variation in the morphologies of the neornithine coracoscaphular joint, other functional correlations may exist.

The coracoid is a robust bone, which has a comparatively high fossilization potential. As demonstrated above, the different morphologies of the scapular articulation facet are potential indicators of profound changes in the architecture of the pectoral girdle and mark important ecomorphological changes in the stem lineages of certain taxa. Improved knowledge of the functional significance of the different morphologies of the coracoscaphular joint of neornithine birds therefore has the potential to inform the paleobiology of extinct taxa, and it is to be hoped that the present study serves to inspire future research in this direction.

Fig. 4 Different morphologies of the coracoid (left side, dorsal view) and furcula (caudal view) of selected extant birds. **a** *Eupodotis vigorsii* (Otidiformes, Otididae). **b** *Sagittarius serpentarius* (Accipitriiformes, Sagittariidae). **c** *Ciconia ciconia* (Ciconiiformes, Ciconiidae). **d** *C. ciconia*, coracoid of a juvenile individual. **e** *Pelecanus onocrotalus* (Pelecaniformes, Pelecanidae). **f** *Anhima cornuta* (Anseriformes, Anhimidae). **g** The early Eocene stem group galliform *Gallinuloides wyomingensis* (Galliformes, Gallinuloididae. WDC CGR-012). **h** *Pavo cristatus* (Galliformes, Phasianidae). **i** *Rhynchotus rufescens*

(Tinamiformes, Tinamidae). **j** *Phalacrocorax carbo* (Suliformes, Phalacrocoracidae). **k** *Goura victoria* (Columbiformes, Columbidae). **l** *Bubo scandiacus* (Strigiformes, Strigidae). **m** *Colius striatus* (Coliiformes, Coliidae). **n** *Pharomachus pavoninus* (Trogoniformes, Trogonidae). **o** *Micrastur ruficollis* (Falconiformes, Falconidae). **p** *Corvus corax* (Passeriformes, Corvidae). Abbreviations: *csc* cotyla scapularis, *faa* facies articularis acrocoracoidea, *fas* facies articularis scapularis, *fns* foramen nervi supracoracoidei, *ins* incisura nervi supracoracoidei, *ste* sternum. The scale bars equal 10 mm

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