A survey of the uncinate bone and other poorly known ossicles associated with the lacrimal/ectethmoid complex of the avian skull

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Abstract
In several taxa of Neornithes (crown group birds), the lacrimal/ectethmoid complex exhibits small bones, the comparative osteology of which is poorly studied. Some of these ossicles—which are commonly known as uncinate bones (ossa uncinata or osa lacrimopalatina)—were already described two centuries ago, but knowledge of their distribution and morphological variability in higher level clades is incomplete. In the present study, a detailed survey of the occurrence of uncinate bones is given, and these ossicles are for the first time reported in the gruiform Psophiidae, some Rallidae, and in the Otidiformes. Their presence in the latter taxon is of particular interest, because in current molecular analyses, the Otidiformes result as close relatives of the Musophagiformes, in which the uncinate bone is particularly large. The uncinate bones of most other neornithine clades, however, appear to have evolved multiple times independently through parallel evolution from the same ligamentous structures. A few earlier authors assumed that the uncinate bone is homologous to the ectopterygoid of non-avian theropods. Although this remains a viable hypothesis, more data on the occurrence of the ectopterygoid in Mesozoic birds are needed for well-supported conclusions. Here, it is noted that the ontogenetic development of the uncinate bone appears to be correlated with that of the ectethmoid, which is another bone in the skull of neornithine birds that is of unknown origin.

Keywords
Aves, comparative osteology, ectopterygoid, os lacrimale communicans, os lacrimopalatinum, os uncinatum, phylogeny

1 | INTRODUCTION
The avian skeleton contains various small elements, the comparative osteology of which is poorly studied. This is particularly true for ossicles associated with the lacrimal/ectethmoid complex of the skull, which are easily lost during skeleton preparation.

Nitzsch (1811) was the first to describe a “lower accessory bone” (“unterer Anhangsknochen”) on the lacrimal of Sterna hirundo (Charadriiformes, Sterniidae); this ossicle was...
subsequently named ossiculum lacrimosuborbitale by Jollie (1957). Several years after Nitzsch, Brandt (1839) noted an accessory bone near the lacrimal of the suliform Fregatidae and the Procellariiformes, which he termed “ossiculum lacrymo-palatinum” (os [ossiculum] lacrimoplatinum of Jollie, 1957 and Baumel & Witmer, 1993). A rod-shaped element situated between the lacrimal and the jugal bar of the Cariamiformes was described as “os lacrymale communicans” by Burmeister (1854). Magnus (1870) finally introduced the term os uncinatum for an ossicle associated with the lacrimal/ectethmoid complex of the Cuculiformes. Reinhardt (1871) described the large uncinate bone of the Musophagiformes, commented on its possible functional significance, and gave an overview of similar ossicles in other birds. Most often, the ossicles associated with the lacrimal/ectethmoid complex were subsumed under the same name and were either termed os lacrimopalatinum (e.g., Jollie, 1957 and Baumel & Witmer, 1993). A rod-shaped element situated between the lacrimal and the jugal bar of the Cariamiformes was described as “os lacrymale communicans” by Burmeister (1854). Magnus (1870) finally introduced the term os uncinatum for an ossicle associated with the lacrimal/ectethmoid complex of the Cuculiformes. Reinhardt (1871) described the large uncinate bone of the Musophagiformes, commented on its possible functional significance, and gave an overview of similar ossicles in other birds. Most often, the ossicles associated with the lacrimal/ectethmoid complex were subsumed under the same name and were either termed os lacrimopalatinum (e.g., Jollie, 1957) or os uncinatum (e.g., Burton, 1969; Cracraft, 1968). However, os uncinatum and os lacrimopalatinum were listed as distinct elements by Baumel and Witmer (1993), and Livezey and Zusi (2006, p. 122) even applied three different names to these ossicles (os lacrimopalatinum, os uncinatum, and the new term os jago-ectethmoidale for the ossicle in the Steatornithidae). For practical reasons, the English term “uncinate bone,” as used in the following, refers to both, the os lacrimopalatinum sensu Brandt (1839) and the os uncinatum sensu Magnus (1870).

In a study of the lacrimal-ectethmoid complex, Cracraft (1968) commented on uncinate bones in various clades. Subsequently, Burton (1969) studied the morphology and possible function of the uncinate bone of the Musophagiformes and noted the presence of an uncinate bone in “adults of the Struthionidae, Rheidae, Diomedeidae, Procellariidae, Fregatidae, some Cuculiformes, Musophagiformes and Steatornithidae” (Burton, 1969, p. 11). More recently, Elzanowski (1999) and Zusi and Livezey (2006) briefly addressed the occurrence of uncinate bones in neornithine birds.

Still, there exist only few illustrations of the actual morphology of these ossicles in different avian taxa, comparative data are scarce, and their morphological variation across and within higher level clades remains poorly studied. The aim of the present study is to improve our knowledge on the distribution and morphology of uncinate bones, and I report several overlooked instances of their occurrence and comment on the morphological and positional variability of these ossicles.

2 | MATERIAL AND METHODS

Unless specified otherwise, the general osteological terminology follows Baumel and Witmer (1993). For this study, mainly skulls cleaned by dermastid beetle larvae were examined, because uncinate bones are usually lost in specimens prepared by putrefactive maceration. Regarding species-rich taxa in which ossicles associated with the lacrimal/ectethmoid complex occur, skulls of the following species were studied in the ornithological collection of Senckenberg Research Institute Frankfurt (SMF); nomenclature and family-level classification follow the IOC World Bird List (https://www.worldbirdnames.org), an asterisk indicates species, of which only macerated skulls were examined: Diomedeidae: Diomedia antipodensis, D. exulans, Thalassarche chlororhynchos, T. melanophris, Phoebetria fusca. Procellariidae: Aphrodroma brevirostris, Ardenna gravis, A. grisea, A. tenuirostris, Bulveria bulverii, B. fallax, Calonectris diomedia, Ca. leucemas, Daption capense, Fulmarus glacialis, F. glacialoides, Halobaena caerulea, Macronectes giganteus, M. halli, Pachyptila salvini, Pelicanoides georgicus, Pe. urinatrix, Procellaria aequinotialis, Pr. cinerea, Pterodroma hypooleuca, Pt. incerta, Pt. lessonii, Pt. mollis, Puffinus baroli, Pu. gavia, Pu. huttoni, Pu. boydi, Pu. puffinus, Pu. yelkouan. Hydrobatidae: Hydrobates pelagicus, Oceanodroma castro, O. leucorhoa. Oceanitidae: Fregetta tropica, Oceanites oceanicus*, Pelagodroma marina. Threskiornithidae: Bostrychia hagedash, Eudocimus albus, E. ruber, Geronticus calvus, G. eremita, Lophotibis cristata, Platalea ajaja, P. alba, P. leucorodia, P. minor, Plegadis falcinellus, Pl. ridgwayi, Pseudibis papillosa, Theristicus melanops, Threskiornis aethiopicus, T. melanephalus, T. spinicollis. Cuculiformes: Cacomantis flabelliformis, Carpococcyx renaudii, Centopus burchelli, Ce. goliath, Ce. phasianinus, Ce. superciliosus, Ceuthmocharis aequus, Chrysococcyx caprius, Chr. lucidus, Clamator glandarius, Cl. levaillantii, Coccyzus americanus, Coua caerulea, Co. cristata, Co. gigas, Crotophaga ani, Cr. major, Cuclius canorus, Cu. solitarius, Eudynamys scolopacea, Geococcyx californianus, Guira guira, Piaya cayana, Surniculus lugubris*. Musophagiformes: Corythaëola cristata, Crinifer concolor, Cr. leucogaster, Cr. personatus, Cr. piscator, Cr. zonurus, Gallirex (Ruwenzorornis) johnstoni, Menelikornis (Tauraco) leucotis, Tauraco corythaix, T. erythrolophus, T. fischeri, T. hartlaubi, T. leucopholus, T. livingstonii, T. macrorhynchos, T. persa, T. (Musophaga) rossae, T. (Musophaga) violaceus. Otidiformes: Affrotis afracockes, Ardeotis arabs, A. australis*, A. kori, Chlamydotis undulata, Eupodotis melanogaster*, Eu. senegalensis, Eu. vigorsii, Lophotis gindiana, L. savilei*, Neotis denhami*, N. ludwigii, N. nuba*, Otis tarda, Tetrax tetrax*. Rallidae: Amaurornis flavirostris, Am. phoenicurus, Aramides cajanea, Ar. ypecaha, Canirallus oculus, Crex crex, Fulica americana, F. atra, F. cristata, Gallirrex cinerea, Gallinula chloropus, G. comeri, Gallirallus australis, Himantornis...
haematopus, Laterallus leucopyrhus, L. melanophaius, Porphyrio poliocephalus, P. porphyrio, Porzana flaviventer, P. parva, P. porzana, Rallina fascicata, Rallus aquaticus, R. elegans, R. limicola. Sarothruridae: Sarothrura elegans, S. pulchra. Laridae, Larinae: Chroiocephalus brunnicephalus, Ch. cirrhocephalus, Ch. genei, Ch. maculipennis, Ch. novaehollandiae, Hydrocoloeus minutus, Larus argentatus, L. audouini, L. cachinnans, L. californicus, L. canus, L. crassirostris, L. delawarensis, L. dominicanus, L. fuscus, L. glaucoides, L. marinus, L. melanocephalus, L. michahellis, L. occidentalis, L. ridibundus, L. schistisagus, Leucophaeus atricilla, Le. pipixcan, Pagophila eburnea, Rhodostethia rosea, Rissa tridactyla, Xema sabini. Laridae, Sterninae: Chlidonias hybrida, Gelochelidon nilotica, Larosterna inca, Onychoprion anaethetus, O. fuscatus, Sterna caspia, St. dougallii, St. hirundo, St. paradisaea, Sternula albifrons, S. Saundersi, Thalasseus bengalensis, Th. bergii, Th. elegans, Th. sandvicensis. Alcidae: Aethia cristatella, Alca torda, Alle alle, Brachyramphus marmoratus, Cepphus grylle, Cerorhinca monocerata, Cyclorrhynchus psittacula, Fratercula arctica, Fr. cirrhata, Fr. corniculata, Pygospio elegans, Synthliboramphus antiquus, Uria aalge, U. lomvia. Accipitridae: Accipiter cooperi, Ac. gentilis, Ac. nisus, Aegypius monachus, Ae. tracheliotus, Aquila audax, Aq. chrysaetos, Aq. clanga, Aq. heliaca, Aq. nipalensis, Aq. rapax, Aviceda subcristata, Butastur teesa, Buteo buteo, B. jamaicensis, B. lagopus, Circetus gallicus, Circus aeruginosus, C. pygargus, Elanus caeruleus, Gypaetus barbatus, Gyps africanus, G. coprotheres, G. fulvus, Haliaeetus albicilla, H. leucocephalus, H. vocifer, Harpagus bidentatus, Harpia harpyja, Hieraaetus fasciatus, Melierax canorus, Milvus migrans, M. milvus, Necrosyrtes monachus, Neophron percnopterus, Pandion haliaetus, Parabuteo unicinctus, Pernis apivorus, Polyboroides typus, Spilornis cheela, Spizaetus cirrhatus, S. Ornatus.

3 | RESULTS

3.1 | Struthioniformes

The uncinate bone of the ostrich was described by Webb (1957). The ossicle is attached to the ventral margin of the lacrimal and is a small, plate-like element (Figure 1a).

3.2 | Rheiformes

In the Rheiformes (Figure 1b,c), a large, plate-like bone is attached to the ventromedial margin of the lacrimal. This bone is situated in the plane of the ectethmoid, from which it is separated by a gap. Its ventrolateral edge contacts the jugal.

3.3 | Steatornithidae

The uncinate bone of the Steatornithidae is a small, L-shaped ossicle with a mediolaterally wide dorsal portion.

FIGURE 1 The uncinate bones of the Struthioniformes (a) and Rheiformes (b, c); the images show the lacrimal/ectethmoid complex of the left side in caudolateral view. (a) Struthio camelus (SMF 6563; left side). (b) Rhea americana (SMF 5754; right side, mirrored). (c) Rhea (Pterocnemia) pennata (SMF 7286; left side). ect, ectethmoid; jug, jugal; lac, lacrimal; pmx, processus maxillopalatinus; unc, uncinate bone. Scale bar = 5 mm.
FIGURE 2  Uncinate bones of the Steatornithidae (a) and Cuculiformes (b–l); all images except (k) show the lacrimal/ectethmoid complex of the left side in caudoventral view. (a) Steatornis caripensis (SMF 1738). (b) Eudynamys scolopacea (SMF 20837; right side, mirrored). (c) Geococcyx californianus, juvenile individual (SMF 6415). (d) G. californianus (SMF 2850). (e) Carpodacus renauti (SMF 4521; right side, mirrored). (f) Centropus burchellii (SMF 8802). (g) Ce. phasianinus (SMF 5242; right side, mirrored). (h) Ce. superciliosus (SMF 1665; right side, mirrored). (i) Clamator glandarius (SMF 1764; right side, mirrored). (j) Cl. levaillantii (SMF 515; right side, mirrored). (k) Chrysococcyx caprius (SMF 10785; right side in ventromedial view), the uncinate bone is co-ossified with the ectethmoid. (l) Cuculus canorus (SMF 4015). ect, ectethmoid; jug, jugal; lac, lacrimal; pal, palatine (os palatinum); qdr, quadrate; unc, uncinate bone. Scale bar = 5 mm
and a thin, curved lateral projection, which is connected to the jugal by a ligament (Figure 2a). The ossicle is situated next to the ectethmoid, with which it does, however, not articulate (a lacrimal is absent in the Steatornithidae).

### 3.4 | Cuculiformes

An uncinate bone of a representative of the Cuculiformes was first reported by Magnus (1870) for “*Phoenicophaeus virens*” (which, according to Reinhardt, 1871 probably denotes *Phoenicophaeus curvirostris*). Reinhardt (1871) identified the ossicle in *Rhinorta chlorocephaea*, *Zanclostomus javanicus*, and *Eudynamys scolopacea* and considered it to be absent in *Crotophaga*, *Guira*, *Dromococcyx*, *Piaya*, and *Centropus*. Beddard (1898) described an uncinate bone for *Scythrops novaehollandiae* (see also Reinhardt, 1871). Burton (1969, p. 11) noted the presence of a well-developed uncinate bone in *Clamator*, *Eudynamys*, and *Centropus* and “a short uncinate bone joining the palatine by means of a ligament” in *Piaya*, *Ramphococcyx*, and *Crotophaga*. An uncinate bone is also present in *Neomorphus geoffroyi* (Posso & Donatelli, 2010) and *Coccycus* (*Hyetornis ruficularis* (Posso & Donatelli, 2007). However, the existing variability in the morphology of this ossicle was not addressed in earlier studies on the osteology of cuckoos (Hughes, 2000; Posso & Donatelli, 2006; Pycraft, 1903), and a number of taxa have not yet been studied.

The uncinate bone forms a plate-like element in some taxa, whereas it is a feeble ossicle in others. Usually, it is attached to the ventral portion of the ectethmoid, and often it articulates with a small rostral projection of the latter bone. In general, the uncinate bone is vestigial in cuculiform taxa with a large ectethmoid, whereas the latter bone is smaller in taxa with a large uncinate bone.

A large, plate-like uncinate bone was figured by Beddard (1898, fig. 3) for *Scythrops novaehollandiae*. A well-developed uncinate bone is also present in *Eudynamys scolopacea* (Reinhardt, 1871; own obs., Figure 2b), where it is attached to the ventral portions of the lacrimal and barely contacts the ectethmoid. A large uncinate bone is here for the first time reported for *Carpococcyx renauldi*, in which it is attached to the ventral portion of the ectethmoid (Figure 2e). The uncinate bone is furthermore well-developed in *Centropus* (*C. burchelli* and *C. phasianinus*, in *C. superciliosus* it is co-ossified with the ectethmoid; Figure 2f–h, contra Reinhardt, 1871). In *Clamator glandarius* (SMF 1764), a smaller, plate-like uncinate bone is situated on the ventral margin of the ectethmoid (Figure 2i).

The uncinate bone is an L-shaped element attached to the ectethmoid in *Phoenicophaeus curvirostris* (“*Phoenicophaeus virens*”; Magnus, 1870, pl. 6, fig. 9). In taxa of the Cuculinae, it is vestigial and merely consists of a ligamentous sheet with a small ossification center that forms two ligamentous spines at its ventral margin. Such is true for *Clamator levillantii* (SMF 515; Figure 2j), *Cethmocharaes aereus* (SMF 521), and *Cacomantis flabeliformis*. An uncinate bone was not found in *Coccyx* and most specimens of *Cuculus* (in one individual of *Cuculus canorus* [SMF 4015], a small ossicle is attached to the jugal near the ventral tip of the lacrimal; Figure 2i).

A spike-like process is co-ossified with the ventral portion of the ectethmoid in *Geococcyx californianus* (Figure 2d; an isolated ossicle was found in a juvenile specimen, Figure 2c), *Surniculus lugubris*, *Chrysococcyx caprius* (Figure 2k), *C. klaas*, and *C. lucidus*. Possibly, a small uncinate bone is also co-ossified with the ectethmoid in *Piaya cayana* (SMF 9605, SMF 20161). An uncinate bone is absent in the taxa *Coua*, *Guira*, and *Crotophaga* (Livezey & Zusi, 2006) scored an “oss uncinatum” as present in *Crotophaga*, but I could not confirm this observation, even though in one of the examined specimens of *Crotophaga ani*, the ossicle may be co-ossified with the ectethmoid; SMF 12515).

### 3.5 | Musophagiformes

The exceptionally large uncinate bone of the Musophagiformes was first described by Reinhardt (1871). Burton (1969, p. 8) provided a detailed description and noted that “[i]n its extreme condition, seen in *Corvethaera cristata* and *Crinifer zonurus* (…), the uncinate bone is inflated, with a wide dorsal end articulating with the ectethmoid, a flattened lateral surface, and a narrow, blade like ventral edge. The lower half is expanded and bulges out laterally under the jugal bar. The jugal bar thus lies in a groove at the front of the orbit formed by the uncinate bone and lacrimal.” In *Corvethaera* (Figure. 3a,b) and *Crinifer* (Fig. 3c–f), the uncinate bone exhibits pneumatic openings on the rostral and/or caudal surface of its ventral portion, which is more strongly pneumatized and wider in *Crinifer leucogaster* (Figure 3e) than in *Corvethaera cristata* (Figure 3a,b) and the other species of the taxon *Crinifer* (Cr. piscator, Cr. zonurus, Cr. personatus, and Cr. concolor).

The uncinate bone forms a rostroventrally wide ventral process in *Corvethaera* and *Crinifer*, whereas it is narrower and more strut-like in the species of *Tauraco* (including *Musophaga*; Figure 3k,l). In *Gallirex johnstoni* (Figure 3g), which has not been studied by previous authors, its proportions are intermediate between those of *Tauraco/Musophaga* (Figure 3h–j) and *Crinifer*. A skull of the closely related (Veron & Winney, 2000)
FIGURE 3  The uncinate bone of the Musophagiformes; if not indicated otherwise, the images show the lacrimal/ectethmoid complex of the left side in caudoventral view. Corythaeola cristata (SMF 8219) in (a) left lateral and (b) caudoventral view. C. concolor (SMF 3499) in (c) left lateral and (d) caudoventral view. (e) Crinifer leucogaster (SMF 6990). (f) C. piscator (SMF 18722). (g) Gallirex johnstoni (SMF 20379). (h) Tauraco violaceus (SMF 8451). (i) T. erythrolophus (SMF 21252). (j) T. corythaix (SMF 20439); the small arrows denote the lateral bulge of the palatine, which braces the uncinate bone. Isolated uncinate bones (left side, rostral view) of (k) Crinifer piscator (SMF 12554) and (l) T. schuetti (SMF 12550). ect, ectethmoid; jug, jugal; lac, lacrimal; pal, palatine (os palatinum); pnf, pneumatic foramen; unc, uncinate bone. Scale bar = 5 mm.
Gallirex porphyreolophus was not available for study, but Reinhardt (1871, p. 329) noted that the uncinate bone of this species is somewhat stouter and wider than in Tauraco. Within the Musophagiformes, Gallirex is the sister taxon of a clade including Tauraco/Musophaga (Veron & Winney, 2000), which conforms with the intermediate size of its uncinate bone.

A distinctive and previously undescribed morphology occurs in Tauraco corythaix, in which the uncinate bone is braced by a lateral bulge of the palatine (Figure 3j). This morphology is not found in the closely related (Veron & Winney, 2000) species T. fischeri and T. livingstonii.

3.6 | Otidiformes

The occurrence of an uncinate bone in the Otidiformes has not been noted before, which is due to the fact that the ossicle is usually co-ossified with the ectethmoid. A free uncinate bone was, however, found on one side of an adult (12-years-old) individual of Eupodotis senegalensis, where it is attached to the lateral margin of the ectethmoid and contacts the ventromedial margin of the lacrimal (Figure 4a). The contralateral uncinate bone of this individual, however, is co-ossified with the ectethmoid (Figure 4b). In most other Otidiformes, the uncinate bone is likewise co-ossified with the ventrolateral portion of the ectethmoid and forms a rostrally directed, spine-like projection, which occurs in Eupodotis vigorsii, Tetrax tetra, Otis tarda, Afrotis afraoides (Figure 4c), Lophotis gindiana, and L. savilei. In Ardeotis arabs, A. kori, A. australis, and Neotis denhami, ectethmoid and lacrimal are co-ossified.

3.7 | Psophiidae

Uncinate bones are here for the first time reported for the gruiform Psophiidae. In multiple specimens of Psophia crepitans (e.g., SMF 19551; Figure 4d), a small, sub-rectangular and plate-like ossicle is attached to the

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**Figure 4** Uncinate bones in taxa of the Otidiformes (a–c) and Gruiformes (d–i); all images except (b) and (i) show the lacrimal/ectethmoid complex of the left side in caudodorsal or caudoventral view. (a) Eupodotis senegalensis (Otidiformes; SMF 21520), left side with free uncinate bone. (b) Eupodotis senegalensis, (Otidiformes; SMF SMF 21520), right side with co-ossified uncinate bone. (c) Afrotis afraoides (Otidiformes; SMF 1988) with co-ossified uncinate bone. (d) Psophia crepitans (Psophiidae; SMF 19551). (e) Porphyrio porphyrio (Rallidae; SMF 199918). (f) P. poliocephalus (Rallidae; SMF 19916). (g) Porzana porzana (Rallidae; SMF 5702). (h) Aramides ypecaha (Rallidae; SMF 5417). (i) Sarothrura pulchra (Sarothruridae; SMF 8311; right side). The encircled areas in (a), (d), (e), and (i) show enlarged details of the uncinate bone. ect, ectethmoid; lac, lacrimal; pal, palatine (os palatinum); unc, uncinate bone. Scale bar = 5 mm
ventral portion of the ectethmoid; laterally, it abuts on the medial margin of the ventral process of the lacrimal.

3.8 | Rallidae and Sarothruridae

Also for the first time, an uncinate bone is here reported for species of the gruiform Rallidae. The ossicle is particularly well developed in *Porphyrio porphyrio* and *P. poliocephalus*, where it is situated between the ectethmoid and the lacrimal (Figure 4e,f). It is small and not in contact with the latter two bones in *Porzana porzana* (Figure 4g) and is a vestigial osseous splint in *Aramides ypecaha* (Figure 4h).

In one specimen of *Sarothrura pulchra* (Sarothuridae; SMF 8311, Figure 4i), the ventral portion of the ectethmoid forms a spike-like rostral process, which resembles the co-ossified uncinate bone of some Cuculiformes (Figure 2d). This projection has not been found in other individuals of the species or other Rallidae.

3.9 | Charadriiformes

Nitzsch (1811) already noted the presence of a caudally directed ossicle in the Sterninae, which he considered to be located on the ventral end of the lacrimal. However, the lacrimal and ectethmoid bones are co-ossified in adult Sterninae, and a juvenile individual of *Thalasseus sandvicensis* shows that the ossicle is located at the contact zone between the ventral end of the lacrimal and the lateral tip of the ectethmoid (Figure 5d). Concerning the

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**FIGURE 5** Ossicles associated with the lacrimal/ectethmoid complex of the charadriiform Lari; all images except (a) show the lacrimal/ectethmoid complex of the right side in lateral or caudolateral view. (a), (b) *Sterna hirundo* (Sterninae; SMF 10232); in (a) the ligamentum jugolacrimale is still in place (the image shows the left side). (c) *Sternula albifrons* (Sterninae; SMF 8178). (d) *Thalasseus sandvicensis*, juvenile individual (Sterninae; SMF 17792); the encircled shows an enlarged detail, the small arrows denote the tips of the lacrimal and ectethmoid, respectively. (e) *Larus fuscus* (Larinae; SMF 6347). (f) *Larus crassirostris* (Larinae; SMF 5868). (g) *Larus dominicanus* (Larinae; SMF 19255). (h) *Alca torda* (Alcidae; SMF 10231). (i) *Fratercula arctica* (Alcidae; SMF 5916). ect, ectethmoid; hel, helical ossicle (see text); lac, lacrimal; ljl, ligamentum jugolacrimale; oss, ossicle associated with lacrimal/ectethmoid complex (ossiculum lacrimosuborbitale of Jollie, 1957). Scale bar = 5 mm.
Sterninae examined in the present study, the ossicle—the ossicular lacrimosuborbitale of Jollie (1957)—was found in Gelochelidon nilotica, Hydroprogne caspia, Larosterna inca, Onychoprion anaethetus, O. fuscatus, Sterna hirundo (Figure 5a,b), S. paradisaea, Sternula albifrons, Thalassasus bengalensis, Th. berti, and Th. elegans. In S. albifrons, the bone is particularly well developed (Figure 5c). Within the studied Larinae, I found this ossicle only in individuals of Larus fuscus (SMF 6347; Figure 5e), L. dominicanus (SMF 19255; Figure 5g), and L. crassirostris (SMF 5868; Figure 5f); in the latter species, it is co-ossified with the ectethmoid. Reinhardt (1871, p. 327) reported its occurrence in L. glaucus, L. marinus, and L. argentatus. In the Alcidae, it is present in Alca torda (SMF 10231; Figure 5h), where it was already noted by Shufeldt (1888; see also Mayr, 2011, fig. 4h). A small ossicle is furthermore present in individuals of Uria aalge (SMF 9553) and minute ones are also present in individuals of Alle alle (SMF 5711), Fratercula arctica (SMF 5916; Figure 5i), and F. corniculata. Jollie (1957) indicated that the ossicle also seems to be present in juveniles of Stercorarius skua (Stercorariidae) depicted by Maillard (1948, fig. 34); in adult Stercorariidae it is absent.

Here, it is noted that some Alcidae furthermore exhibit a peculiar helical ossicle that is situated next to the ventral border of the ectethmoid (Figure 5h). This ossicle, which probably is an ossified nasal concha, was identified in Alca torda, Fratercula arctica, Alle alle, and Cepphus grylle, but it may be present in other species as well.

### 3.10 Procellariiformes

In the Procellariiformes, uncinate bones occur in the Diomedeidae and Procellariidae (Brandt, 1839; Reinhardt, 1871). In the Diomedeidae, the bone is a weakly curved, rod-shaped element, which runs along the ventromedial border of the descending process of the lacrimal and directs toward the palatine (Figure 6a). The uncinate bone of the Procellariidae, by contrast, is a rod-shaped element that is only attached to the ventral end of the lacrimal. Within the Procellariidae, the ossicle is best developed in Puffinus (Figure 6b–d), Ardenna (Figure 6e), Calonectris (Figure 6f), Bulweria, Pterodroma, Halobaena, and Pachyptila (Figure 6h), whereas it is only a very thin splint in Macronectes (Figure 6i) and Fulmarus and has not been found in Daption (of which, however, only a single skull was examined). The uncinate bone is variably developed in Puffinus and Ardenna: In Puffinus puffinus (Figure 6b) and P. baroli (Figure 6c), its dorsal portion forms a distinct, medially directed and rod-like process, so that the ossicle has an inverse L-shape. In P. gavia (Figure 6d), P. boydi, and the species of Ardenna (Figure 6e), by contrast, the dorsal portion is distinctly widened but lacks a medial projection.

In Puffinus, Ardenna, Calonecrtis, Procellaria, and Bulweria, the lacrimal is not co-ossified with the surrounding bones. By contrast, in many Procellariidae with a reduced uncinate bone (Macronectes, Fulmarus, Daption), lacrimal, ectethmoid, and frontal are tightly fused. Co-ossification of the lacrimal with the ectethmoid and frontal bones also occurs, however, in Halobaena and Pachyptila, in which the uncinate bone is well developed.

An uncinate bone is here also reported for Pelecanoides (Figure 6j,k), in which it is a short, rod-shaped ossicle, which in one specimen has no contact to the lacrimal and runs along the dorsal margin of the palatine (Figure 6k). An uncinate bone was already reported for Pelecanoides urinatrix by Reinhardt (1871), whereas Burton (1969) found only a ligament to be present in the taxon.

Livezey and Zusi (2006, p. 122) considered an uncinate bone (“os lacrimopalatinum”) to be present in Oceanites (Oceanitinae). I could only examine a macerated skull of this taxon, but found an uncinate bone to be present in the closely related taxa Pelagodroma (of which more than 20 skulls were available) and Fregata. An uncinate bone is likewise absent in the species of the Hydrobatinae.

### 3.11 Fregatidae and Sulidae

The uncinate bone of the Fregatidae was first described by Brandt (1839). It is a slightly curved, rod-like bone, which runs along the ventromedial border of the descending process of the lacrimal and reaches to the palatine (Figure 7a); the morphology of the ossicle closely resembles that of the procellariiform Diomedeidae. A possible uncinate bone was noted by Olson (1977) for the early Eocene stem group frigatebird Limnofregata, whereas it does not seem to be preserved in the skulls figured by Olson and Matsuoka (2005). Limnofregata distinctly differs from crown group Fregatidae in the morphology of the lacrimal/ectethmoid complex, and whereas the ectethmoid is greatly reduced in extant Fregatidae, it is well developed in Limnofregata (Olson, 1977; Olson and Matsuoka, 2005).

The Fregatidae are the sister taxon of the Suliformes, which include the Sulidae, Phalacrocoracidae, and Anhingidae (Hackett et al., 2008; Kuhl et al., 2021; Prum et al., 2015). Jollie (1957) identified a putative uncinate
FIGURE 6  The uncinate bone of the Procellariiformes; all images show the lacrimal/ectethmoid complex of the left side in lateral or caudolateral view. (a) *Thalassarche chlororhynchos* (Diomedeidae; SMF 8922). (b) *Puffinus puffinus* (Procellariidae; SMF 19586). (c) *P. baroli* (Procellariidae; SMF 18065). (d) *P. gavia* (Procellariidae; SMF 5245). (e) *Ardenna gravis* (Procellariidae; SMF 19367). (f) *Calonectris diomedea* (Procellariidae; SMF 2752). (g) *Pterodroma hypoleuca* (Procellariidae; SMF 3957). (h) *Pachyptila salvini* (Procellariidae; SMF 8798, right side, mirrored). (i) *Macronectes giganteus* (Procellariidae; SMF 8847). (j) *Pelecanoides* sp. (Procellariidae; SMF 8829). (k) *P. georgicus* (Procellariidae; SMF 8796, right side, mirrored). ect, ectethmoid; lac, lacrimal; mem, membrane between jugal and palatine; pal, palatine (os palatinum); unc, uncinate bone. Scale bar = 5 mm.
bone in the taxon *Morus* (Sulidae), which is here also reported for *Sula* (Figure 7g). The bone contacts the mesethmoid and is similar in its size and position to the ectethmoid of the Anhingidae. Most likely, therefore, it represents an ectethmoid that is not co-ossified with the mesethmoid rather than an uncinate bone.

Suliform birds furthermore exhibit a peculiar ossicle near the lacrimal, which is situated on the dorsal surface of the jugal bar and is particularly well-developed in the Anhingidae (Figure 7h; in the Phalacrocoracidae, there is only a small splint of bone, whereas the ossicle appears to be co-ossified with the jugal bar in the Sulidae). The occurrence of this ossicle was first noted by Brandt (1839), who introduced the term os suprajugale for it. The homology of this ossicle is unknown, but its position rostral of the lacrimal does not suggest an os uncinatum.

### 3.12 | Threskiornithidae

The occurrence of an uncinate bone in the threskiornithid taxon *Plegadis* was first noted by Cracraft (1968). It is a curved, rod-shaped bone, which runs along the ventral border of the lacrimal and connects the tip of the ectethmoid with the jugal bar (Figure 7b). A rod-like ossicle that extends from the ventral tip of the lacrimal to the
jugal bar is also present in *Platalea ajaja* (SMF 9691) and *P. minor* (SMF 8234; Figure 7c). In *Threskiornis aethiopicus* (Figure 7d; SMF 18318), by contrast, a rod-shaped uncinate bone runs from the lateral tip of the ectethmoid along the ventral margin of the lacrimal. In *Bostrychia hagedash* (SMF 11738), the ossicle appears to be co-ossified with the ectethmoid. Vestigial uncinate bones were also found in other Threskiornithidae, that is, *Eudocimus ruber* (SMF 7440), *Pseudibis papillosa* (SMF 19788; Figure 7e), and *Geronticus eremita* (SMF 21541; Figure 7f).

### 3.13 Cariamiformes

A small ossicle between the tip of the lacrimal and the jugal of the Cariamidae was first mentioned by Burmeister (1854). It is present in both extant species, *Cariama cristata* (Figure 8a) and *Chunga burmeisteri* and was also identified in the extinct Phorusrhacidae (Degrange, 2021; Degrange et al., 2015).

### 3.14 Accipitriformes

Elzanowski (1999) reported uncinate bones in some Accipitridae, but did not specify their occurrence. I found the ossicle to be present in *Haliaeetus vocifer* (Figure 8b); vestigial ossicles are present in individuals of *Melierax canorus* (Figure 8c), *A. heliaca*, and *A. nipalensis*. In a specimen of *Pernis apivorus*, a small ossification occurs within a membrane extending from the ventromedial margin of the ectethmoid to the palatine.
3.15 | Piciformes

In species of the piciform Picidae, the ventrolateral portion of the ectethmoid forms a long, rostrally directed process, which runs along the dorsal margin of the jugal bar. This process is an autapomorphy of the subclade Malarpicini (Manegold & Töpfer, 2013) and was designated as an “os uncinatum” by Shufeldt (1900). In a juvenile specimen of Dryocopus martius, a small ossicle was indeed found on the ventrolateral tip of the ectethmoid (Figure 8g,h). This suggests that the long process of this bone is formed by fusion with a separate ossification. Whether the latter indeed represents an uncinate bone is, however, anything but certain.

3.16 | Ossicles associated with the lacrimal/ectethmoid complex in individuals of the galliform Megapodiidae, the Columbiformes, and the Trogoniformes

The above-listed taxa regularly exhibit ossicles associated with the lacrimal/ectethmoid complex. In three further cases, however, unusual ossifications were only identified in a single individual or species of a given clade, so that the occurrences of these structures may represent anomalous conditions.

In one captive individual of Alectura lathami (Galliformes, Megapodiidae; SMF 7243, Figure 8d), a small ossicle was found attached to the rostral surface of the ectethmoid bone. This bone is absent in other skulls of the species. Skulls of other Megapodiidae were not available for examination.

In several captive individuals of Goura victoria (Columbiformes), I found a small, plate-like ossicle attached to the ventrolateral surface of the palatine bone (Figure 8e). This ossicle has not been reported before and was not identified in other species of the Columbiformes.

Reinhardt (1871) noted the presence of a putative uncinate bone in a species of the Trogoniformes (cf. Trogon surrucura [“T. aurantius”]). The structure in question is a long, hook-like, and medially projected process of the lacrimal, which may constitute a co-ossified uncinate bone. A similar projection is here reported for Trogon collaris (SMF 19799; Figure 8f), but was not found in other Trogoniformes.

4 | DISCUSSION

4.1 | Morphology, development, and homology

As shown in the present study, uncinate bones are not a rare exception in neornithine birds, but have a wide distribution. Often these ossicles are, however, rudimentary and prone to be lost during skull preparation. It is therefore to be expected that more instances of their occurrence will be identified in future studies and this is particularly true for taxa, in which the uncinate bone is eventually co-ossified with the lacrimal (as in some Laridae) or ectethmoid (as in most Otidiformes and some Cuculiformes). The latter may be the case in Rhynochetos jubatus (Rhynchetidae), in which the tip of the ectethmoid shows a rostral projection similar to that in the Otidiformes, which may represent a co-ossified uncinate bone.

The ossicles associated with the lacrimal/ectethmoid complex exhibit different morphologies and positional relationships across neornithine birds (Table 1). Most likely, not all of these structures are therefore homologous and caution is warranted in their phylogenetic interpretation.

The rod-shaped element between the ventral end of the lacrimal and the jugal bar of the Cariamiformes, for example, represents an ossified ligamentum jugolacrimale (Degrange et al., 2015), and as noted in the introduction, the term os lacrimale communicans is available for this ossicle. By contrast, Burton (1969) found a ligamentum jugolacrimale to be present in the Musophagiformes and noted that the uncinate bone of turacos develops from the ossification of a ligament between the ectethmoid and the palatine.

The plate-like uncinate bones of the Musophagiformes and the corresponding ossicles of the Cuculiformes, Otidiformes, Psophiidae, some Rallidae, some Accipitriformes, and Steatornithidae exhibit similar topological relationships. Their position is variable, but usually they are situated between the ectethmoid and the lacrimal. Although the bones sometimes articulate with both the lacrimal and the ectethmoid, in most taxa their contact with the ectethmoid is more extensive. If the ossicles co-ossify with bones of the lacrimal/ectethmoid complex, this fusion also involves the ectethmoid (Cuculiformes, Otidiformes). Plate-like uncinate bones likewise occur in the Struthioniformes and Rheiformes, where they mainly articulate, however, with the lacrimal.

In the Fregatidae, Procellariiformes, and Threskiornithidae, by contrast, the uncinate bone is rod-shaped and attached to the ventral or medial portion of the lacrimal. Its morphology in adult birds is therefore different from that in the aforementioned taxa. For this study, ontogenetic stages were only available for the Musophagiformes and the procellariiform Diomedeidae, but these show a similar development of the uncinate bone. Even though the ossicle is associated with the ectethmoid in adult individuals of the Musophagiformes, it develops from an ossification center near the ventral
end of the lacrimal, which occurs late in skull ontogeny and at a stage when the lacrimal is already fully ossified (Figure 9a). The ossification center for the uncinate bone is situated in a ligamentous structure connected to a membranous sheet that develops into the ectethmoid. In a juvenile individual of Phoebastria irrorata (Diomedeidae), there is also a ligamentous structure in the position of the uncinate bone, which is conflu- ent with a ligamentous membrane representing an early developmental stage of the ectethmoid (Figure 9b).

The ossicle on the tip of the lacrimal in the Lari is likewise not derived from an ossified ligamentum jugolacrimale, and in one specimen of Sterna hirundo in the collection of SMF the ligament and the ossicle are clearly visible as separate structures (Figure 5a). Livezey & Zusi (2006) considered the ossicle in the Lari to be a sesamoid bone and its homology remains uncertain.

Here it is hypothesized that the ossicles in the Cuculiformes, Musophagiformes, and Otidiformes and those of the Fregatidae, Procellariiformes, and Threskiornithidae evolved convergently through parallel evolution. Although these ossicles therefore originated multiple times independently, it is proposed to apply the term “os uncinatum” to all uncinate bones that developed from the same ligamentous structures. The different shapes of the ossicles in, for example, the Musophagiformes and Procellariiformes may justify the application of different names, but uncinate bones appear to have evolved several times independently even within the Aequornithes. Under the application of a concept of strict homology, the term “os lacrimopalatinum” could therefore not be used for both Fregatidae and Procellariiformes (let alone Threskiornithidae), and the term “os uncinatum” may have to be restricted to the ossicle in the Cuculiformes. This would result in a very impractical terminology. Although the term “os lacrimopalatinum” has first been suggested, it is here proposed to use the name “os uncinatum” for these structures, because these ossicles are often mainly attached to the ectethmoid rather than the lacrimal.

### 4.2 Phylogenetic considerations

In most recent analyses of nuclear sequence data, the Struthioniformes and Rheiformes resulted as successive sister taxa of all other palaeognathous birds (e.g., Hackett et al., 2008; Prum et al., 2015; Kuhl et al., 2021). This suggests that an uncinate bone is plesiomorphic for the Palaeognathae. However, a recent whole-genome analysis supported a sister group relationship between the Rheiformes and a clade including the Apterygiformes and Casuariiformes (Cloutier et al., 2019). Under this phylogenetic scenario, the uncinate bones of the Struthioniformes and Rheiformes would be more likely to be of convergent origin (Livezey & Zusi, 2006) scored an uncinate bone [“os uncinatum”] as present in Dromaius [Casuariiformes], but I could not confirm this observation.

### TABLE 1 Overview of different types of ossicles associated with the lacrimal/ectethmoid complex of neornithine birds

| Taxon                  | Shape of bone | Main articulation | Identification               |
|------------------------|---------------|-------------------|------------------------------|
| Struthionidae          | Plate-like    | lacrimal          | os uncinatum                 |
| Rheidae                | Plate-like    | lacrimal          | os uncinatum                 |
| Diomedeidae            | Rod-shaped    | lacrimal          | os uncinatum ("os lacrimopalatinum") |
| Procellariidae         | Rod-shaped    | lacrimal          | os uncinatum ("os lacrimopalatinum") |
| Fregatidae             | Rod-shaped    | lacrimal          | os uncinatum ("os lacrimopalatinum") |
| Sulidae                | Plate-like    | mesethmoid        | ectethmoid                   |
| Threskiornithidae      | Rod-shaped    | lacrimal/ectethmoid | os uncinatum ("os lacrimopalatinum") |
| Steatornithidae        | Hook-shaped   | none              | os uncinatum                 |
| Cuculidae              | Plate-like/rod-like | ectethmoid         | os uncinatum                 |
| Musophagidae           | Plate-like    | ectethmoid        | os uncinatum                 |
| Otididae               | Plate-like    | ectethmoid        | os uncinatum                 |
| Rallidae               | Plate-like    | ectethmoid        | os uncinatum                 |
| Lari (Sternidae, Laridae, Alcidae) | Plate-like | lacrimal   | uncertain (“ossiculum lacrimosuborbitale”) |
| Cariamidae             | Rod-shaped    | lacrimal          | os lacrimale communicans    |
| Accipitridae           | Plate-like    | ectethmoid        | os uncinatum                 |
| Picidae                | Tiny ossicle  | ectethmoid        | uncertain                    |
Within the Neognathae, taxa with well-developed uncinate bones are phylogenetically nested within the clade. Most likely, therefore, the stem species of the Neognathae had only a vestigial uncinate bone or just a ligamentous structure was present, and a large uncinate bone represents an apomorphy of neognathous subclades (a multiple independent origin of a larger uncinate bone in Neognathae also places a caveat on the above comments concerning palaeognathous birds).

Of particular interest from a phylogenetic point of view is the occurrence of uncinate bones in the Otidiformes, Cuculiformes, and Musophagiformes. The interrelationships of these taxa are controversially resolved in current phylogenetic analyses. In the analysis of Hackett et al. (2008), the Otidiformes resulted as the sister taxon of the Aequornithes. The analyses of Jarvis et al. (2014) and Prum et al. (2015), by contrast, supported a clade (Cuculiformes + [Musophagiformes + Otidiformes]), whereas a more recent analysis of Kuhl et al. (2021) recovered a clade (Musophagiformes + Otidiformes), which resulted as the sister taxon of a clade including the Cuculiformes, Columbiformes, Pterocliformes, and Mesitornithiformes. The presence of an uncinate bone in the Otidiformes and Musophagiformes is consistent with the results of the analyses of Jarvis et al. (2014), Prum et al. (2015), and Kuhl et al. (2021), and the ossicle would be the first morphological apomorphy of the clade (Otidiformes + Musophagiformes). Alternatively, an uncinate bone may be an apomorphy of a more inclusive clade, which also includes the Cuculiformes, and a final assessment of the significance of this feature depends on a robust

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**FIGURE 9** Early developmental stages of the uncinate bone in juvenile individuals of (a) *Tauraco* (Musophaga) *violaceus* (Musophagiformes; SMF 9705, left side) and (b) *Phoebastria irrorata* (Diomedeidae; SMF 2437, right side, mirrored). Uncinate bones contacting the palatal membrane between the jugal and the palatine in (c) *Carpococcyx renauldi* (Cuculiformes; SMF 4207) and (d) *Puffinus puffinus* (Procellariidae; SMF 19607). (e) Ectopterygoid of the late Jurassic *Archaeopteryx siemensii* (Wyoming Dinosaur Center, Thermopolis, USA; WDC-CSG-100) compared to (f) the uncinate bone of *Rhea americana* (Rheiformes; SMF 5754). ecp, ectopterygoid; ect, ectethmoid; jug, jugal; lac, lacrimal; lig, ligament; mem, membrane between jugal and palatine; oss, ossicle of uncertain homology; pal, palatine (os palatinum); unc, uncinate bone. Scale bar = 5 mm
placement of the Cuculiformes and on whether a well-developed uncinate bone is plesiomorphic for the latter taxon.

Only a few comprehensive analyses of the interrelationships of the Cuculiformes exist and these studies also show conflicting results (Johnson et al., 2000; Sorenson & Payne, 2002, 2005). In all analyses, however, the species with a well-developed uncinate bone are phylogenetically nested within the clade. Most likely, therefore, only a ligamentous structure was present in the stem species of the Cuculiformes. In the phylogeny of Sorenson and Payne (2005), a large uncinate bone evolved three or four times independently, in a clade including the taxa Carpococcyx, Centropus, and Coua (the latter lacks an os uncinatum, so that the bone either evolved two times independently or was secondarily lost in Coua), as well as in the cuculine taxa Eudynamys and Scythrops. By contrast, the analysis of Johnson et al. (2000) recovered a sister group relationship between Centropus and Geococcyx (Carpococcyx was not included in the study) and supported a sister group relationship between Scythrops and Eudynamys. The presence of a large uncinate bone in the latter two taxa may support this phylogenetic placement. However, until a robust phylogeny of the Cuculiformes is available, the exact phylogenetic significance of a large uncinate bone in the members of this clade remains elusive.

An uncinate bone also occurs in representatives of the Aequornithes, with the ossicle being found in the Fregatidae, Procellariiformes, and some Threskiornithidae. These three taxa are phylogenetically nested within the Aequornithes (Hackett et al., 2008; Kuhl et al., 2021; Prum et al., 2015), which suggests that the uncinate bone evolved at least three times independently. However, Crompton (1953) identified a “cartilago uncinata” in the embryo of the Sphenisciformes, so that it also appears possible that an uncinate bone is plesiomorphic for the Aequornithes and was lost multiple times independently (Livezey & Zusi, 2006, p. 122, considered an uncinate bone “os lacrimopalatinum” to be present in adult Sphenisciformes, which I could not confirm).

The uncinate bone is well developed in the Diomedeidae, and within the Procellariidae it is comparatively large in the taxa Puffinus, Ardenna, and Calonectris. The position of the Diomedeidae within the Procellariiformes is controversially resolved in current molecular phylogenies, and albatrosses are either obtained as the sister taxon of all crown group Procellariiformes except for the Oceanitinae (Hackett et al., 2008) or, more often, they result as the sister taxon of all other crown group Procellariiformes (Estandia et al., 2021; Kuhl et al., 2021; Prum et al., 2015). In both cases, an uncinate bone either evolved convergently in the Diomedeidae and Procellariidae or it was lost one or two times, in the Oceanitinae and Hydrobatinae. Within the Procellariidae, the ossicle is vestigial in Pelecanoides and a very thin bony strand in the taxa Macronectes, Fulmarus, and Daption, which form a clade together with Thalassoica and Pagodroma (Estandia et al., 2021; Kennedy & Page, 2002; Nunn & Stanley, 1998; Penhallurick & Wink, 2004; specimens of Thalassoica and Pagodroma could not be examined). This tendency toward reduction of the uncinate bone within the Procellariidae may suggest that the ossicle was lost in the Hydrobatinae and Oceanitinae and that it was present in the stem species of the Procellariiformes.

In the Threskiornithidae, a well-developed, rod-shaped uncinate bone is present in Plegadis, Platalea, and Threskiornis, which is notable, because molecular analyses suggest a clade including these three taxa (Ramirez et al., 2013). However, in some taxa, the ossicle appears to be co-ossified with the ectethmoid (Bostrychia hagedash) and others show vestiges of an uncinate bone. Possibly, therefore, an uncinate bone is also plesiomorphic for the Threskiornithidae and was reduced several times within the clade.

The distribution of the ossicle associated with the lacrimal/ectethmoid complex of the charadriiform Lari also exhibits homoplasy, but in the case of these birds a multiple independent origin of an uncinate bone appears most likely. The ossicle occurs in most Sterninae and is likely to be plesiomorphic for this taxon, but its occurrence in only a few, and phylogenetically nested, species of the Larinae and Alcidae suggests that it convergently evolved in the latter taxa.

### 4.3 Functional significance and evolutionary origin

So far, functional considerations mainly addressed the exceptionally large uncinate bone of the Musophagiformes. Cracraft (1968) hypothesized that the ossicle braces the palate, and this was also assumed by Burton (1969), who detailed that it may resist tensile forces pulling the palatines down. Korzoum et al. (2001, p. 965), by contrast, proposed that the uncinate bone of turacos stabilizes the mandible, “particularly when [the] jaws act as a pair of scissors.”

It is beyond the scope of this study to assess the functional significance of the uncinate bone, which would require a detailed study of associated soft tissue structures. However, earlier authors largely disregarded the different morphologies found within the Musophagiformes, and functional hypotheses may be improved by a better understanding of why the ossicle is more massive in the taxa Corythaeea and Crinifer than in Tauraco (Figure 3k,l).
The peculiar morphology of *Tauraco corythaix*, in which the uncinate bone is braced by a lateral bulge of the palatine (Figure 3), could also provide further clues on the function of the ossicle, if it can be correlated with characteristics of the feeding biology of this species.

Burton (1969, p. 8) already noted that the uncinate bone of turacos “does not touch the palatine, but its ventral edge makes direct contact with the dorsal surface of the dermal material covering the palate.” In the Proc-ellariiformes and Fregatidae, the uncinate bone also contacts the palatal membrane between the jugal and the palatine (Figures 6d and 9d), and this is likewise true for some Cuculiformes (Figure 9c). Possibly, the primary function of the uncinate bone is therefore not the bracing of other bones (palatine or jugal), but the stabilization of soft tissue structures between the jugal and palatine.

In the Cuculiformes, large uncinate bones occur in taxa with a comparatively massive beak, such as *Carpococcyx* and *Scythrops*. Within the Railidae, the taxon *Porphyrio*, in which the uncinate bone is particularly large, also has a more massive beak than other taxa that lack an uncinate bone. Across higher level clades, however, there appears to be no clear correlation between the occurrence of uncinate bones and beak shape, skull morphology, or feeding habits. Judging from their different morphologies and orientations, the ossicles associated with the lacrimal/ectethmoid complex of neornithine birds probably have different functions, and in some taxa, such as the Accipitriformes, Otidiformes, Psophiidae, and some Cuculiformes, the uncinate bone is only rudimentary and unlikely to play a functional role.

As detailed above, a large, ossified uncinate bone represents an evolutionary novelty of certain clades of neognathous birds and appears to have evolved several times independently from a ligamentous structure. Whether an ossified uncinate bone was present in the stem species of crown clade birds (Palaeognathae + Neognathae) is uncertain, so that it remains an open question whether the ossicle is part of the ancestral bauplan of the avian skull.

Crompton (1953) assumed that the uncinate bone is homologous to the anuran and reptilian “processus maxillaris posterior” (e.g., Roček, 1990). Müller (1963, p. 108) likewise hypothesized that it stems from an ossification of the “processus maxillaris posterior” and develops together with the ectethmoid by endochondral ossification in the planum antorbital.

More recently, however, the avian uncinate bone was considered to be possibly homologous to the ectopterygoid (Elzanowski, 1999; McDowell, 1978). This bone is absent in crown group avians (Neornithes) but well developed in non-avian theropods and early Mesozoic birds, such as *Archaeopteryx* (Mayr et al., 2007), *Sapeornis* (Hu et al., 2020), and some Enantiornithines (Chiappe et al., 2001; Elzanowski, 1995; Wang et al., 2021). In particular, the uncinate bone of the Rheiformes (Figure 9f) shows a morphological resemblance to the ectopterygoid of Mesozoic avians, that is, *Archaeopteryx* (Figure 9e) and *Sapeornis*. The ectopterygoid of the enantiornithine taxon *Gobipteryx* (Elzanowski, 1995, fig. 2) also resembles the uncinate bone of the Rheiformes in its shape. Unlike the ectopterygoid of Mesozoic birds, however, the uncinate bone of the Rheiformes and other representatives of the Neornithes is situated in a more rostral position and does not articulate with the pterygoid. An ectopterygoid has furthermore not yet been identified in early stem group representatives of the Ornithuromorpha, the clade including neornithine birds.

The uncinate bone develops late in skull ontogeny, together with the ectethmoid, and the connection between the ligamentous structure forming the uncinate bone and the membranous early developmental stage of the ectethmoid suggest that the ontogenetic development of both bones is correlated. Possibly as a consequence thereof, an uncinate bone is usually absent in taxa, which lack a well-developed ectethmoid (an exception are the Fregatidae, in which the ectethmoid is, however, well developed in stem group representatives [see above]). Future studies will also have to investigate whether the uncinate bone and the ectethmoid represent a single element, which develops from two ossification centers.

The neornithine ectethmoid is another bone, the homology of which is unresolved. Even though an ectethmoid has been tentatively identified in the Late Cretaceous enantiornithine *Gobipteryx* (Chiappe et al., 2001), it has not been reported for other in Mesozoic stem group birds. Jollie (1957, p. 425) noted that the bone (his “lateral ethmoid”) is a “secondary chondral membral ossification which appears at the very end of the developmental period (...) and as such indicates its phylogenetic newness in the bird.” These comments conflict with the assumption that the ectethmoid, as well as the developmentally correlated uncinate bone, represent vestiges of skull elements present in non-avian theropods, but a homology of the uncinate bone of neornithine birds and the ectopterygoid of Mesozoic avians should nevertheless be scrutinized in future studies. Clearly, however, more data on the ontogeny of the lacrimal/ectethmoid complex of the neornithine skull as well as an improved understanding of the skull morphology of Mesozoic ornithuromorph taxa at the base of Neornithes are required before a well-founded hypothesis on the evolutionary significance of uncinate bones can be established.
ACKNOWLEDGMENTS

The author would like to thank Sven Tränkner for taking the photographs. Comments from Federico Degrange and an anonymous reviewer improved the manuscript.

AUTHOR CONTRIBUTION

Gerald Mayr: Conceptualization; data curation; formal analysis; investigation; methodology; project administration; resources; supervision; validation; visualization; writing—original draft; writing—review and editing.

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How to cite this article: Mayr, G. (2022). A survey of the uncinate bone and other poorly known ossicles associated with the lacrimal/ectethmoid complex of the avian skull. *The Anatomical Record*, 305(9), 2312–2330. [https://doi.org/10.1002/ar.24869]