On the comparative morphology of the juvenile avian skull: An assessment of squamosal shape across avian higher-level taxa

Gerald Mayr1 | Albrecht Manegold2

1Ornithological Section, Senckenberg Research Institute and Natural History Museum Frankfurt, Frankfurt am Main, Germany
2Staatliches Museum für Naturkunde Karlsruhe, Karlsruhe, Germany

Correspondence
Gerald Mayr, Senckenberg Research Institute and Natural History Museum Frankfurt, Ornithological Section, Senckenberganlage 25, D-60325 Frankfurt am Main, Germany.
Email: gerald.mayr@senckenberg.de

Abstract
The comparative morphology of juvenile avian skulls is poorly known. Here, we survey the shape of the squamosal (os squamosum) across juvenile skulls of avian higher-level clades. In all palaeognathous birds, the rostral end of the squamosal does not surpass the parietal and does not reach the frontal. This morphology is likely to be plesiomorphic for neornithine birds. A short squamosal also occurs in some Neognathae, but in most neognathous birds the squamosal contacts the frontal, and in some taxa the bone is strongly elongated and distinctly surpasses the parietal. Some clades show a notable variation in squamosal morphology. This is, for example, true for Strigiformes, where the taxon *Athene* differs from the other examined owls in squamosal size, and for the Passeriformes, where Old World Suboscines are characterized by a distinctive squamosal morphology. A unique derived squamosal morphology is for the first time reported for the Apodidae and Hemiprocnidae, in which the bone forms a elongated rostral process that runs along most of the orbital rim. In non-avian theropods, the squamosal articulates with the postorbital and delimits the upper temporal opening. Extant birds lack a postorbital, but a topological correlation between the squamosal and the postorbital process is maintained in most taxa of the Neognathae. The phylogenetic significance of squamosal morphology is diminished by the fact that closely related taxa often show very disparate shapes of the bone, and squamosal morphology appears to be determined by multiple functional constraints including skull geometry, brain morphology and, possibly, nostril type.

Keywords
Aves, neurocranium, ontogeny, phylogeny, skull evolution

1 | INTRODUCTION

In adult neornithine (crown group) birds, the neurocranium forms a solid unit and its component bones are...
tightly co-ossified, so that their sizes and shapes can only be evaluated through the study of juvenile specimens. However, even though avian osteology has been intensely studied during the past two centuries, the comparative morphology of juvenile bird skulls still is insufficiently known.

Earlier authors provided descriptions of the ontogenetic development of the skull of selected taxa, with detailed studies having been performed for palaeognathous birds (Maxwell, 2009; Müller, 1963; T.K. Parker, 1866, Parker, 1891a), the domestic chicken (Erdmann, 1940; Jollie, 1957), Laridae (Weber, 1990), Strigidae (May, 1961), Falconidae (Sutschkin, 1899, Psittacidae (Tokita, 2003), and Coliidae (Goldschmid, 1972). More anecdotal data exist for other taxa (e.g., Böhm, 1930: Balaenicpitidae; Posso & Donatelli, 2005: Cuculidae; Brusaferro & Simonetta, 1998: Meropidae; Pycraft, 1905: Eurylaimidae).

Most of these analyses focus on a particular taxon and few comparative data exist on the variation across neornithine higher level clades. Although earlier authors emphasized the need for more detailed studies across a broader taxonomic range (e.g., Marugán-Lobón & Buscalioni, 2009; Zusi, 1993), such have not yet been performed, with comparative descriptions of particular skull bones being particularly scarce (Mayr, 2020; Zusi & Livezey, 2006).

The dorsal and lateral portions of the cranial vault of birds are mainly formed by four paired bones, the frontal (os frontale), parietal (os parietale), laterosphenoid (os laterosphenoidale; “orbitosphenoid” of Jollie, 1957, “pleurospheoid” of Müller, 1963 and Zusi, 1993, but see Clark, Welman, Gauthier, & Parrish, 1993), and the squamosal (os squamosum). The squamosal is the only bone of the cranial vault which derives from the caudal (posterior) portion of the mandibular-stream cranial neural crest, whereas the frontal, parietal, and laterosphenoid originate from the mesoderm and—in the case of the rostral portion of the frontal—the rostral (anterior) portion of the mandibular-stream cranial neural crest (Maddin, Piekarski, Sefton, & Hanken, 2016). The squamosal is situated in the laterocaudal portion of the neurocranium (Figure 1a). Caudally, it articulates with the exoccipital and supraoccipital, medially it is bounded by the parietal, and laterally it abuts the laterosphenoid; the relations to the frontal are variable across different neornithine taxa. The ventral portion of the squamosal bears the zygomatic process and a more caudally situated processus supramaxillaris as well as the articulation facet for the capitulum squamosum of the quadrate.

Even though it was noted previously that the squamosal differs in its relation to the surrounding bones (Zusi, 1993), this variation remained unstudied. In the

![Figure 1](image)

**Figure 1** Squamosal shape in juvenile skulls (left lateral view) of the Passeriformes (a–c), Piciformes (d), Trogoniformes (e), Charadriiformes (f), and Columbiformes (g). (a) Lamprotornis superbus (Sturnidae; SMF 4455). (b) Falculea palliata (Vangidae; SMF 2830). (c) Pitta sordida (Pittidae; SMF 4613). (d) Dendrocopos major (Picidae; SMF 1986). (e) Trogon viridis (Trogonidae; SMF 3669). (f) Sterna albifrons (Laridae; SMF 5633). (g) Streptopelia decaocto (Columbidae; SMF 2499). The squamosal is shaded gray. Abbreviations: exo, exoccipital; frt, frontal; lts, laterosphenoid; squ, squamosal; par, parietal; ppo, processus postorbitalis; qdr, quadrate. Scale bars equal 5 mm.
present study, we provide the first account of squamosal morphology across a broad number of avian higher-level taxa. We comment on the stem species pattern for neornithine and neognathous birds and discuss the phylogenetic and functional implications of the observed variation in squamosal shape.

2 MATERIAL AND METHODS

The nomenclature of the extant species follows the IOC World Bird List (https://www.worldbirdnames.org), except for the Gruidae, where the taxon Bugeranus is maintained. Skulls of juveniles of the following species were examined in the ornithological collection of Senckenberg Research Institute Frankfurt (SMF); skulls with dissociated cranial elements are highlighted with an asterisk: Palaeognathae: Apterygidae: Apteryx australis (SMF 7409, SMF 7410, SMF 7418*); Struthionidae: Struthio camelus (SMF 6610, SMF 19998); Rheidae: Rhea americana (SMF 9541, SMF 19371, SMF 20424); Casuariidae: Casuarius casuarius (SMF 12460, SMF 19510), Dromaius novaehollandiae (SMF 14286); Tinamidae: Nothura boraquira (SMF 2475). Galliformes: Megapodiidae: Alectura lathami (SMF 140*, SMF 15582*), Otidiphaps nobilis (SMF 8261), Pavo cristatus (SMF 5988), Cuca cristata (SMF 8189), Cuculus canorus (SMF 10579). Musophagiformes: Musophaga violacea (SMF 9680), Tauraco sp. (SMF 6634). Accipitriformes: Circus aeruginosus (SMF 9839), Pernis apivorus (SMF 18256). Falconiformes: Falco eleonorae (SMF 4072).

MATERIAL AND METHODS

The nomenclature of the extant species follows the IOC World Bird List (https://www.worldbirdnames.org), except for the Gruidae, where the taxon Bugeranus is maintained. Skulls of juveniles of the following species were examined in the ornithological collection of Senckenberg Research Institute Frankfurt (SMF); skulls with dissociated cranial elements are highlighted with an asterisk: Palaeognathae: Apterygidae: Apteryx australis (SMF 7409, SMF 7410, SMF 7418*); Struthionidae: Struthio camelus (SMF 6610, SMF 19998); Rheidae: Rhea americana (SMF 9541, SMF 19371, SMF 20424); Casuariidae: Casuarius casuarius (SMF 12460, SMF 19510), Dromaius novaehollandiae (SMF 14286); Tinamidae: Nothura boraquira (SMF 2475). Galliformes: Megapodiidae: Alectura lathami (SMF 140*, SMF 15582*), Otidiphaps nobilis (SMF 8261), Pavo cristatus (SMF 5988), Cuca cristata (SMF 8189), Cuculus canorus (SMF 10579). Musophagiformes: Musophaga violacea (SMF 9680), Tauraco sp. (SMF 6634). Accipitriformes: Circus aeruginosus (SMF 9839), Pernis apivorus (SMF 18256). Falconiformes: Falco eleonorae (SMF 4072).

MATERIAL AND METHODS

The nomenclature of the extant species follows the IOC World Bird List (https://www.worldbirdnames.org), except for the Gruidae, where the taxon Bugeranus is maintained. Skulls of juveniles of the following species were examined in the ornithological collection of Senckenberg Research Institute Frankfurt (SMF); skulls with dissociated cranial elements are highlighted with an asterisk: Palaeognathae: Apterygidae: Apteryx australis (SMF 7409, SMF 7410, SMF 7418*); Struthionidae: Struthio camelus (SMF 6610, SMF 19998); Rheidae: Rhea americana (SMF 9541, SMF 19371, SMF 20424); Casuariidae: Casuarius casuarius (SMF 12460, SMF 19510), Dromaius novaehollandiae (SMF 14286); Tinamidae: Nothura boraquira (SMF 2475). Galliformes: Megapodiidae: Alectura lathami (SMF 140*, SMF 15582*), Otidiphaps nobilis (SMF 8261), Pavo cristatus (SMF 5988), Cuca cristata (SMF 8189), Cuculus canorus (SMF 10579). Musophagiformes: Musophaga violacea (SMF 9680), Tauraco sp. (SMF 6634). Accipitriformes: Circus aeruginosus (SMF 9839), Pernis apivorus (SMF 18256). Falconiformes: Falco eleonorae (SMF 4072).
preserved specimens. Data on the juvenile skull of other higher-level data were obtained from the literature.

The exact individual age of all specimens is unknown, but most are from hatchlings of a comparable, relatively late developmental stage, in which the skull bones are well ossified but are still separated by sutures. Skulls of differently aged juveniles were available for the Spheniscidae (Spheniscus humboldti), Phoenicopteridae, Laridae (Larus argentatus), and Gruidae (Balearica, Bugeranus).

Developmental data suggest that the avian parietal is actually homologous to the postparietal of other tetrapods and that the frontal is a frontoparietal (Maddin et al., 2016). However, to avoid unnecessary confusion in relation to earlier studies, the traditional terminology is maintained in the present article.

3 | RESULTS

As indicated by its Latin name, the squamosal usually has a squamiform (scale-like) shape. Even though the morphology of the bone appears to be consistent within neornithine “families”, it shows considerable variation between superordinate higher-level taxa in shape, size, and orientation.

Crown group birds (Neornithes) are divided into the sister taxa Palaeognathae and Neognathae, with the latter being further split into Galliformes and Neaves (all other neognathous birds). In juveniles of the palaeognathous Apterygidae (Figure 2a) and Casuariidae (Figure 2b), the squamosal has a subrectangular outline and bears a long processus zygomaticus in its rostroventral portion. A similar morphology occurs in other juvenile palaeognathous birds (Figure 3a), in which the zygomatic process is likewise the only well-developed projection of the squamosal. On the medial surface of the bone there is a fossa for a diverticulum of the middle ear air sac (Jollie, 1957).

In juveniles of neognathous birds, by contrast, squamosal shape is much more variable and the bone forms distinct processes. Often there is a long rostrodorsally directed process, which articulates with the frontal (Figure 2), but several taxa also exhibit a shorter caudomedial process, which separates the ventrolateral portion of the parietal from the exoccipital and occurs in, for example, the Charadriiformes and Passeriformes (Figure 2o–p). The development of the processus zygomaticus is highly variable in neognathous birds and this is also true for the processus suprameaticus; in some taxa, such as the Charadriiformes, Gruidae, Railidae, and Strigiformes, processus zygomaticus and processus suprameaticus are of subequal length and form a U-shaped notch (Figure 2o,p). The fossa for the diverticulum of the middle ear air sac, on the medial surface of the bone, is well delimited in some neognathous taxa (e.g., the procellariiform Diomedeidae; Figure 2j), but less developed or absent in others, such as the Passeriformes (Figure 2l).

The squamosal of neornithine birds not only differs in shape and size, but also in its relation to the surrounding bones. The different morphologies may, at least provisionally, be assigned to three categories, which are summarized in Table 1.

In the Palaeognathae, including the extinct Dinornithidae (Worthy & Scofield, 2012, figure 4) and Aepyornithidae (Balonoff & Rowe, 2007), the squamosal does not contact the frontal, and the laterosphenoid is therefore not separated from the parietal. This lack of contact between squamosal and frontal also occurs in some neognathous birds, and among the studied taxa it was found in the Caprimulgidae (Figure 3d), Spheniscidae (Figure 4a), Threskiornithidae (Figure 4e), Ardeidae (Figure 4f), Phalacrocoracidae, Rhynochetidae, Musophagidae (Figure 3g), and most Strigiformes (except Athene). According to Pycraft (1898: pl. 8), the squamosal likewise does not contact the frontal in the Sulidae (Figure 4i) and Phaethontidae (Figure 4j).

In all other studied Neognathae, by contrast, the squamosal separates the laterosphenoid from the parietal and contacts the frontal, even though the geometry of the involved bones shows much variation. In various only distantly related taxa, the squamosal does not extend beyond the boundary between parietal and frontal. In some taxa, the bone has a broad rostral end, so that the suture between squamosal and frontal (sutura frontosquamosalis) forms a line with that between frontal and parietal (sutura frontoparietalis). This morphology occurs in the Balaenicipitidae (Figure 4g), Otidae, Accipitridae (Figure 3k; see also Jollie, 1977: figures 50 and 51), and Psittacidae (Figure 3j). In other taxa, the squamosal tapers rostrodorsally, so that it contacts the frontal only with a narrow tip. Such is the case in the Podicipedidae (Figure 5l), Ciconiidae (Figure 4d), Cuculidae (Figure 3f; see also Pycraft, 1903a; Posso & Donatelli, 2005), Falconidae (Figure 3i), Meropidae (Brusaferro & Simonetta, 1998), Alcedinidae, and Piciformes.

A tapering squamosal is also found in the Phoenicopteridae (Figure 5g), Gruidae (Figure 5n–p), and Trogonidae (Figure 1e). These latter taxa exhibit a distinctive morphology in that the rostroventral edge of the parietal forms a slender, rostrally directed extension, which reaches the tip of the squamosal and largely separates its dorsal margin from the frontal. At least in the Gruidae, this derived morphology emerges during skull development and is not present in early ontogenetic stages of Balearica and Bugeranus (Figure 5n–p). It is absent in the
FIGURE 2  Isolated squamosals of juvenile skulls in lateral (left image) and medial (right image) view; the bones are from the left side and are shown in their approximate orientation in the horizontally positioned skull. (a,b) Apteryx australis (Apterygiformes, Apterygidae; SMF 7418). (c,d) Dromaius novaezelandiae (Casuariiformes, Casuariidae; SMF 140). (e,f) Crax sp. (Galliformes, Cracidae; SMF 497); right side, mirrored. (g,h) Heteronetta atricapilla (Anseriformes, Anatidae; SMF 15582); the attached parietal was digitally removed and the suture between squamosal and parietal is indicated by the dotted line. (i,j) cf. Phoebastria irrorata (Procellariiformes, Diomedeidae; SMF 2433). (k,l) Spheniscus humboldti (Sphenisciformes, SMF 5849). (m,n) Phalacrocorax harrisi (Suliformes, Phalacrocoracidae; SMF 2429). (o,p) Rhinoptilus chalcopeterus (Charadriiformes, Glaucidae; SMF 13431). (q,r) Alca torda (Charadriiformes, Alcidae; SMF 18872); right side, mirrored. (s,t) Psarocolius montezuma (Passeriformes, Icteridae; SMF 4688); right side, mirrored. Abbreviations: cmp, caudomedial process; cqs, cotyla quadratica squamosi; pnf, fossa for middle ear air sac; psm, processus suprameaticus; pzg, processus zygomaticus; rsp, rostral process. Scale bars equal 10 mm.
Podicipedidae and Rallidae, which are the sister taxa of the Phoenicopteridae and Gruidae, respectively (Hackett et al., 2008; Jarvis et al., 2014; Prum et al., 2015).

Squamosal morphology of juvenile Galloanseres was surveyed by Zusi and Livezey (2000). In these birds, the bone has a subrectangular shape, broadly contacts the frontal, and extends well beyond the suture between parietal and frontal (Figure 3b,c). The squamosal also surpasses the parietal in the Opisthocomidae (Figure 4k), Diomedeidae (Zusi & Livezey, 2006, figure 4b), Procellariidae (Figure 4b;
In several only distantly related neoavian taxa, the squamosal not only surpasses the parietal, but also extends rostrodorsally well beyond the postorbital process. Such a very long squamosal occurs in the procellariiform Hydrobatinae (Oceanodroma; Figure 4c), most Charadriiformes apart from the Burhinidae (Figure 4c), as well as in the Rallidae (Figure 5m), Columbidae (Figures 1g and 3h), Pteroclidae (Figure 3i), and Passeriformes (Figure 1a–c). Squamosal shape shows, however, much variation in these birds. The bone is particularly long in the charadriiform Laridae, Sternidae, and Alcidae, in which it projects beyond the cranial vault and forms a small projection in the adult skull, which caudolaterally delimits the fossae glandulae nasales (Figure 5d–j). This distinctive morphology also occurs in the procellariiform Hydrobatinae (Oceanodroma; Figure 4c). The rostrodorsal process of the squamosal is broad in oscine Passeriformes (Figure 1a,b), whereas it is narrow and of subfalcate shape in the suboscine Pittidae (Figure 1c). A narrow squamosal was also reported for Eurylaimus ochromalus (Eurylaimidae) by Pycraft (1905, pl. 2), but is not present in the only juvenile specimen of a New World suboscine available to us (cf. Lessonia rufa; Tyrannidae) and therefore appears to be a characteristic of Old World Suboscines. In both, Charadriiformes and Passeriformes, the long squamosal broadly overlaps with the frontal.

A unique and previously unreported squamosal morphology is finally found in the Hemiprocnidae and Apodidae, in which the bones is extremely elongated and forms a rostral process that runs along most of the orbital rim (Figure 3e). In the adult skull of both Apodidae and Hemiprocnidae the long squamosal is reflected by a ridge-like rim along the orbit, which is medially bordered by a narrow sulcus for musculus cucullaris capitis (Zusi, 2013, figure 4). This rim and sulcus are also present in the Trochilidae, which suggests that hummingbirds, of which no juvenile skulls were available for study, have an equally elongated squamosal. By contrast, the squamosal is short in the Caprimulgidae (Figure 3d). The morphology in other representatives of the Strisores (the clade including Apodiformes and the paraphyletic “caprimulgiform” birds; Mayr, 2010) is unknown.

### 4 | DISCUSSION

#### 4.1 | Stem species pattern

In non-avian theropods, the squamosal articulates with the postorbital and delimits the ventral margin of the upper...
temporal opening; unlike in neornithine birds the bone is therefore not fully incorporated into the cranial vault (e.g., Elzanowski & Wellnhofer, 1996; Tsuihiji et al., 2014; Wang & Hu, 2017). The squamosal of *Archaeopteryx* still resembles that of non-avian theropods and exhibits a postorbital and a quadratojugal process (Elzanowski & Wellnhofer, 1996); the latter was considered homologous to the zygomatic process of neornithine birds (Elzanowski, 2001). Squamosal shape is poorly known in other Mesozoic birds and the bone is often left away in skull reconstructions (e.g., Wang & Hu, 2017). In the only enantiornithine specimen with an identifiable squamosal, the bone is very small, triradiate, and appears not to have been incorporated into the braincase (O’Connor &

**FIGURE 4** Juvenile neurocrania of taxa of the Aequornithes (a–i), Phaethontiformes (j), and Opisthocomiformes (k) in left lateral view. In all photographs, the skull is digitally brightened and the squamosal is highlighted in a darker tone; sutures delimiting the parietal are enhanced by fine dotted lines. (a) *Spheniscus humboldti* (Sphenisciformes; SMF 10117). (b) *Calonectris edwardsii* (Procellariiformes, Procellaridae; SMF 932); caudal portion of neurocranium without frontals. (c) *Oceanodroma leucorhoa* (Procellariiformes, Hydrobatinae; from Pycraft, 1899). (d) *Ciconia ciconia* (Ciconiiformes; SMF 10755). (e) *Platalea sp.* (Pelecaniformes, Threskiornithidae; SMF 10121). (f) *Botaurus stellaris* (Pelecaniformes, Ardeidae; SMF 19986). (g) *Balaeniceps rex* (Pelecaniformes, Balaenicipitidae; from Böhm, 1930, mirrored). (h) *Pelecanus occidentalis* (Pelecaniformes, Pelecanidae; SMF 9389); right side, mirrored. (i) *Sula leucogaster* (Suliformes, Sulidae; from Pycraft, 1898). (j) *Phaethon lepturus* (Phaethontidae; from Pycraft, 1898). (k) *Opisthocomus hoazin* (Opisthocomidae; from W.K. Parker, 1891b). Abbreviations: frt, frontal; lts, laterosphenoid; squ, squamosal; par, parietal; ppo, processus postorbitalis; qdr, quadratojugal. Scale bars equal 10 mm; (c,g) and (i–k) are not to scale.
Chiappe, 2011; Sanz et al., 1997). Even in the Late Cretaceous ornithurine *Ichthyornis*, in which the postorbital is reduced, the squamosal seems to have not yet been fully integrated into the neurocranium (Field et al., 2018). The reconstruction of Field et al. (2018) furthermore indicates that the squamosal of *Ichthyornis* did not contact the frontal, so that the laterosphenoid abutted the parietal.

Outgroup comparisons with *Ichthyornis* suggest that the short squamosal of palaeognathous birds is plesiomorphic for Neornithes as a whole. It is, however, not quite clear
how the shape of the squamosal of *Ichthyornis* was determined by Field et al. (2018), because the cranial bones of this Late Cretaceous bird are co-ossified and sutures delimiting the squamosal cannot be discerned. If the squamosal morphology of *Ichthyornis* was actually deduced from comparisons with extant palaeognathous birds, any conclusions on the plesiomorphic morphology of neornithine birds based on *Ichthyornis* as an outgroup taxon would become circular.

For Neognathae, it is more parsimonious to assume that a squamosal contacting the frontal represents the plesiomorphic condition. A contact between squamosal

**FIGURE 5** Juvenile neurocrania of the Charadriiformes (a–c), Phoenicopteriformes (d), Pocipediformes (e–g), and Piciformes (h) in left lateral view. All skulls are digitally brightened and the squamosal is highlighted in a darker tone; the fine dotted lines enhance sutures delimiting the parietal. (a) *Tyto alba* (Tytonidae; SMF 20000); right side, mirrored. (b) *Asio otus* (Strigidae; SMF 10813); right side, mirrored. (c) *Athena noctua* (Strigidae; SMF 8421); right side, mirrored. (d) *Urocopus macrourus* (Colliriidae; SMF 5933). (e) *Tockus nasutus* (Bucerotidae; SMF 18951). (f) *Tockus sp.* (Bucerotidae; SMF 9726); right side, mirrored. (g) *Upupa epops* (Upupidae; SMF 17694); right side, mirrored. (h) *Dendrocoptes major* (Picidae; SMF 19029); right side, mirrored. Abbreviations: frt, frontal; lts, laterosphenoid; squ, squamosal; par, parietal; ppo, processus postorbitalis; qdr, quadrat. Scale bars equal 10 mm.

**FIGURE 6** Juvenile neurocrania of the Strigiformes (a–c), Coliiformes (d), Pocipediformes (e–g), and Piciformes (h) in left lateral view. All skulls are digitally brightened and the squamosal is highlighted in a darker tone; the fine dotted lines enhance sutures delimiting the parietal. (a) *Tyto alba* (Tytonidae; SMF 20000); right side, mirrored. (b) *Asio otus* (Strigidae; SMF 10813); right side, mirrored. (c) *Athena noctua* (Strigidae; SMF 8421); right side, mirrored. (d) *Urocopus macrourus* (Colliriidae; SMF 5933). (e) *Tockus nasutus* (Bucerotidae; SMF 18951). (f) *Tockus sp.* (Bucerotidae; SMF 9726); right side, mirrored. (g) *Upupa epops* (Upupidae; SMF 17694); right side, mirrored. (h) *Dendrocoptes major* (Picidae; SMF 19029); right side, mirrored; hyoid digitally removed. Abbreviations: frt, frontal; lts, laterosphenoid; squ, squamosal; par, parietal; ppo, processus postorbitalis; qdr, quadrat. Scale bars equal 10 mm.
and frontal is absent in various taxa of the Aequornithes, the clade including most aquatic and semiaquatic birds, as well as in the Phaethontidae, Rynchochetidae, Caprimulgidae, Musophagidae, and Strigiformes (Table 1). In Aequornithes, there exists variation in the size of the squamosal, which is rostrodorsally shorter than the parietal in the Spheniscidae, Phalacrocoracidae, Sulidae, Threskiornithidae, and Ardeidae, as long as the parietal in the Ciconiidae and Balaenicipitidae (Böhm, 1930), and longer than the parietal in the Pelecanidae. Based on this distribution and current phylogenies (Hackett et al., 2008; Jarvis et al., 2014; Prum et al., 2015; Figure 7), it is most parsimonious to assume that a short squamosal is plesiomorphic for Aequornithes. The taxa of the Aequornithes form a clade together with Phaethontidae and Eurypygiformes (Rynchochetidae + Eurypygidae) in current molecular phylogenies (Figure 7; Jarvis et al., 2014; Prum et al., 2015) and a short squamosal is likely to have already been present in the stem species of this clade. The short squamosal of the Caprimulgidae may also be plesiomorphic for Strisores, the clade including “caprimulgiform” and apodiform birds, because the Caprimulgidae result as the sister taxon of other taxa of the Strisores in current molecular phylogenies (Prum et al., 2015).

The early divergences within Neoaves are controversially resolved in different molecular analyses (Ericson et al., 2006; Hackett et al., 2008; Jarvis et al., 2014; Prum et al., 2015), but in all phylogenies most taxa with a short squamosal are among the early diverging clades, and only the Strigiformes are nested within Telluraves, the clade including most arboreal landbirds (Figure 7). However, even though a short squamosal, which does not contact the frontal, is mainly found in phylogenetically more “basal” neognathous taxa, it is more parsimonious in all current phylogenies to assume that it represents a derived condition for Neognathae and evolved convergently in the clades showing this feature. In the phylogeny of Prum et al. (2015), for example, a short squamosal may have developed only four times independently in neognathous birds (in the Strisores, Musophagiformes, the clade formed by Eurypygiformes, Phaethontiformes, Aequornithes, and in Strigiformes; Figure 7). By contrast, at least nine independent origins are required for a squamosal reaching the frontal (in Galloanseres, Apodiformes, Otidiformes + Cuculiformes, Musophagiformes + Mesitornithiformes + Pterocliformes, Gruiformes, Phoenicopteriformes + Podicipediformes + Charadriiformes, Ciconiidae, Pelecaniformes, and Opisthocomiformes + Telluraves). From a parsimony point of view, it is therefore more likely that a squamosal, which

**FIGURE 7** Phylogenetic interrelationships of neornithine birds as recovered in the molecular analysis of Prum et al. (2015). Taxa shown in blue have a short squamosal, which does not reach the frontal, whereas the bone contacts or exceeds the frontal in taxa highlighted in red. Squamosal morphology of taxa in light gray is unknown.
reaches the frontal, represents the plesiomorphic condition for neognathous birds.

Galloanseres, which are the sister taxon of all other neognathous birds, exhibit a long, rectangular-shaped squamosal, which surpasses the parietal, and this morphology is also found in multiple neoavian clades. However, these very long squamosals show a great diversity of shapes, so that a squamosal, which distinctly surpasses the parietal, is likely to have evolved independently in Galloanseres and various neoavian clades.

Although the postorbital bone is completely reduced in adult neoornithine birds, in some juveniles a small ossification on the tip of the postorbital process of the laterosphenoid was considered to be a remnant of the bone (Bittner, 1912); this ossicle was, however, identified as a "secondary membral ossification" by Jollie (1957, p. 411). Irrespective of whether an embryological anlage of a postorbital is present in some Neornithes, a topological correlation between the squamosal and the postorbital process of the laterosphenoid seems to be maintained in most Neognathae, in which the rostral tip of the squamosal reaches to the postorbital process. The fact that the squamosal projects beyond the cranial vault and is therefore not fully integrated into the neurocranium in the charadriiform Lari (Laridae, Alcidae, and allies; Figure 5d–j) and the procellariiform Hydrobatinae (Oceanodroma; Figure 4c) may indicate an atavism, which reflects the evolutionary history of the bone. If the postorbital process is topologically equivalent to the postorbital bone, squamosal development may therefore still be influenced by ontogenetic factors correlated with the formation of the postorbital.

4.2 Phylogenetic and functional considerations

The phylogenetic significance of squamosal shape is diminished by the fact that closely related taxa often show very disparate morphologies, which is the case for, for example, Sphenisciformes (Figure 4a) and Procellariiformes (Figure 4b,c), Balaenicipitidae (Figure 4g) and Pelecanidae (Figure 4h), or the strigiform taxon Athene (Figure 6c) and other Strigiformes (Figure 6a,b). Moreover, there appears to be a great amount of homoplasy in the distribution of squamosal types among neoornithine birds. However, even though it is difficult to identify derived squamosal morphologies characterizing major neoavian clades, a number of taxa exhibit distinctive squamosal shapes of potential phylogenetic and functional interest.

A unique apomorphy of the Apodidae, Hemiprocnidae, and—presumably (see above)—Trochilidae is the extreme elongation of the rostrocaudal process of the squamosal, which runs along the dorsal margin of the orbit (Figure 3e). In the adult skull of these apodiform birds, the rostrocaudal process of the bone borders a distinct sulcus for musculus cucullaris capitis (Zusi, 2013, figure 4), and we consider it possible that the extreme elongation of the squamosal is related to a particular development of this muscle.

Columbidae and Pteroclidae form a clade together with the Mesitornithidae in molecular phylogenies (Hackett et al., 2008; Jarvis et al., 2014; Prum et al., 2015). However, whereas the former two taxa have a greatly elongated squamosal, which exceeds the postorbital process in rostrocaudal direction, an elongated squamosal is absent in the Mesitornithidae (although the exact shape of the bone could not be determined in the alcohol-preserved specimen available to us). From a mere morphological point of view, this morphology may represent a synapomorphy of Pteroclidae and Columbidae. However, if the molecular phylogenies correctly reflect the interrelationships of the above taxa, the squamosal was either secondarily shortened in mesites or the morphology in Columbidae and Pterooidae evolved convergently.

Certainly, functional and ontogenetic constraints on squamosal development are multifactorial and differ across Neognathae. Some of the observed variation may be due to different skull geometries of the involved taxa. It has been shown that the development and shape of the frontals and parietals is correlated with brain morphology (Fabbri et al., 2017; Marugán-Lobón & Buscalioni, 2009). Possibly, therefore, differences in brain shape and associated changes in the sizes of the frontal and parietal may affect the shape of the squamosal.

Different skull geometries are also likely to account for the observed variation of squamosal shape in strigiform birds (Figure 6a–c), which was already recognized by Pycraft (1903b) for the two species studied by him (Athene cucullaria and Strix aluco). As shown by the latter author and the present study, the taxon Athene has a much longer squamosal than other Strigiformes (Figure 6a–c). Current phylogenies support a sister group relationship between a clade including Athene, Surnia, Glaucidium, and Aegolius and all other Strigidae (e.g., Wood et al., 2016), and whether a long squamosal is a derived characteristic of this latter clade or represents an autopomorphy of Athene needs to be examined once juvenile skulls of Surnia, Glaucidium, and Aegolius become available. Whereas in Tyto and most Strigidae the portion of the skull roof that forms the caudodorsal margin of the orbital rim is flattened, it exhibits the usual neoornithine morphology (sharp ridge) in Athene. Even though the short squamosal of strigiform birds is therefore associated with a derived cranial morphology, it
is more parsimonious to assume that a short squamosal is plesiomorphic for Strigiformes (i.e., Strigidae + Tytonidae).

In the Charadriiformes, by contrast, all examined taxa except the Burhinidae have a greatly elongated squamosal (Figure 5a–j). Because the Burhinidae are phylogenetically nested within other Charadriiformes (e.g., Mayr, 2011), an elongated squamosal is certainly plesiomorphic for the clade. Burhinidae differ from other charadriiform taxa in that the squamosal does not form a long rostrodorsal process and in that the nostrils are holorhinal, whereas they are schizorhinal in other charadriiform birds (Mayr, 2011). Charadriiformes therefore not only provide an example for a secondary shortening of the squamosal (in the Burhinidae), but also indicate that a correlation may exist between squamosal shape and nostril type.

The squamosal is the only bone of the cranial vault that derives from the cranial neural crest, which also gives rise to the facial part of the skull, the quadrate, and the palatal area (Maddin et al., 2016). Therefore mutually interdependent ontogenetic constraints on squamosal morphology and the feeding apparatus may exist and this so much the more, since the squamosal provides an articulation facet for the quadrate. However, no obvious correlation exists between squamosal shape and beak length, and similar squamosal shapes occur in birds with very different beak shapes and feeding ecologies, such as the charadriiform Laridae and the Columbiformes.

We studied squamosal shape in a large number of birds, but the morphology of this bone remains unknown for various critical taxa, including many Strisores (Steatornithidae, Nycitibidae, Podargidae, and Aegothelidae), some Aequornithes (Gaviidae, Fregatidae), the eurypygiform Eurypygidae, the accipitriform Cathartidae and Sagittariidae, as well as many taxa of Telluraves (Leptosomidae, Coraciidae, the piciform Galbulae). Examination of the squamosal morphology in these birds may further improve our understanding of the phylogenetic and functional significance of the observed variation shown by this bone, and future studies of the comparative morphology of other bones of the juvenile avian skull are likely to augment these data.

ACKNOWLEDGMENT
We thank S. Tränkner for taking the photographs. Comments from two anonymous reviewers improved the manuscript. Open access funding enabled and organized by Projekt DEAL.

AUTHOR CONTRIBUTIONS

Albrecht Manegold: Conceptualization; formal analysis; investigation; visualization.

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

REFERENCES

Balanoff, A. M., & Rowe, T. (2007). Osteological description of an embryonic skeleton of the extinct elephant bird, Aepyornis (Palaeognathae: Ratitae). Journal of Vertebrate Paleontology, 27, Memoir, 9, 1–53.

Bittner, F. (1912). Über die Schläfenregion am Schädel der Vögel und dessen Beziehungen zu dem der Reptilien. Archiv für Naturgeschichte, 78, 1–23.

Böhm, M. (1930). Über den Bau des jugendlichen Schädel's von Balænicercex rex nebst Bemerkungen über dessen systematische Stellung und über das Gaumenskelet der Vögel. Zeitschrift für Morphologie Und Ökologie der Tiere, 17, 677–718.

Brusaferro, A., & Simonetta, A. M. (1998). Morphology of the feeding apparatus in nestlings of Merops. Italian Journal of Zoology, 65, 249–259.

Clark, J. M., Welman, J., Gauthier, J. A., & Parrish, J. M. (1993). The laterosphenoid bone of early archosauromorphs. Journal of Vertebrate Paleontology, 13, 48–57.

Elzanowski, A. (2001). A novel reconstruction of the skull of Archaeopteryx. Netherlands Journal of Zoology, 51, 207–216.

Elzanowski, A., & Wellinhofer, P. (1996). Cranial morphology of Archaeopteryx: Evidence from the seventh skeleton. Journal of Vertebrate Paleontology, 16, 81–94.

Erdmann, K. (1940). Zur Entwicklungsgeschichte der Knochen im Schädel des Huhnes bis zum Zeitpunkt des Ausschlüpfens aus dem Ei. Zeitschrift für Morphologie Und Ökologie der Tiere, 36, 315–400.

Ericson, P. G. P., Anderson, C. L., Britton, T., Elzanowski, A., Johansson, U. S., Källersjö, M., ... Mayr, G. (2006). Diversification of Neovaves: Integration of molecular sequence data and fossils. Biology Letters, 2, 543–547.

Fabbri, M., Koch, N. M., Pritchard, A. C., Hanson, M., Hoffman, E., Bever, G. S., ... Bhullar, B.-A. S. (2017). The skull roof tracks the brain during the evolution and development of reptiles including birds. Nature Ecology and Evolution, 1, 1543–1550.

Field, D. J., Hanson, M., Burnham, D., Wilson, L. E., Super, K., Ehret, D., ... Bhullar, B.-A. S. (2018). Complete Ichthyornis skull illuminates mosaic assembly of the avian head. Nature, 557, 96–100.

Goldschmid, A. (1972). Die Entwicklung des Craniums der Mausvögel (Coliliformes, Colilidae, Aves): IV. Die Entwicklung des Osteocraniums. Gegenbaurs Morphologisches Jahrbuch, 118, 553–569.

Hackett, S. J., Kimball, R. T., Reddy, S., Bowie, R. C. K., Braun, E. L., Braun, M. J., ... Yuri, T. (2008). A phylogenomic study of birds reveals their evolutionary history. Science, 320, 1763–1767.

Jarvis, E. D., Mirarab, S., Aberer, A. J., Li, B., Houde, P., Li, C., Ho, S. Y. W., Faircloth, B. C., Nahholz, B., Howard, J. T., Suh, A., Weber, C. C., da Fonseca, R. R., Li, J., Zhang, F., Li, H., Zhou, L., Narula, N., Liu, L., Ganapathy, G., Boussau, B., Bayzid, M. S., Zavidovych, V., Subramanian, S.,...
Gabaldón, T., Capella-Gutiérrez, S., Huerta-Cepas, J., Rekepalli, B., Munch, K., Schierup, M. et al. (2014). Whole-genome analyses resolve early branches in the tree of life of modern birds. *Science*, 346, 1320–1331.

Jollie, M. T. (1957). The head skeleton of the chicken and remarks on the anatomy of this region in other birds. *Journal of Morphology*, 100, 389–436.

Jollie, M. (1977). A contribution to the morphology and phylogeny of the Falconiformes, part 2. *Evolutionary Theory*, 2, 115–208.

Maddin, H. C., Piekarski, N., Sefton, E. M., & Hanken, J. (2016). Homology of the cranial vault in birds: New insights based on embryonic fate-mapping and character analysis. *Royal Society Open Science*, 3, 160356.

Marugán-Lobón, J., & Buscalioni, A. D. (2009). New insight on the anatomy and architecture of the avian neurocranium. *The Anatomical Record*, 292, 364–370.

Maxwell, E. E. (2009). Comparative ossification and development of the skull in palaeognathous birds (Aves: Palaeognathae). *Zoological Journal of the Linnean Society*, 156, 184–200.

May, W. (1961). Die Morphologie des Chondrocranium und Osteocranium eines Waldkauzembryos (Strix aluco L.). *Zeitschrift für Wissenschaftliche Zoologie*, 166, 135–202.

Mayr, G. (2010). Comparative morphology of the avian maxillary bone (os maxillare) based on an examination of macerated juvenile skeletons. *Acta Zoológica*, 101, 24–38.

Müller, H. J. (1963). Die Morphologie und Entwicklung des Crani-ums von *Rhea americana* Linné. II. Viszeralskelett, Mittelohr und Osteocranium. *Zeitschrift für Wissenschaftliche Zoologie*, 168, 35–118.

O’Connor, J. K., & Chiappe, L. M. (2011). A revision of enantiornithine (Aves: Ornithothoraces) skull morphology. *Journal of Systematic Palaeontology*, 9, 135–157.

Parker, T. J. (1891a). Observations on the anatomy and development of the skull in palaeognathous birds (Aves: Palaeognathae). *Zoological Journal of the Linnean Society*, 156, 184–200.

Parker, W. K. (1891b). On the morphology of a reptilian bird, *Opisthocomus cristatus*. *Transactions of the Zoological Society of London*, 13, 43–85.

Piro, A., & Hospitaleche, C. A. (2019). Skull morphology and ontogenetic variation of the southern Giant petrel *Macronectes giganteus* (Aves: Procellariiformes). *Polar Biology*, 42, 27–45.

Posso, S. R., & Donatelli, R. J. (2005). Skull and mandible formation in the cuckoo (Aves, Cuculidae): Contributions to the nomenclature in avian osteology and systematics. *European Journal of Morphology*, 42, 163–172.

Prum, R. O., Berv, J. S., Dornburg, A., Field, D. J., Townsend, J. P., Moriarty Lemmon, E., & Lemmon, A. R. (2015). A comprehensive phylogeny of birds (Aves) using targeted next-generation DNA sequencing. *Nature*, 526, 569–573.

Pycraft, W. P. (1898). Contributions to the osteology of birds. Part I. *Proceedings of the Zoological Society of London*, 1898, 82–101.

Pycraft, W. P. (1899). Contributions to the osteology of birds. Part III. *Proceedings of the Zoological Society of London*, 1899, 381–411.

Pycraft, W. P. (1903a). Contributions to the osteology of birds. Part VI. *Cuculiformes. Proceedings of the Zoological Society of London*, 1903, 258–291.

Pycraft, W. P. (1903b). A contributions towards our knowledge of the morphology of owls. Part II. *Osteology. Transactions of the Linnean Society of London*, 9, 1–46.

Pycraft, W. P. (1905). Contributions to the osteology of birds. Part VII. *Eurylaemidae; with remarks on the systematic position of the group. Proceedings of the Zoological Society of London*, 1905, 30–56.

Sanz, J. L., Chiappe, L. M., Perez-Moreno, B. P., Moratalla, J. J., Hernandez-Carrasquilla, F., Buscalioni, A. D., ... Martinez-Delclòs, X. (1997). A nestling bird from the lower cretaceous of Spain: Implications for avian skull and neck evolution. *Science*, 276, 1543–1546.

Sushkin, P. F. (1899). Zur Morphologie des Vogelskelettes. I. Schädel von Tinnunculus. *Nouveaux Mémoires de la Société Impériale Des Naturalistes de Moscou*, 16, 1–163.

Tokita, M. (2003). The skull development of parrots with special reference to the emergence of a morphologically unique craniofacial hinge. *Zoological Science*, 20, 749–758.

Tsuhijii, T., Barsbold, R., Watabe, M., Tsogtbaatar, K., Chinzorig, T., Fujiyama, Y., & Suzuki, S. (2014). An exquisitely preserved troodontid theropod with new information on the palatal structure from the upper cretaceous of Mongolia. *Naturwissenschaften*, 101, 131–142.

Wang, M., & Hu, H. (2017). A comparative morphological study of the jugal and quadratojugal in early birds and their dosaurian relatives. *The Anatomical Record*, 300, 62–75.

Weber, E. (1990). Zur Kraniiognese bei der Lachmöwe (Larus ridibundus L.), zugleich ein Beitrag zur Rekonstruktion des Grundplans der Vögel. *Gegenbaurs Morphologisches Jahrbuch*, 136, 335–387.

Wood, J. R., Mitchell, K. J., Scofield, R. P., De Pietri, V. L., Rawlence, N. J., & Cooper, A. (2016). Phylogenetic relationships and terrestrial adaptations of the extinct laughing owl, *Sceloglaux albifacies* (Aves: Strigidae). *Zoological Journal of the Linnean Society*, 179, 907–918.

Worthy, T. H., & Scofield, R. P. (2012). Twenty-first century advances in knowledge of the biology of moa (Aves: Dinornithiformes): A new morphological analysis and moa diagnoses revised. *New Zealand Journal of Zoology*, 39, 87–153.

Zusi, R. L. (1993). Patterns of diversity in the avian skull. In J. Hanken & B. K. Hall (Eds.), *The skull (Vol. 2, Patterns of Structural and Systematic Diversity, pp. 391–437). Chicago: University of Chicago Press.*

Zusi, R. L. (2013). Introduction to the skeleton of hummingbirds (Aves: Apodiformes, Trochilidae) in functional and phylogenetic contexts. *Ornithological Monographs*, 77, 1–94.
Zusi, R. L., & Livezey, B. C. (2000). Homology and phylogenetic implications of some enigmatic cranial features in Galliformes and Anseriformes birds. *Annals of Carnegie Museum, 69*, 157–193.

Zusi, R. L., & Livezey, B. C. (2006). Variation in the os palatinum and its structural relation to the palatum osseum of birds (Aves). *Annals of Carnegie Museum, 75*, 137–180.

**How to cite this article:** Mayr G, Manegold A. On the comparative morphology of the juvenile avian skull: An assessment of squamosal shape across avian higher-level taxa. *Anat Rec.* 2021;304:845–859. https://doi.org/10.1002/ar.24504