

Osteology of the Shoulder Girdle in the Piciformes, Passeriformes and Related Groups of Birds

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Abstract. A comparative study of the bones of the shoulder girdle in the Piciformes, Passeriformes and Coraciiformes, and also in related orders of birds such as the Trogoniformes, Coliiformes, Apodiformes, Strigiformes and Caprimulgiformes, is presented and discussed. A number of observed characters justify inclusion only the families Indicatoridae, Picidae, Capitonidae and Ramphastidae in the order Piciformes, while also demonstrating a close resemblance with the Passeriformes that suggests a monophyletic origin for these two orders. On the other hand, although the closely related Bucconidae and Galbulidae are not included in the Piciformes they more closely resemble the Coraciiformes, particularly the Meropidae, Coraciidae and Brachypteraciidae. Among the Coraciiformes, it was observed that the Upupidae closely resemble the Phoeniculidae and, to a lesser extent, the Bucerotidae (particularly *Tockus*). For other coraciiforms, observation of shoulder girdle osteology alone did not provide sufficient evidence to justify a family grouping or a clearer definition of the boundaries of this order.

Key words. Birds, comparative anatomy, clavicle, scapula, coracoid.

1. INTRODUCTION

Many systematic groupings of recent birds have been proposed by countless authors since the publication of *Sistema Naturae* by LINNAEUS (1758), and many of them differ in their views about the groups comprised in the traditional orders Piciformes and Coraciiformes. The Ramphastidae (toucans) and Capitonidae (barbets) are generally included in the order Piciformes, suborder Picoidea (or Pici), together with the families Picidae (woodpeckers) and Indicatoridae (honey-guides); while the Galbulidae (jacamars) and Bucconidae (puff-birds) are classed in the suborder Galbuloidea (or Galbulae). This traditional view of the Piciformes is adopted by several authors (STRESEMANN 1934; STEINBACHER 1935; STEINBACHER 1937; VERHEYEN 1955; SWIERCZEWSKY & RAIKOW 1981; SIMPSON & CRACRAFT 1981; CRACRAFT 1981; RAIKOW & CRACRAFT 1983). The isozymic pattern found by AVISE & AQUADRO (1987) for malate dehydrogenase (S-MDH) is a character of the group that includes the Ramphastidae, Capitonidae, Indicatoridae and Picidae, suggesting that this is a monophyletic group. However, Galbulidae and

Bucconidae do not present the same pattern, and neither do the Coraciiformes.

PRUM (1988) conducted a phylogenetic analysis of the capitonids and compared the findings with the DNA-DNA hybridization data published in SIBLEY et al. (1988), concluding that the capitonids are a polyphyletic group and proposing their separation into six subfamilies (Trachyphonidae, Calorhamphidae, Lybiidae, Megalaimidae, Capitoninae and Semnorninae), which together with the Ramphastinae would form the family Ramphastidae. LANYON & HALL (1994) also concluded that the Capitonidae are polyphyletic, with the New World barbets being a sister group of the toucans.

SIBLEY & AHLQUIST (1972, 1990), OLSON (1982, 1983), BURTON (1984), LANYON & ZINK (1987) and SIBLEY et al. (1988) aver that the Galbulidae and Bucconidae are more closely related phylogenetically with the Coraciiformes than the Piciformes. Thus SIBLEY et al. (1988), SIBLEY & AHLQUIST (1990), SIBLEY & MONROE JR. (1990) and MONROE JR. & SIBLEY (1993) propose the order Galbuliformes, classifying Galbulidae and Bucconidae in the superorder Galbulimorphae, parvclass Coraciae.

Thus is it possible to identify two separate viewpoints, one which postulates inclusion of the Galbulidae and Bucconidae among the Piciformes, and another which excludes them in order to classify them among the Coraciiformes or in a group of their own.

Just as it is for the Piciformes, the monophyletic origin of the Coraciiformes is also questioned by several authors. BURTON (1984) includes the Galbulidae and Bucconidae with the Leptosomidae, Coraciidae and Brachypteraciidae in the suborder Coracii, order Coraciiformes, while placing the Bucerotidae, Upupidae and Phoeniculidae in a separate order, the Upupiformes.

MAURER & RAIKOW (1981) include the family Trogonidae in the order Coraciiformes and argue for monophyly on the basis of the hypothesis put forward by GADOW (1896) regarding the evolution of plantar tendons in birds. They therefore propose a classification of the Coraciiformes that includes the family Trogonidae, and in this they are followed by CRACRAFT (1981). The group is traditionally considered an independent order (Trogoniformes).

In light of DNA-DNA hybridization, SIBLEY et al. (1988) propose the creation of the parvclass Coraciae to include the orders Galbuliformes (Galbulidae and Bucconidae), Bucerotiformes (Bucerotidae and Bucorvidae), Upupiformes (Upupidae, Phoeniculidae and Rhinopomastidae), Trogoniformes (Trogonidae), and Coraciiformes, with two suborders: Coracii (Coraciidae, Brachypteraciidae and Leptosomidae), and Alcedini (Momotidae, Todidae, Alcedinidae, Dacelonidae, Cerylidae and Meropidae). SIBLEY et al. (op. cit.) accept the proposal advanced by CRACRAFT (1971) to group Coraciidae and Brachypteraciidae together in the superfamily Coracioidea, and classify the Leptosomidae in the superfamily Leptosomoidea, both of which would belong to the suborder Coracii. This classification is maintained in SIBLEY & AHLQUIST (1990), SIBLEY & MONROE JR. (1990), and MONROE JR. & SIBLEY (1993).

With regard to the Passeriformes, LOWE (1946) argues for inclusion of the families Indicatoridae, Picidae, Ramphastidae and Capitonidae in the suborder Pici, order Passeriformes, and of the traditional Passeriformes in the suborder Passeres. In a study of cranial and appendicular anatomy in the family Picidae, SHUFELDT (1900) suggests that woodpeckers are more akin to the Passeriformes. MAYR & AMADON (1951) also suggest that the Pici (= Piciformes) seem to be closer to the Passeriformes, phylogenetically speaking. However, on the basis of an analysis of DNA-DNA hybridization BLEIWEISS et al. (1994) rebut the suggestion that the Piciformes and Passeriformes are closely related, suggesting instead that the Piciformes are located on the first branch of radiation in non-

passeriform groups, and that the Passeriformes are phylogenetically more related to the Coliidae and Alcedinidae.

FEDUCCIA (1977) argues against monophyly of the Passeriformes and for creation of the order Tyranniformes encompassing the families that are characteristic of the New World ("suboscines"). However, bearing in mind the organization of spermatozooids in the testicles of "oscines" (HENLEY et al. 1978), FEDUCCIA (1979) found that "suboscines" also possess this derived character, which is unique to vertebrates. Moreover, examination of the *columella* under a scanning microscope evidenced differences that had not been observed previously (FEDUCCIA 1977), leading to reconsideration of monophyly of the Passeriformes. After reviewing the 18 characters of the Passeriformes, RAIKOW (1982) accepted that this order is monophyletic.

The present paper analyzes the osteology of the shoulder girdle in the Piciformes, Passeriformes and other bird groups, as a contribution to an enhanced systematic grouping of birds.

2. MATERIALS AND METHODS

The study was based on an examination of 109 main skeletons belonging to 83 different bird species, 31 families of the orders Strigiformes, Caprimulgiformes, Apodiformes, Coliiformes, Trogoniformes, Coraciiformes, Piciformes and Passeriformes, although skeletons of all other orders of birds, almost all families of non-passeriform birds and most families of Passeriformes were also examined.

The osteological material belonged to the National Museum of Natural History's Smithsonian Institution, Washington, USA (USNM), and the private collection of Herculano Alvarenga, Taubaté, Brazil (HA), as detailed below:

Strigidae – *Ciccaba virgata* (Cassin, 1848): 1♂ (HA: 1230).
Podargidae – *Podargus strigoides* (Latham, 1801): 1♀ (HA: 1209).
Nyctibiidae – *Nyctibius griseus* (Gmelin, 1789): 2♂ (HA: 118, 682).
Caprimulgidae – *Lurocalis semitorquatus* (Gmelin, 1788): 1♀ (HA: 1270).
Apodidae – *Streptoprocne zonaris* (Shaw, 1796): 1 indetermined (HA: 249).
Coliidae – *Colius striatus* (Gmelin, 1789): 1 indetermined (HA: 124).
Trogonidae – *Pharomachrus mocinno* de la Llave, 1832: 1♂ (HA: 554).
Priotelus temnurus (Temminck, 1825): 1♂ (HA: 559).
Trogon viridis Linnaeus, 1766: 1♀ (HA: 263).
T. surrucura Vieillot, 1817: 1♂ (HA: 1337).
Alcedinidae – *Ceryle torquata* (Linnaeus, 1766): 1♀ (HA: 127).
Chloroceryle amazona (Latham, 1790): 1♀ (HA: 306).
C. americana (Gmelin, 1788): 1♂ (HA: 767).
Alcedo atthis Linnaeus, 1758: 1 indetermined (HA: 128).
Dacelo novaeguineae (Hermann, 1783): 1 indetermined (HA: 126).
Todidae – *Todus subulatus* Gray, 1847: 1 indetermined (HA: 129).
Momotidae – *Momotus momota* (Linnaeus, 1766): 1♂ (HA: 393); 1 indetermined (HA: 1356).
Meropidae – *Merops apiaster* Linnaeus, 1758: 1♂ (HA: 131); 1 indetermined (HA: 1356).

Coraciidae – *Coracias caudata* Linnaeus, 1766: 1 indetermined (HA: 1551). *Eurystomus orientalis* (Linnaeus, 1766): 1♀ (HA: 133). **Brachypteraciidae** – *Brachypteracias leptosomus* (Lesson, 1832): 1 indetermined (USNM: 223863). **Leptosomidae** – *Leptosomus discolor* (Hermann, 1783): 1 indetermined (USNM: 291845). **Upupidae** – *Upupa epops* Linnaeus, 1758: 1 indetermined (HA: 135). **Phoeniculidae** – *Phoeniculus purpureus* (Miller, 1784): 1 indetermined (USNM: 320948). **Bucerotidae** – *Tockus erythrorhynchus* (Temminck, 1823): 1♂ (HA: 137). *Aceros undulatus* (Shaw, 1811): 1 indetermined (HA: 138). **Galbulidae** – *Galbula albirostris* Latham, 1790: 1 indetermined (HA: 1226). *G. ruficauda* Cuvier, 1817: 1♀ (HA: 293). **Bucconidae** – *Notharchus macrorhynchus* (Sclater, 1855): 1♀ (HA: 508). *Nystalus chacuru* (Vieillot, 1816): 1♀ (HA: 1312); 1♂ (HA: 1335). *Malacoptila rufa* (Spix, 1824): 1 indetermined (HA: 1225). *Monasa nigrifrons* (Spix, 1824): 1♀ (HA: 140); 1♂ (HA: 298). **Capitonidae** – *Capito niger* (Müller, 1776): 1♂ (HA: 1364). *Semnornis ramphastinus* (Jardine, 1855): 1 indetermined (HA: 145). *Psilopogon pyrolophus* Müller, 1835: 1♂ (USNM: 343420). *Megalaima asiatica* (Latham, 1790): 1♀ (HA: 1525); 1♂ (HA: 1527). *M. haemacephala* (Müller, 1776): 1♀ (HA: 146). *Tricholaema hirsuta* (Swainson, 1821): 1♀ (USNM: 322560). *Lybius bidentatus* (Shaw, 1798): 1♂ (USNM: 291092). *L. dubius* (Gmelin, 1788): 1♀ (HA: 1550). *Trachyphonus vaillantii* Ranzani, 1935: 1♂ (USNM: 558564). **Indicatoridae** – *Indicator indicator* (Sparman, 1777): 1♂ USNM: 430329). *I. minor* Stephens, 1815: 1♂ (USNM: 558565). **Ramphastidae** – *Pteroglossus inscriptus* (Swainson, 1822). 2♂ (HA: 304, 615). *P. bitorquatus* Vigors, 1826: 1♂ (HA: 1141). *P. aracari* (Linnaeus, 1758): 1♀ (HA: 143). *P. castanotis* Gould, 1833: 1♀ (HA: 400); 2♂ (HA: 413, 1229). *P. torquatus* (Gmelin, 1788): 1 indetermined (HA: 551). *Selenidera maculirostris* (Lichtenstein, 1823): 1♀ (HA: 738); 1♂ (HA: 416). *S. gouldii* (Natterer, 1837): 2♂ (HA: 144, 1212). *Baillonius baillonii* (Vieillot, 1819): 1♀ (HA: 839); 2♂ (HA: 394, 1297); 1 indetermined (HA: 1365). *Ramphastos dicolorus* Linnaeus, 1766: 2♂ (HA: 599, 1288). *R. vitellinus* Lichtenstein, 1823: 2♀ (HA: 303, 350); 3♂ (HA: 352, 713, 799). *R. sulfuratus* Lesson, 1830: 1♂ (HA: 531). *R. toco* Müller, 1776: 1♂ (HA: 1014); 1 indetermined (HA: 142). *R. tucanus* Linnaeus, 1758: 2♂ (HA: 254, 1238). **Picidae** – *Jynx torquilla* Linnaeus, 1758: 1 indetermined (HA: 148). *Picumnus cirratus* Temminck, 1825: 1♀ (HA: 1071); 3♂ (HA: 149, 1032, 1326). *P. aurifrons* Hargitt, 1889: 1 indetermined (HA: 506). *Picooides major* Linnaeus, 1758: 1 indetermined (HA: 1359). *Piculus flavigula* (Boddaert, 1783): 1♀ (HA: 376). *Melanerpes flavifrons* Vieillot, 1818: 1♀ (HA: 762). *Veniliornis spilogaster* (Wagler, 1827): 1♀ (HA: 817). *V. passerinus* Linnaeus, 1766: 1♂ (HA: 694). *Colaptes campestris* (Vieillot, 1818): 2♀ (HA: 486, 1010). *Celeus flavescens* Gmelin, 1788: 1♀ (HA: 226). *Dryocopus lineatus* Linnaeus, 1766: 1♀ (HA: 459). *Campephilus robustus* (Lichtenstein, 1823): 1♂ (HA: 1123). **Dendrocolaptidae** – *Nasica longirostris* (Vieillot, 1818): 1♂ (HA: 632). *Dendrocolaptes platyrostris* Spix, 1825: 1♂ (HA: 1115). *Campilorhamphus falcularius* (Vieillot, 1822): 1♂ (HA: 1078). **Thamnophilidae** – *Thamnophilus ruficapillus* Vieillot, 1816: 1♂ (HA: 1052).

Phlegopsis nigromaculata (Lafresnaye & d'Orbigny, 1837): 1♂ (HA: 1290). **Furnariidae** – *Philydor leucophrus* (Jardine & Selby, 1830): 1♂ (HA: 1112). **Cotingidae** – *Tijuca atra* Férussac, 1829: 1♀ (HA: 1338). *Pyroderus scutatus* (Shaw, 1792): 1♀ (HA: 726). **Formicariidae** – *Chamaeza ruficauda* (Cabanis & Heine, 1859): 1♀ (HA: 1449). *Grallaria varia* (Boddaert, 1783): 1♂ (HA: 1079). *Hylopezus nattereri* (Pinto, 1937): 1♀ (HA: 1320). **Tyrannidae** – *Pitangus sulphuratus* (Linnaeus, 1766): 1♀ (HA: 1108); 1 indetermined (HA: 522). *Myiarchus ferox* (Gmelin, 1789): 1♀ (HA: 167). **Muscicapidae** – *Turdus rufiventris* Vieillot, 1818: 1♀ (HA: 1127). **Corvidae** – *Corvus brachyrhynchus* Brehm, 1822: 1♂ (HA: 442).

The bones of the shoulder girdle were analyzed using a Wild M3 (9.6×–60×) stereoscopic microscope. Drawings were made only of those considered most interesting because they are not yet found in the literature or illustrate details relevant to the present study.

The nomenclature used is based on MORONY et al. (1975), with modifications. Bone terminology is basically that used by BAUMEL et al. (1993), supplemented by HOWARD (1929) and GILBERT et al. (1981).

3. RESULTS AND DISCUSSION

3.1. Clavicle

The *omalis* extremity (Fig. 1: oe) of the clavicle in the Passeriformes (Fig. 1: A–E), Picidae (Fig. 1: H–K), Indicatoridae (Fig. 1: F, G), Ramphastidae (Fig. 1: L–O) and Capitonidae (Fig. 1: T–Z) is triangular in shape and distinctly truncated at the apex, with a large cranial expansion; the adjacent portion of diaphysis is rectilinear or slightly curved cranially. In these groups the above-mentioned cranial expansion is articulated with the acrocoracoid process (ap – Fig. 7) of the coracoid bone; this expansion is particularly well-developed in Indicatoridae (Fig. 1: F, G) and in such Picinae as *Picooides major* and *Campephilus robustus* (Fig. 1: H, I). Pneumatic foramina are relatively abundant in these groups, albeit often absent in smaller species.

In the Ramphastidae the lateral face of the *omalis* extremity is almost flat and contains a variable number of pneumatic foramina, mainly located in the cranial portion. This number may vary in a single exemplar, as observed in the case of *Ramphastos toco*, where the left clavicle has seven foramina and the right clavicle has four. The size of these foramina also varies, but generally speaking they are larger in the larger species. For example, a specimen of *R. tucanus* was found to have one large foramen, while species of a smaller size, such as *Baillonius baillonii*, may not have any pneumatic foramina at all. No pneumatic foramina were found in the Capitonidae.

Pneumatic foramina located at the *omalis* extremity of the clavicle were observed not only in the Ramphasti-

dae, but also in the Picidae (except the genus *Picumnus*), *Indicator indicator* and the Passeriformes. They are also present in *Eurystomus orientalis* (Coraciidae), the Momotidae and Trogonidae.

In the Bucconidae (Fig. 1: Q–S), Galbulidae (Fig. 1: P), Coraciiformes (*sensu lato*) (Fig. 2: AA–OO), Apodiformes (Fig. 2: PP), Caprimulgiformes (Fig. 2: QQ–SS) and Strigiformes (Fig. 2: TT), in contrast with the previous group, the *omalis* extremity is not truncat-

ed at the apex, the pneumatic foramina are relatively rare, and the adjacent portion of diaphysis is almost always caudally curved. The Galbulidae and Bucconidae present a strikingly distinct coracoid process (Fig. 1: cp), situated obliquely as in the Meropidae (Fig. 2: FF). A cranial projection (small and secondary) can be observed only in the Coliidae (Fig. 2: DD), Meropidae (FF), some cerylines (Fig. 2: GG–II) and the Todidae. In *Chloroceryle amazona* (Fig. 2: JJ) and

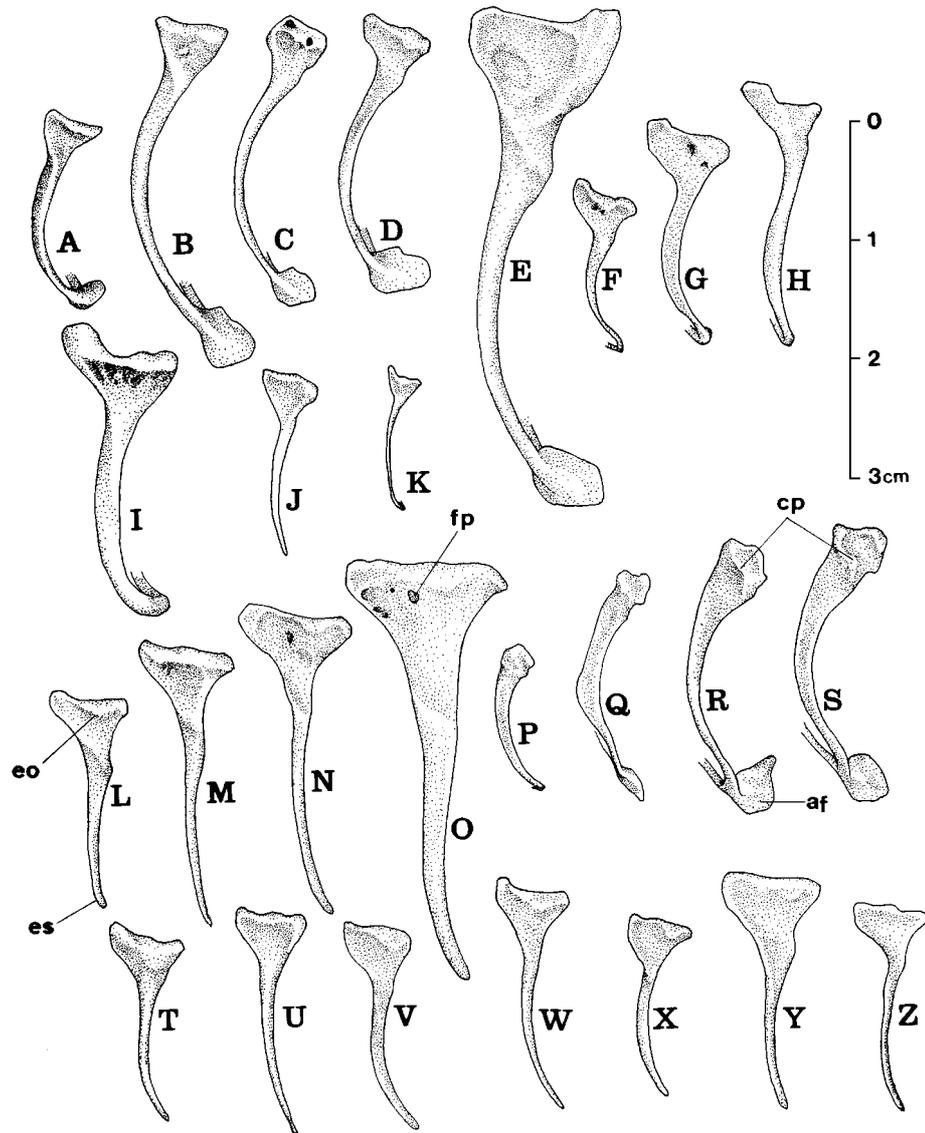


Fig. 1. Side view of the left clavicle: af – apophysis of the furcula; cp – coracoid process; eo – *omalis* extremity; es – sternal extremity; fp – pneumatic foramen; A – *Dendrocolaptes platyrostris*; B – *Grallaria varia*; C – *Pitangus sulphuratus*; D – *Turdus rufiventris*; E – *Corvus brachyrhynchus*; F – *Indicator minor*; G – *Indicator indicator*; H – *Picoides major*; I – *Campephilus robustus*; J – *Jynx torquilla*; K – *Picumnus cirratus*; L – *Bailloniidae baillonii*; M – *Selenidera maculirostris*; N – *Pteroglossus castanotis*; O – *Ramphastos tucanus*; P – *Galbula albirostris*; Q – *Nystalus chacuru*; R – *Monasa nigrifrons*; S – *Notharchus macrorhynchus*; T – *Capito niger*; U – *Semnornis ramphastinus*; V – *Trachyphonus vaillantii*; W – *Lybius bidentatus*; X – *Tricholaema hirsuta*; Y – *Psilopogon pyrolophus*; Z – *Megalaima haemacephala*.

Ceryle torquata (Fig. 2: KK), which are also alcedinids, the cranial projection is smaller. In the Momotidae (Fig. 2: MM), Trogonidae (Fig. 2: NN–OO) [classified as Coraciiformes by some authors: MAURER & RAIKOW (1981); CRACRAFT (1981)], in the orders Apodiformes (Fig. 2: PP), Caprimulgiformes (Fig. 2: QQ–SS), Strigiformes (Fig. 2: TT) and others not represented here, the *omalis* extremity of the clavicle tends to be slim, i.e. not craniocaudally expanded. The sternal extremity (*extremitas sternalis* Fig. 1: es) of the clavicle is relatively strong, with a large apoph-

ysis of the furcula (*hypocleideum*) in the Passeriformes (Fig. 1: A–E) and Bucconidae (Fig. 1: Q–S), especially *Monasa nigrifrons* (Fig. 1: R) and *Notharchus macrorhynchus* (Fig. 1: S). A small *hypocleideum* can be seen in the Trogonidae (Fig. 2: NN, OO), Caprimulgiformes (Fig. 2: QQ–SS) and Strigiformes (Fig. 2: TT). In the Picidae (Fig. 1: H–K), Indicatoridae (Fig. 1: F–G), Galbulidae (Fig. 1: P) and Coraciiformes (*sensu lato* – Fig. 2: AA–MM), the sternal extremity is tenuous and there is no *hypocleideum*. In *Jynx torquilla* (Fig. 1: J) the sternal extremity is very

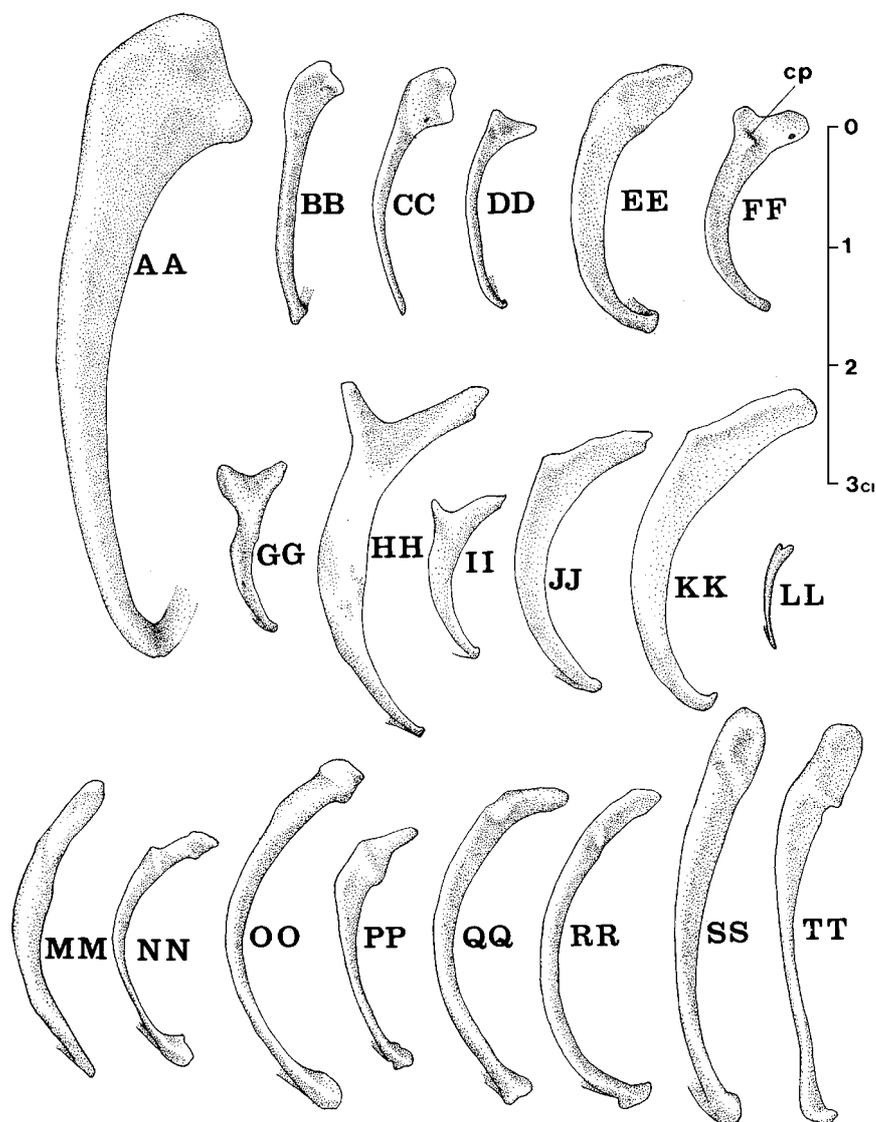


Fig. 2. Side view of the left clavicle: cp – coracoid process. AA – *Aceros undulatus*; BB – *Tockus erythrorhynchus*; CC – *Upupa epops*; DD – *Colius striatus*; EE – *Eurystomus orientalis*; FF – *Merops apiaster*; GG – *Alcedo atthis*; HH – *Dacelo novaeguineae*; II – *Chloroceryle americana*; JJ – *Chloroceryle amazona*; KK – *Ceryle torquata*; LL – *Todus subulatus*; MM – *Momotus momota*; NN – *Trogon surrucura*; OO – *Pharomachrus mocinno*; PP – *Streptoprocne zonaris*; QQ – *Lurocalis semitorquatus*; RR – *Nyctibius griseus*; SS – *Podargus strigoides*; TT – *Ciccaba virgata*.

thin, as it also is in *Picumnus cirratus*; no furcula was observed in the specimen examined, probably owing to damage during preparation.

STEINBACHER (1937) also observes a difference between the Galbulidae and Bucconidae as regards the presence of the apophysis of the furcula only in the latter family, and SHUFELDT (1891) had earlier noticed the absence of this apophysis in the Picidae.

The sternal extremity (*extremitas sternalis* – es) of the clavicle in the Ramphastidae (Fig. 1: L–O) and Capitonidae (Fig. 1: T–Z) is small, and the apex is slightly

skewed caudally. The two clavicles are distinctly separate and do not form a furcula.

OWEN (1854) is probably the first to have noticed that the clavicles in the toucans do not form a furcula and are attached to the sternum solely by collagenous ligaments. Later authors also mention this aspect of the clavicles (NEWTON 1896; BEDDARD 1898; STRESEMANN 1934; STEINBACHER 1937; VERHEYEN 1955; PRUM 1988).

In the Capitonidae (Fig. 1: T–Z), the shape of the clavicle is similar to that of the Ramphastidae. VERHEYEN

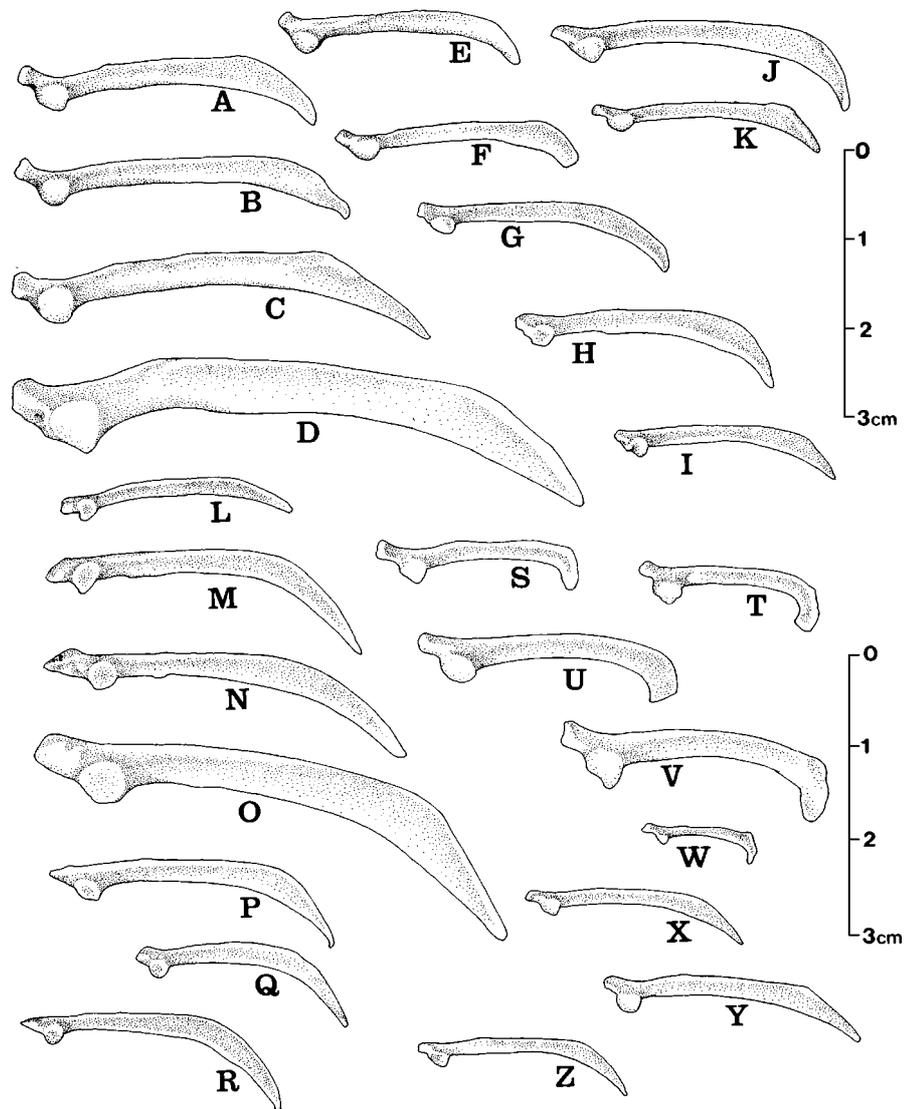


Fig. 3. Side view of the left scapula. A – *Baillonius baillonii*; B – *Selenidera maculirostris*; C – *Pteroglossus castanotis*; D – *Ramphastos tucanus*; E – *Semnornis ramphastinus*; F – *Capito niger*; G – *Trachyphonus vaillantii*; H – *Lybius bidentatus*; I – *Tricholaema hirsuta*; J – *Psilopogon pyrolophus*; K – *Megalaima haemacephala*; L – *Dendrocolaptes platyrostris*; M – *Gallaria varia*; N – *Tijuca atra*; O – *Pyroderus scutatus*; P – *Turdus rufiventris*; Q – *Philydor leucophrus*; R – *Chamaeza ruficauda*; S – *Picoides major*; T – *Piculus flavigula*; U – *Colaptes campestris*; V – *Campephilus robustus*; W – *Picumnus cirratus*; X – *Jynx torquilla*; Y – *Indicator indicator*; Z – *Indicator minor*.

(1955) reports that in some Old World capitonids, the two clavicles are connected ventrally by a slightly curved bone to form a furcula; even in adult individuals of a certain age, the junctions of this bone with the two clavicles remain distinct. VERHEYEN (op. cit.) also refers to the fact that in the genera *Megalaima*, *Pogoniulus*, and probably *Lybius*, the clavicles are similar to those of the Ramphastidae, i.e. short and shaped like a stiletto. PRUM (1988) observes the presence of this interclavicular bone in *Lybius torquatus*, calling it a “metaclavicle” and suggesting that it may be a “neomorphic character”. PRUM (op. cit.) also says there is no “metaclavicle” in the Neotropical Capitonidae, in the oriental genera *Megalaima* and *Psilopogon*, and in the Ethiopian genera *Buccanodon* and *Pogoniulus*. Among the capitonids examined for the present study, the “metaclavicle” was observed only in *Lybius dubius*; in some specimens, it may have been lost during preparation.

STEINBACHER (1937) notes that the clavicles in the Capitonidae present a weaker connection or are smaller in size, corresponding to only half that of the coracoids, with a membranous formation which extends as far as the sterno-clavicular ligament. STRESEMANN (1934) refers to this aspect in connection with *Capito* sp.

In recent birds, besides the Ramphastidae and some Capitonidae, NEWTON (1896) reports the clavicles being united by cartilage or fibrous tissue in *Ocydromus* (= *Gallirallus*), *Cariama*, *Didus* (= *Raphus*), *Carpophaga* (= *Ducula*), many Psittacidae and Strigidae, the Musophagidae, *Buceros* and *Alcedo*. In small psittacids of the genera *Agapornis* and *Neophema* (FÜRBRINGER 1888; BEDDARD 1898; BELLAIRS & JENKIN 1960; pers. obs.), the clavicle is confined to the *omalis* extremity. In *Cariama cristata* (Cariamidae), *Alcedo atthis* (Acedinidae) and *Ducula aenea* (Columbidae), we observed that the clavicles meet medially to form the furcula. In a study of the anatomy of the Columbidae, GARROD (1874) makes no reference to the absence of a furcula in any species. The absence of clavicles has been noted in the ratites and also in *Mesitornis* (Mesitornithidae) (NEWTON 1896; BEDDARD 1898).

3.2. Scapula

The body of the scapula is a narrow, curved (or slightly curved) blade-shaped bone, especially in the Passeriformes, and also in the Picidae, Indicatoridae, Ramphastidae and Capitonidae (Fig. 3). In the latter, the acromial process is relatively large with a truncated apex, giving the scapula an almost quadrangular shape. In many passeriforms, however, the acromial process is obliquely truncated, forming an apex with a more pointed tip (Fig. 3: N, P, R).

In the Ramphastidae, the acromial process is large and slightly skewed toward the dorsum (Fig. 3: A–D). The cranial extremity of this process is articulated with the clavicle, which (as mentioned above) presents a cranial expansion at the *omalis* extremity. The subacromial region (between the acromion and the *facies articularis humeralis*) in the Ramphastidae is almost always perforated by pneumatic foramina.

In the Capitonidae the scapula is similar to that of the Ramphastidae, except that the caudal region of the blade is more markedly curved (Fig. 3: E–K), and most species do not have pneumatic foramina. Subacromial pneumatic foramina were found only in *Semnornis ramphastinus*.

In both species of the Indicatoridae examined (Fig. 3: Y–Z), the scapula is also similar to that of the Ramphastidae, with the addition of subacromial pneumatic foramina in *Indicator indicator*. However, the acromial process lacks the dorsal projection found in the Ramphastidae and is more cranially projected.

In the Picidae, including *Picumnus* (Fig. 3: S–W), the caudal portion of the scapula is sharply curved (nearly 90°), suggesting a shared character in the family, while in *Jynx* (Fig. 3: X) it is shaped like those of the Indicatoridae (Fig. 3: Y, Z) and other piciforms.

Subacromial pneumatic foramina were found in eight genera of woodpeckers examined (*Campephilus*, *Celeus*, *Picoides*, *Veniliornis*, *Piculus*, *Colaptes*, *Melanerpes* and *Dryocopus*); they were absent in *Jynx torquilla* and *Picumnus cirratus*. According to BELLAIRS & JENKIN (1960), small birds such as these two species are less pneumatized than large ones. The acromial process in the Picidae is developed, as it is in the Ramphastidae, but in several genera, especially *Jynx*, it is cranially projected.

In the Galbulidae (Fig. 4: AA) and Bucconidae (Fig. 4: BB–DD), the scapula is more rectilinear in shape, although the caudal region is ventrally curved to a slight extent, and hence resembles some coraciiforms such as *Leptosomus*, *Upupa*, *Phoeniculus*, *Dacelo*, and *Tockus* among others. No subacromial pneumatic foramina were found in either family, except for one specimen of *Nystalus chacuru* which had a tiny foramen in the left scapula.

In *Upupa epops* (Fig. 4: EE; Upupidae) and in *Phoeniculus purpureus*, the scapula has an almost rectilinear blade, similar to that of the Bucconidae, and a large subacromial pneumatic foramen. At the costal margin, the acromion, which is of moderate size, forms at its base a ramification that gives rise to a second, ventromedially positioned, process (vp) which is articulated with the extremity of the procoracoid process of the coracoid, as exemplified for *Ceryle torquata* in Fig. 8.

In the Bucerotidae (Fig. 4: FF), the body of the scapula is similar to that of *Leptosomus discolor* (Fig. 4: GG; Leptosomidae) and also presents a ventromedial process (vp). In *Aceros undulatus* there are small subacromial pneumatic foramina, while in *Tockus erythrorhynchus* there are none. Both the ventromedial process and pneumatic foramina at the apex of the acromion are found in *Merops apiaster* (Fig. 4: II; Meropidae) where the scapula is more curved.

In the Alcedinidae (Fig. 4: KK–OO), the cranial portion of the scapula is rectilinear, while the caudal portion often forms sharp angles at various levels and has a ventrally directed apex. The ventromedial process is pronounced (vp – Fig. 8) in this group, as it is in the Momotidae (Fig. 4: QQ) and Todidae (Fig. 4: PP). In the latter two families, the general appearance of the scapula is similar to that of the Alcedinidae.

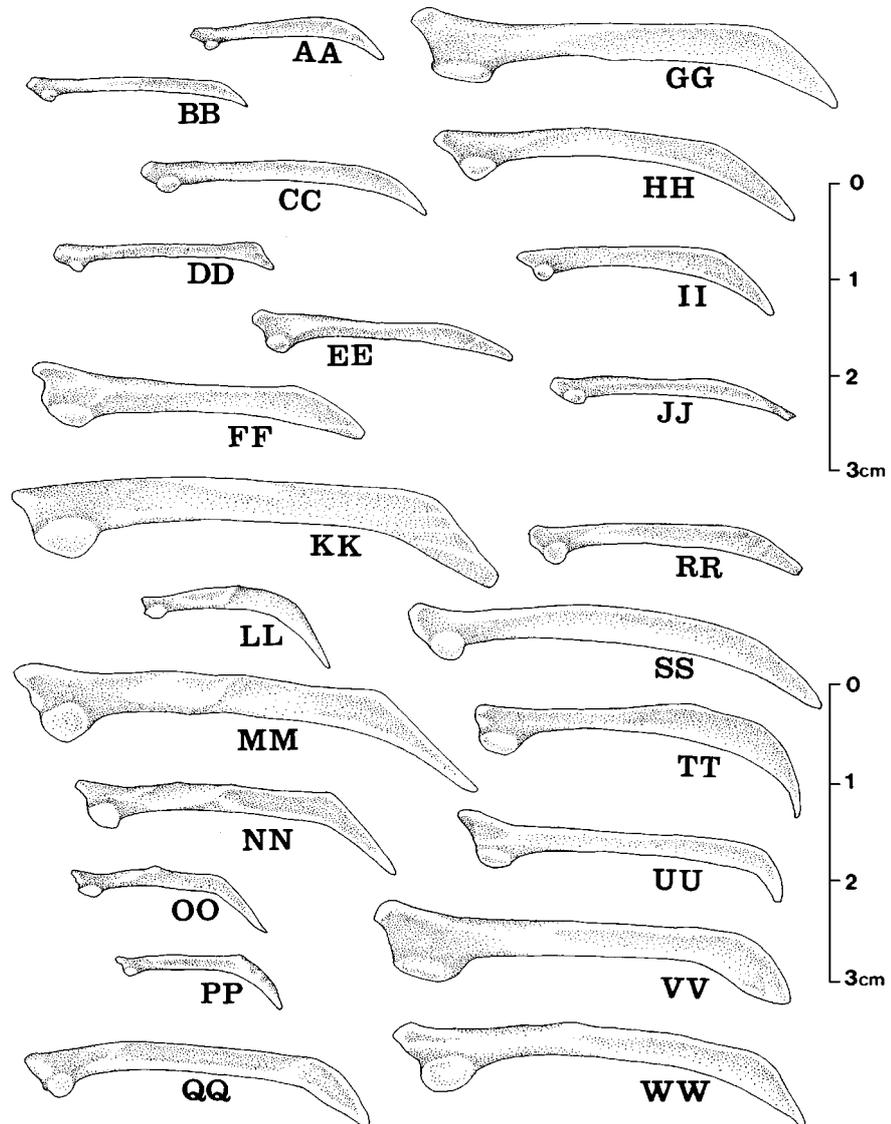


Fig. 4. Side view of the left scapula. AA – *Galbula albirostris*; BB – *Malacoptila rufa*; CC – *Monasa nigifrons*; DD – *Nyctalus chacuru*; EE – *Upupa epops*; FF – *Tockus erythrorhynchus*; GG – *Leptosomus discolor*; HH – *Eurystomus orientalis*; II – *Merops apiaster*; JJ – *Colius striatus*; KK – *Dacelo novaeguineae*; LL – *Alcedo atthis*; MM – *Ceryle torquata*; NN – *Chloroceryle amazona*; OO – *Chloroceryle americana*; PP – *Todus subulatus*; QQ – *Momotus momota*; RR – *Trogon surrucura*; SS – *Pharomachrus mocinno*; TT – *Nyctibius griseus*; UU – *Lurocalis semitorquatus*; VV – *Podargus strigoides*; WW – *Ciccaba virgata*.

In the Trogonidae (Fig. 4: RR and SS), the scapula is slightly curved throughout its length; the acromial process is small and lacking in a ventromedial process.

In the Caprimulgiformes (Fig. 4: TT–VV) and Strigiformes (Fig. 4: WW), the body of the scapula tends toward a flat or moderately curvaceous blade-like shape, and the acromion lacks the ventromedial process that occurs in several groups of the Coraciiformes.

A large pneumatic foramen at the extremity of the acromion is found only in the Strigiformes.

3.3. Coracoid

The third element of the scapular girdle, the coracoid, is the strongest bone in the entire structure. The *omalis* extremity presents a complex articular region compris-

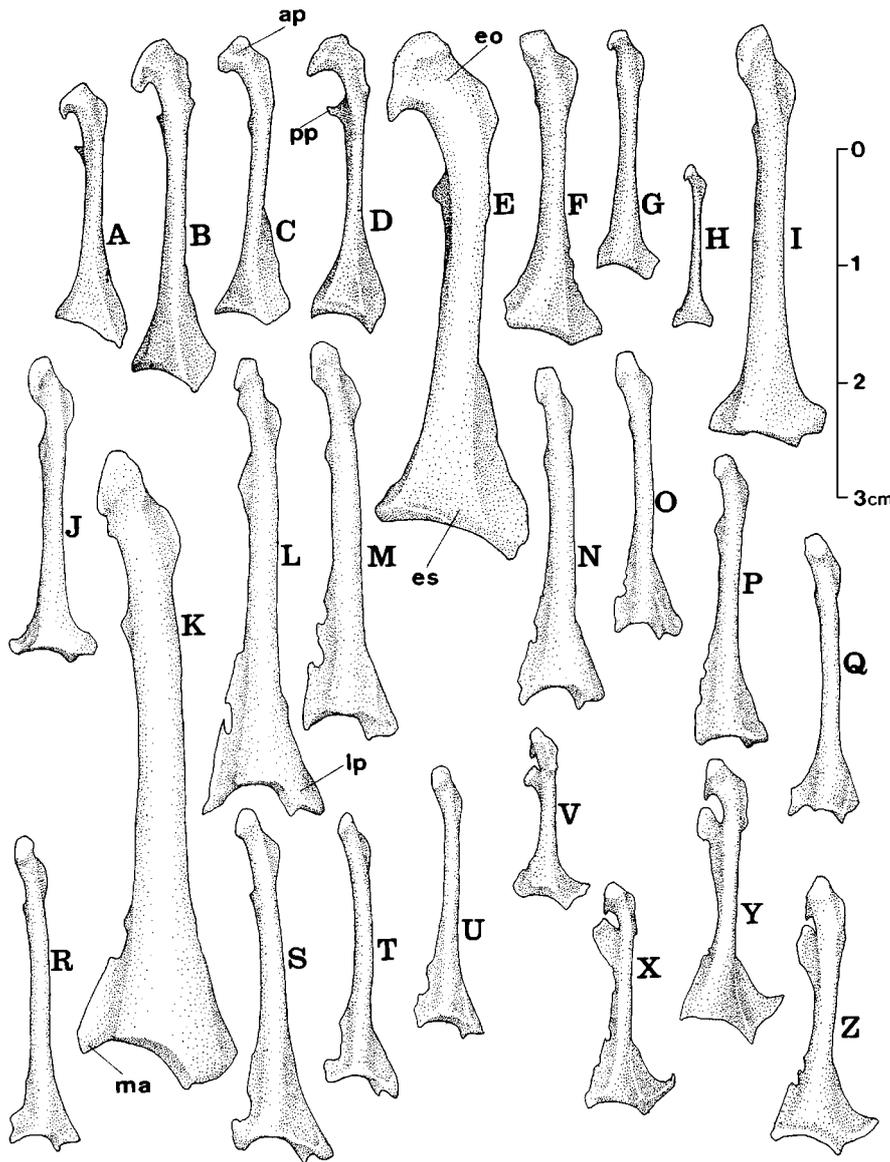


Fig. 5. Ventral view of the left coracoid: ap – acrocoracoid process; eo – *omalis* extremity; es – sternal extremity; lp – lateral process; ma – medial angle; pp – procoracoid process. A – *Dendrocolaptes platyrostris*; B – *Grallaria varia*; C – *Turdus rufiventris*; D – *Pitangus sulphuratus*; E – *Corvus brachyrhynchus*; F – *Indicator indicator*; G – *Jynx torquilla*; H – *Picumnus cirratus*; I – *Campephilus robustus*; J – *Picoides major*; K – *Ramphastos tucanus*; L – *Pteroglossus castanotis*; M – *Selenidera maculirostris*; N – *Bailloniopsis baillonii*; O – *Capito niger*; P – *Semnormis ramphastinus*; Q – *Trachyphonus vaillantii*; R – *Lybius bidentatus*; S – *Psilopogon pyrolophus*; T – *Megalaima haemacephala*; U – *Tricholaema hirsuta*; V – *Galbula albirostris*; X – *Nystalus chacuru*; Y – *Monasa nigrifrons*; Z – *Notharchus macrorhynchus*.

ing the clavicle, scapula and humerus. The three bones of the scapular girdle are bound together by a complex system of ligaments which also joins them to the fore limb.

The coracoid has a procoracoid process (pp – Fig. 5: D) near the *omalis* extremity. This process is the main element in the formation of the triosseous canal, of which the scapula and clavicle also form part of the walls of this canal, permitting passage of the tendon of the *supracoracoideus* muscle which inserts on the dor-

sal margin of the humerus. In many birds, only the procoracoid process and the scapula form the canal for this tendon, while in others this conduit is formed by the procoracoid process alone (FÜRBRINGER 1888; BAUMEL et al. 1993). In the latter case, the procoracoid process merges with the medial region of the acrocoracoid process (ap – Fig. 5: C), termed the brachial tuberosity (bt – Fig. 9) by HOWARD (1929) and GILBERT et al. (1981), as can be observed in *Tockus erythrorhynchus* (Fig. 6: FF), *Upupa epops* (Fig. 6: GG),

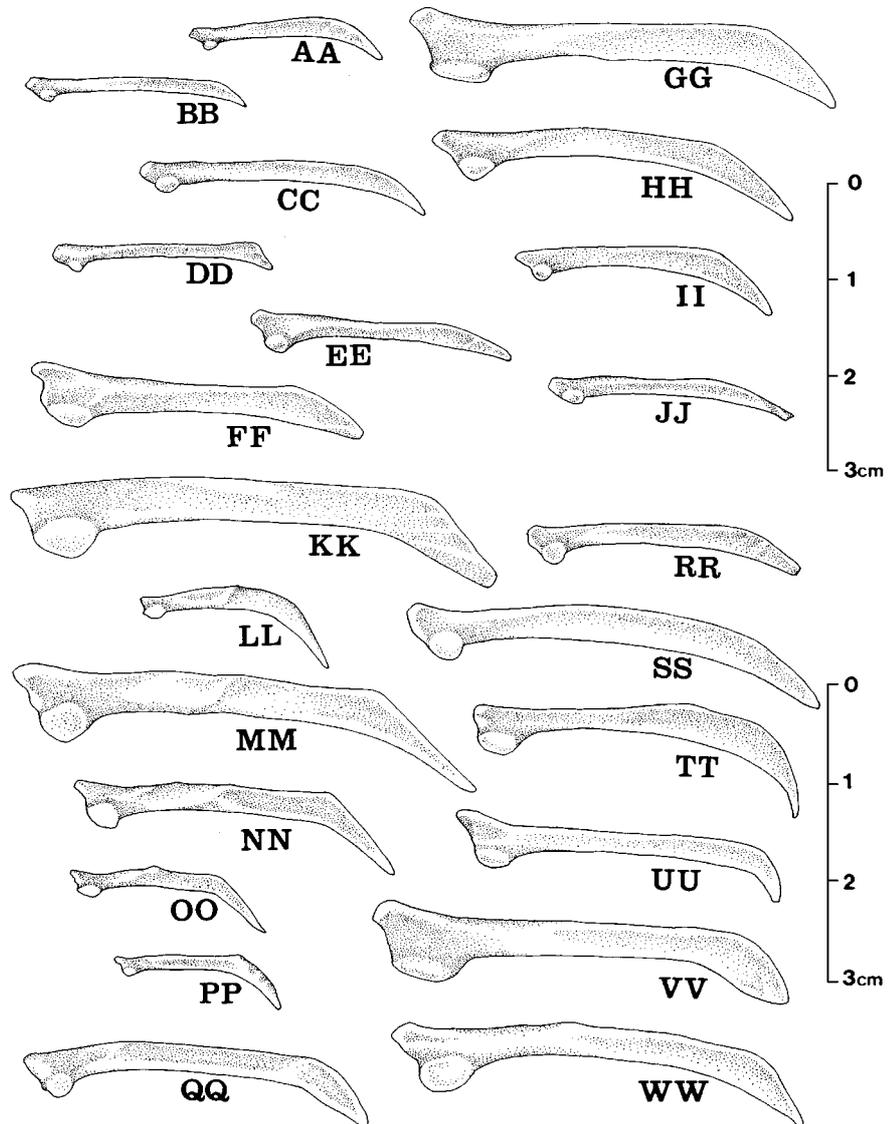


Fig. 6. Ventral view of the left coracoid: ap – acrocoracoid process; pp – procoracoid process. AA – *Eurystomus orientalis*; BB – *Brachypteracias leptosomus*; CC – *Leptosomus discolor*; DD – *Colius striatus*; EE – *Aceros undulatus*; FF – *Tockus erythrorhynchus*; GG – *Upupa epops*; HH – *Alcedo atthis*; II – *Dacelo novaeguineae*; JJ – *Ceryle torquata*; KK – *Chloroceryle amazona*; LL – *Chloroceryle americana*; MM – *Todus subulatus*; NN – *Momotus momota*; OO – *Merops apiaster*; PP – *Trogon surrucura*; QQ – *Pharomachrus mocinno*; RR – *Streptoprocne zonaris*; SS – *Lurocalis semitorquatus*; TT – *Ciccaba virgata*; UU – *Nyctibius griseus*; VV – *Podargus strigoides*.

Phoeniculus purpureus and *Alcedo atthis* (Fig. 6: HH). In the Ramphastidae, the coracoid is characterized by a narrow, elongated body (Fig. 5: K–N), with an elongated acrocoracoid process that forms a discreet angle with the axis of the body. The procoracoid process is very small; the sternal extremity of the coracoid presents a strongly curvaceous articular margin, accentuated by the medial angle (ma – Fig. 5) and the lateral process (lp – Fig. 5: L), both of which expand ventrally toward the sternum.

In the Capitonidae (Fig. 5: O–U), the coracoid has the same configuration as that found in the Ramphastidae, but the lateral process is usually somewhat more devel-

oped. In the Indicatoridae (Fig. 5: F) and Picidae (Fig. 5: G–J), the coracoid is somewhat more elongated. At the sternal extremity the medial angle and lateral process are more discreet and do not project ventrally. In the Passeriformes (Fig. 5: A–E), which also have a coracoid with an elongated body, the procoracoid process is somewhat more pronounced and the sternal extremity more expanded; the most conspicuous characteristic is the medial portion of the elongated acrocoracoid process on the side of the procoracoid process.

In the Galbulidae (Fig. 5: V) and Bucconidae (Fig. 5: X–Z), the coracoid differs from those of other Piciformes by having a more expanded sternal extremity, forming a large lateral process; the *omalis* extremity forms a medial expansion ventrally skewed toward the procoracoid process, as in the Passeriformes (Fig. 5: A–E), and this latter process is far broader and more developed.

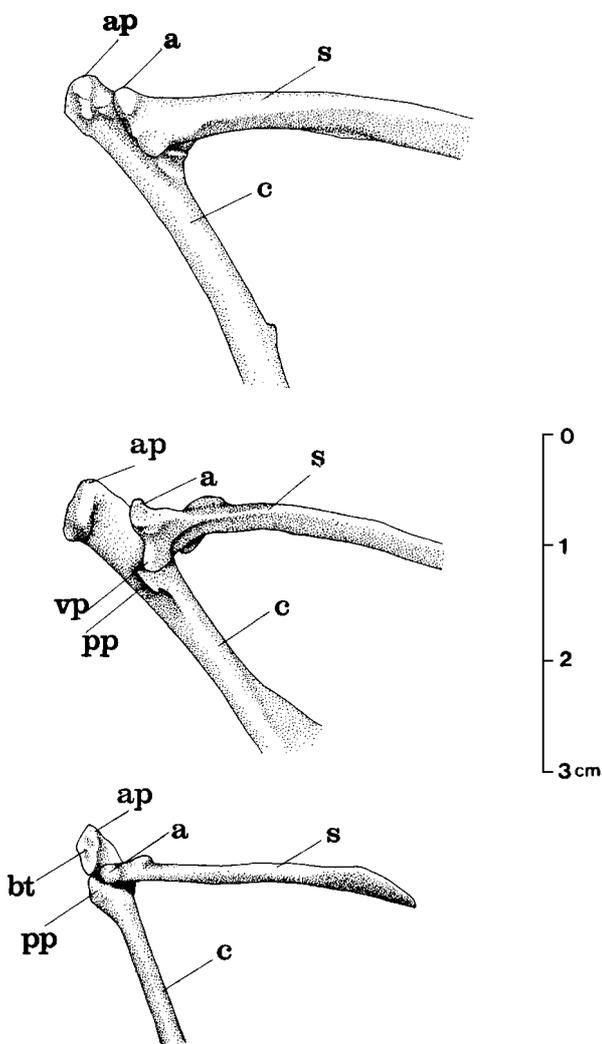
In general, the Coraciiformes (Fig. 6: AA–OO), Trogoniformes (Fig. 6: PP–QQ), Apodiformes (Fig. 6: RR), Caprimulgiformes (Fig. 6: SS, UU, VV) and Strigiformes (Fig. 6: TT), have an elongated procoracoid process developed similar to that found in the Bucconidae and Galbulidae.

A noteworthy characteristic is the absence of the coracoid foramen in all the Piciformes, Passeriformes, Coraciiformes, Trogoniformes and Coliiformes, whereas this foramen is apparently present in most orders of birds. Indeed, this may be a common character in these groups; however, in *Leptosomus discolor* (Coraciiformes), this foramen is evident. On the other hand, the coracoid foramen is not found in other discrete groups such as the Galliformes (HOLMAN 1964) and Ardeidae (pers. obs.).

4. CONCLUSIONS

A number of homologous characters found in the three osseous elements of the shoulder girdle, that support some assertions of relationship between the piciforms and related groups; these are: 1) the shape of the both extremities of the clavicle and coracoid; 2) the presence of the furcula and *hipocleideum*; 3) the shape of the scapular lamina; 4) the presence of the ventromedial process of the scapula; 5) the development of the procoracoid process and 6) the presence of the coracoid foramen. The analysed characters allowed the following conclusions:

a) The monophyly of the Pici. The Picidae, Indicatoridae, Capitonidae, and Ramphastidae form a fairly homogeneous group that must be monophyletic, and constitute the “genuine” representatives of the order Piciformes. The analysis also shows that the Ramphastidae are closely akin to the Capitonidae, while the Indicatoridae are directly related to the Picidae.



Figs. 7–9. Right scapulo-coracoid articulation, medial view: **7.** *Ramphastos dicolorus*. **8.** *Ceryle torquata*. **9.** *Notarchus macrorhynchus*: a – acromion; ap – acrocoracoid process; bt – brachial tuberosity; c – coracoid; pp – procoracoid process; s – scapula; vp – ventromedial process of the acromion.

In the Ramphastidae and Capitonidae, the sternal extremities of the clavicles are short and slender and do not meet to form a furcula; however, in some Asian and African Capitonidae the two clavicles are joined by a slightly curved bone called the "metaclavicle" (PRUM, 1988), which seems to be a structure worthy of further ontogenetic study and understanding as to its phylogenetic value. The general morphology of the clavicle, scapula and coracoid is very similar between the members of these two families.

On the other hand, the Picidae and Indicatoridae present complete clavicles, which meet at the sternum forming a furcula. The general format of the clavicle is very similar in the two families, differing from that of the Ramphastidae and Capitonidae, not only due to the furcula but also by the cranial expansion in the omalis extremity being much more prominent. The coracoid morphology of the Indicatoridae also brings them closer to the Picidae.

b) Monophyly of the Bucconidae and the Galbulidae. The clavicles with the apex of the omalis extremity rounded off and the prominent crest forming the coracoid process, besides the straight scapula and the coracoid with the procoracoidal process expanded into a laminar form and a pointed lateral process, are some of the characters which bring these two families close together, thus supporting the monophyletic hypothesis.

c) Non-relationship between the Pici and the Galbuloidea. The traditional concept whereby the order Piciformes is composed of the suborders Pici and Galbuloidea has no foundation when based on the morphology of the shoulder girdle. On the contrary, in the present study, these two groups do not present any characteristic which suggests this relationship.

d) Relationship of the Galbuloidea to the Coraciiformes. The characters observed on the shoulder girdle of the Galbulidae and Bucconidae, show a pronounced similarity to those in the Brachypteraciidae, Coraciidae and Meropidae. The similarity of the coracoid of the Bucconidae, Brachypteraciidae and Coraciidae, is especially outstanding, as OLSON (1983) had already noted. It appears to us evident that the Galbuloidea should be included amongst the Coraciiformes or, as concluded by SIBLEY & AHLQUIST (1990), in a distinct order, the Galbuliformes.

e) Relationship of the Piciformes to the Passeriformes. The above presented conclusions based on shoulder girdle morphology are quite close to the conclusions of SIBLEY & AHLQUIST (1990) which are centered on DNA hybridization. However, as to their phylogenetically placing the Passeriformes quite apart from the Piciformes, we herein note some characters shared by these two orders which appear to suggest the opposite. Representatives of both orders possess: (1) the triangular shaped omalis extremity of the clavicle, (2) dis-

tinctly truncated at the apex, and (3) with relatively abundant pneumatic foramina; (4) a very slender and elongated coracoid, almost rounded in transversal section at the middle, with a (5) much reduced procoracoid process; (6) the general morphology of the scapula, even though not contributing much in the present study, is much the same in the two groups.

f) Monophyly of the Coraciiformes. Most of the Coraciiformes share a scapula with a very rectilinear cranial half, besides a ventromedial process which is articulated to the extremity of the procoracoid process of the coracoid. In the clavicles of the Coraciiformes, the apex of the omalis extremity is usually rounded off. The more typical structure of the coracoid of the Coraciiformes appears to be: at the sternal extremity, the procoracoid process is wide and flat forming together with the main part of the coracoid a groove for the tendon of the supracoracoid muscle; this description of the coracoid can be especially applied to the Brachypteraciidae, Coraciidae, Meropidae, Upupidae, and also *Alcedo atthis* amongst the Alcedinidae. In the remaining Alcedinidae, Momotidae, Todidae and Bucerotidae this basic architecture appears to have become modified through a lengthening of the coracoid and a reduction of the procoracoid process.

g) Non-relationship between the Trogonidae and Coraciiformes. The scapula of the Trogonidae does not present a rectilinear cranial part as it is found in the Coraciiformes. The ventromedial process is also absent. The omalis extremity of the Trogonidae clavicle is almost always expanded which is not so in the Coraciiformes. The procoracoidal process of the Trogonidae coracoid is not laminar and wide as in the Coraciiformes. In the sternal extremity of the coracoid, the lateral and medial process are expanded and rounded off in the Trogonidae, different from what we observed in the Coraciiformes. Such characters separate very well the Trogonidae from the Coraciiformes, opposite to the opinions of MAURER & RAIKOW (1981) and CRACRAFT (1981), and this leads us to accept this family as being placed in its own order, the Trogoniformes.

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REFERENCES

- AVISE, J. C. & AQUADRO, C. F. (1987): Malate dehydrogenase isozymes provide a phylogenetic marker for the Piciformes (woodpeckers and allies). *Auk* **104**: 324–328.
- BAUMEL, J. J., KING, A. S., BREAZILE, J. E., EVANS, H. E. & BERGE, J. C. V. eds. (1993): *Handbook of avian anatomy: Nomina anatomica avium*. Cambridge, Nuttall Ornithological Club. 779 p.
- BEDDARD, F. E. (1898): *The structure and classification of birds*. London, Longmans. 548 p.
- BELLAIRS, A. D'A. & JENKIN, C. R. (1960): *The skeleton of birds*. Pp. 241–300 in: MARSHALL, A. J. (ed.) *Biology and comparative physiology of birds*. New York, Academic Press. v. 1.
- BLEIWEISS, R., KIRSCH, J. A. W. & LAPOINTE, F.-J. (1994): DNA-DNA hybridization-based phylogeny for "higher" nonpasserines: reevaluating a key portion of the avian family tree. *Mol. Phylogenet. Evol.*, Orlando, **3**: 248–255.
- BURTON, P. J. K. (1984): Anatomy and evolution of the feeding apparatus in the avian orders Coraciiformes and Piciformes. *Bull. Br. Mus. nat. Hist. Zool.*, London, **47**: 331–443.
- CRACRAFT, J. (1971): The relationship and evolution of the rollers: families Coraciidae, Brachipteraciidae and Leptosomatidae. *Auk* **88**: 723–752.
- CRACRAFT, J. (1981): Toward a phylogenetic classification of the recent birds of the world (Class Aves). *Auk* **98**: 681–714.
- FEDUCCIA, A. (1977): A model for the evolution of perching birds. *Syst. Zool.*, New York, **26**: 19–31.
- FEDUCCIA, A. (1979): Comments on the phylogeny of perching birds. *Proc. Biol. Soc. Wash.* **92**: 689–696.
- FÜRBRINGER, M. (1888): *Untersuchungen zur Morphologie und Systematik der Vögel zugleich ein Beitrag zur Anatomie der Stütz und Bewegungsorgane*. 1751 pp. Amsterdam, T. J. Van Holkema.
- GADOW, H. (1896): Muscular system. Pp. 602–620 in: NEWTON, A. (ed.) *A dictionary of birds*. London, Adam & Charles Black.
- GARROD, A. H. (1874): On some points in the anatomy of the Columbæ. *Proc. zool. Soc. Lond.*, 249–259.
- GILBERT, M., MARTIN, L. D. & SAVAGE, H. G. (1981): Avian osteology. 252 pp. Laramie, B. Miles Gilbert.
- HENLEY, C., FEDUCCIA, A. & COSTELLO, D. P. (1978): Oscine spermatozoa: a light- and electronmicroscopy study. *Condor* **80**: 41–48.
- HOLMAN, J. A. (1964): Osteology of gallinaceous birds. *Q. Jl. Fla. Acad. Sci.* **27**: 230–252.
- HOWARD, H. (1929): The avifauna of Emeryville shellmound. *Univ. Calif. Publ. Zool.* **32**: 301–394.
- LANYON, S. C. & ZINK, R. M. (1987): Genetic variation in Piciform birds: monophyly and genera and familial relationships. *Auk* **104**: 724–732.
- LANYON, S. C. & HALL, J. G. (1994): Reexamination of barbet monophyly using mitochondrial-DNA sequence data. *Auk* **111**: 389–397.
- LOWE, P. R. (1946): On the systematic position of the woodpeckers (Pici), honey-guides (Indicator), hoopoes and others. *Ibis* **88**: 103–126.
- MAURER, D. R. & RAIKOW, R. J. (1981): Appendicular myology, phylogeny, and classification of the avian order Coraciiformes (including Trogoniformes). *Ann. Carneg. Mus.* **50**: 417–434.
- MAYR, E. & AMADON, D. (1951): A classification of recent birds. *Am. Mus. Novit.* **1494**: 1–42.
- MONROE Jr., B. L. & SIBLEY, C. G. (1993): *A world checklist of birds*. 393 pp. New Haven, Yale University Press.
- MORONY Jr., J. J., BOCK, W. J. & FARRAND Jr., J. (1975): *Reference list of the birds of the world*. 207 pp. American Museum of Natural History, Department of Ornithology.
- NEWTON, A. (1896): *A dictionary of birds*. 1087 pp. London, Adam & Charles Black.
- OLSON, S. L. (1982): A critique of Cracraft's classification of birds. *Auk* **99**: 723–739.
- OLSON, S. L. (1983): Evidence for polyphyletic origin of the Piciformes (Aves). *Auk* **100**: 126–133.
- OWEN, R. (1854): Observations on the anatomy of the toucan. 160 pp. in: GOULD, J. (ed.) *A monograph of the Ramphastidae or family of toucans*. Belém, JARI Companhia Florestal Monte Dourado. Fac-simile 2. ed., 1992.
- PRUM, R. O. (1988): Phylogenetic interrelationships of the barbets (Aves: Capitonidae) and toucans (Aves, Ramphastidae) based on morphology with comparisons to DNA-DNA hybridization. *Zool. J. Linn. Soc.* **92**: 313–343.
- RAIKOW, R. J. (1982): Monophyly of the Passeriformes: test of a phylogenetic hypothesis. *Auk* **99**: 431–445.
- RAIKOW, R. J. & CRACRAFT, J. (1983): Monophyly of the Piciformes: a reply to Olson. *Auk* **100**: 134–138.
- SHUFELDT, R. W. (1891): On the question of saurognathism of the Pici, and other osteological notes upon that group. *Proc. Zool. Soc. Lond.* 122–9.
- SHUFELDT, R. W. (1900). On the osteology of woodpeckers. *Proc. Am. philos. Soc.* **39**: 578–622.
- SIBLEY, C. G. & AHLQUIST, J. E. (1972): A comparative study of the egg-white proteins of non-passerine birds. *Bull. Peabody Mus. nat. Hist.* **39**: 1–276.
- SIBLEY, C. G. & AHLQUIST, J. E. (1990): *Phylogeny and classification of birds*. 976 pp. New Haven, Yale University Press.
- SIBLEY, C. G., AHLQUIST, J. E. & MONROE Jr., B. L. (1988): A classification of the living birds of the world based on DNA-DNA hybridization studies. *Auk* **105**: 409–423.
- SIBLEY, C. & MONROE Jr., B. L. (1990): *Distribution and taxonomy of birds of the world*. 1111 pp. New Haven, Yale University Press.
- SIMPSON, S. F. & CRACRAFT, J. (1981): The phylogenetic relationships of the Piciformes (Aves). *Auk* **98**: 481–494.
- STEINBACHER, G. (1935): Funktionell-anatomische Untersuchungen an Vögelfüßen mit Wendezehen und Rückzehen. *J. Ornithol.* **83**: 214–282.
- STEINBACHER, J. (1937): Anatomische Untersuchungen über die Systematische Stellung der Galbulidae und Bucconidae. *Arch. Naturgesch.* **6**: 417–515.
- STRESEMANN, E. (1934): Sauropsida: Aves. in: KRUMBACH, T. (ed.) *Handbuch der Zoologie*. Berlin, Walter de Gruyter. v. 7, pt. 2.
- SWIERCZEWSKY, E. V. & RAIKOW, R. J. (1981): Hind limb morphology, phylogeny and classification of the Piciformes. *Auk* **98**: 466–480.
- VERHEYEN, R. (1955): Contribution à la systématique des Piciformes basée sur l'anatomie comparée. *Bull. Inst. R. Sci. Nat., Belg.* **31**: 1–43.

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