

Cranial Osteology in Momotidae (Aves: Coraciiformes)

Márcia C. Pascotto^{1*} and Reginaldo J. Donatelli²

¹Departamento de Zoologia, IB/USP, Cidade Universitária, São Paulo, Brasil 05508-900

²Laboratório de Vertebrados, Departamento de Ciências Biológicas, FC, Universidade Estadual Paulista, São Paulo, Brasil 17033-360

ABSTRACT Momotidae (motmots) is found throughout Latin America between Mexico and northern Argentina. Given the absence of detailed studies of cranial osteology of Momotidae in the literature, this article presents a comprehensive description of the variation of the cranial osteology in all nine species of Momotidae and compares the results with published studies of other families of Coraciiformes and families in other orders. In addition, the cranial structures described are related to ecological and behavioral aspects of Momotidae. The cranial osteology of *Baryphthengus ruficapillus* is described in detail and compared with other species of Momotidae. The results indicate the presence in Momotidae of modified cranial structures, among which the most conspicuous are the frontal, lacrimal, squamosal, orbital, and laterosphenoid regions, as well as the palatine, upper jaw, pterygoid, and mandible. *J. Morphol.* 258:32–48, 2003.

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KEY WORDS: Aves; Coraciiformes; Momotidae; cranial osteology; jaw osteology

Momotidae (Coraciiformes), motmots, have a strong curved bill with tomia that are more or less serrated, depending on the species. All species in the family share the following peculiarities: spatula-shaped extremities of the central pair of rectrices (a small apical subportion of which has no barbs, except in *Baryphthengus ruficapillus*, *Aspatha gularis*, and *Hylomanes momotula*); a black facial mask; and typically a large black spot on the breast (Sick, 1997). There is no sexual dimorphism in plumage coloring (Verheyen, 1955; Sibley and Ahlquist, 1990; Sick, 1997).

Momotidae are exclusively neotropical. They are found throughout Latin America between Mexico and northern Argentina (Meyer de Schauensee, 1970; Gill, 1990; Sibley and Ahlquist, 1990; Forshaw, 1998; del Hoyo et al., 2001). Their preferred habitat is tropical forest (Fry et al., 1988).

Motmots feed mainly on arthropods, fruits, and small vertebrates. Insects are the main food item for *Eumomota superciliosa*, *Electron platyrhynchum*, *Hylomanes momotula*, and *Aspatha gularis*. *Baryphthengus ruficapillus* and *Momotus momota* feed either on fruits or insects, the latter being the main component of their diet (Remsen et al., 1993).

Orejuela (1980) related size and morphology of the bill with the size of prey taken by two Momotidae species: *Eumomota superciliosa* prefers small prey due to its long, wide, light, and finely serrated bill compared to *Momotus momota*. The latter is able to eat large prey due to its short, narrow, thick, and deeply serrated bill, which seems suited for crushing large insects. Remsen et al. (1993) observed that the wide and flattened bill of *Electron platyrhynchum* is similar to several tyrant flycatchers, specially *Todirostrum* and *Platyrinchus*, both exclusively insectivorous that sally to forage to capture arthropods.

Momotidae foraging strategy is quite similar to the Galbulidae: they perch fairly low on exposed branches, dart out after insects, and return to their starting point (Sick, 1997). Motmots hold prey with their bill and hit the prey against the branch either to immobilize or to kill it before swallowing or giving it to their nestlings (Skutch, 1964). *Baryphthengus martii* was seen searching for crabs and fishes in a manner similar to kingfishers (Remsen et al., 1993).

Similar to the Alcedinidae, motmots excavate holes in vertical banks to build their nests. They use their feet and bill in excavation; their holes can reach 60 cm up to 2 m deep. During courtship, motmots are able to use tools, such as dry leaves and dead twigs, with their bill when competing for a mate (Skutch, 1964).

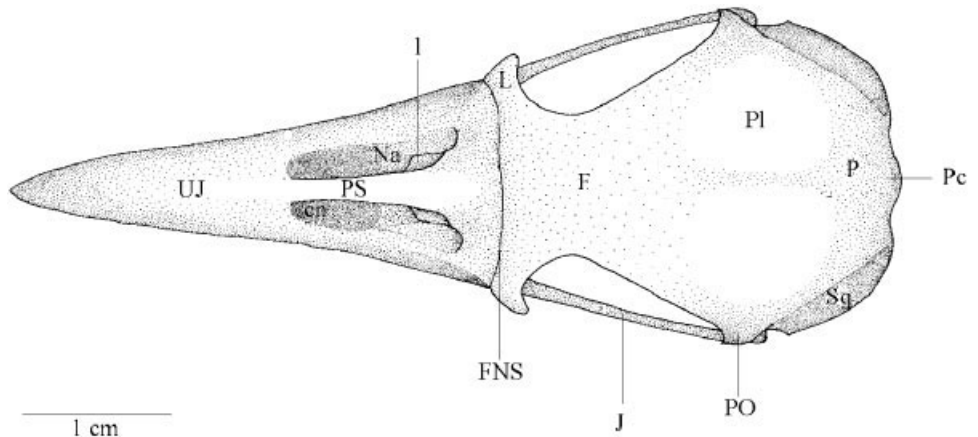
However, few anatomical studies of Coraciiformes have been performed. Most are merely descriptive, comparing a small number of bone structures or emphasizing the myology of some species or groups. Examples include the studies of Sclater (1865) and Murie (1872), as well as more recent work by Lowe (1948), Cracraft (1971), Burton (1984), and Maurer and Raikow (1981). Almost all of these studies are

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*Correspondence to: Márcia Cristina Pascotto, Caixa Postal 181, São Manuel, São Paulo, Brasil 18650-000.
E-mail: mcpascot@hotmail.com

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Fig. 1. Dorsal view of skull in *Momotus mexicanus*. cn, concavity of the nostril; F, frontal region; FNS, frontonasal suture; J, jugal arch; L, lacrimal region; l, lamina of the postnasal foramen; Na, external naris; P, parietal region; Pc, *Prominentia cerebellaris*; Pl, parietal lobes; PO, *Proc. postorbitalis*; PS, *Pila supranasalis*; Sq, squamosal region; UJ, upper jaw.



still insufficient with regard to both the anatomical features described and the number of species analyzed.

The purpose of this study was to compare the variation in cranial osteology, to produce a detailed comparative description of cranial osteology in all nine species: *Baryphthengus ruficapillus*, *Baryphthengus martii*, *Momotus momota*, *Momotus mexicanus*, *Electron platyrhynchum*, *Electron carinatum*, *Eumomota superciliosa*, *Aspatha gularis* and *Hylomanes momotula*, and to compare the results with published studies of other families of Coraciiformes and families in other orders.

MATERIALS AND METHODS

This study is based on 25 adult specimens covering all species of Momotidae. Skulls and mandibles came from the collections of the Museu Paraense Emílio Goeldi, Belém, Pará, Brasil (MPEG); National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM); Museum of Zoology, University of Michigan, Michigan, USA (UMMZ); Museum of Natural History, University of Kansas, Lawrence, Kansas, USA (KUMNH); and the scientific collection of the Laboratório de Vertebrados, Departamento de Biologia, Universidade Estadual Paulista, Bauru, SP, Brasil (LV): *Baryphthengus ruficapillus* (Vieillot) 1818: LV 015: indeterminate sex, captivity; USNM 428199: ♂, Colombia; USNM 613419: ♀, Panama; USNM 613420: ♀, Panama; USNM 612053: indeterminate sex, Brazil. *Baryphthengus martii* (Spix) 1824: USNM 614002: ♂, Panama; UMMZ 133822: Costa Rica; UMMZ 133823: Costa Rica. *Momotus momota* (Linnaeus) 1766: MPEG 1427: ♂, unknown locality; MPEG 967: ♂, unknown locality; USNM 428784: ♀, Columbia; USNM 554691: ♂, Tobago; USNM 345920: ♂, Brazil; USNM 428842: ♂, Colombia. *Momotus mexicanus* Swainson 1827: UMMZ 130943: Mexico; UMMZ 159130: Mexico. *Electron platyrhynchum* (Leadbeater) 1829: USNM 321526: indeterminate sex, Panama; USNM 428583: ♂, Panama; UMMZ 153115: Costa Rica; UMMZ 219194: Panama. *Electron carinatum* (Du Bus de Gisignies) 1847: KUMNH 34812: ♂, Guatemala. *Eumomota superciliosa* (Sandbach) 1837: UMMZ 133818: Costa Rica; UMMZ 133819: Costa Rica. *Hylomanes momotula* Lichtenstein 1839: UMMZ 156476: Mexico. *Aspatha gularis* (Lafresnaye) 1840: USNM 343481: ♂, Guatemala; UMMZ 151586: Guatemala.

Because most of the cranial bones are paired and the species are characterized by bilateral symmetry, this work describes all cranial osteology in the singular.

The osteology of *Baryphthengus ruficapillus* is also described in detail as a reference framework for comparison with other species

of Momotidae. For the comparative study we used a Mitutoyo 0.05 mm caliper with 0.01 mm resolution for measurement and comparison of structures, and a Leica Wild M3B stereomicroscope (9.6 × 60). For detailed study of the quadrate bone in *B. ruficapillus* (LV 015), it was manually detached from the braincase after immersion in water for approximately 10 h.

The osteological nomenclature used in this study follows *Nomina Anatomica Avium* (Baumel et al., 1993). In the absence of nomenclature for certain structures, lettering is used, as in Donatelli (1992, 1996, 1997). The region or structure identified is indicated by the initial letter. Species classification followed Howard and Moore (1998).

RESULTS

Ossa Cranii

The frontal region (*Os frontale*, F, Figs. 1–3, 6–10) is articulated rostrally to the nasal bone by the frontonasal suture (FNS, Figs. 1–3), which is conspicuous in all species of Momotidae. Dorsocaudally it fuses with the parietal bone (P, Figs. 1–3) and rostrolaterally with the lacrimal bone (L, Figs. 1–3), with no evidence of a frontolacrimal suture. Ventromedially it fuses with the interorbital septum (SI, Figs. 6–10) and rostroventrally with the mesethmoid region.

The frontal region is flat in most of the species analyzed. The main exceptions are *Eumomota superciliosa*, where the depth of this region varies individually, and *Momotus momota*, which has a slight frontal depression (*Depressio frontalis*) in the medial region. This depression extends to the rostral portion of the parietal region, where it is more pronounced and divides the parietal lobes (Pl, Figs. 1–3, 6–10).

The parietal region (*Os parietale*, P, Figs. 1–3) is bounded laterally by the squamosal region (Sq, Figs. 1–3), with a prominent superior temporal crest (*Crista temporalis*, etc, Figs. 4–10), and caudally by the supraoccipital region (SO, Figs. 4, 5), with a transverse nuchal crest (*Crista nuchalis transversa*, CrNT, Figs. 4, 5).

The caudolateral portion of the parietal region, dorsomedially to the postorbital process, contains

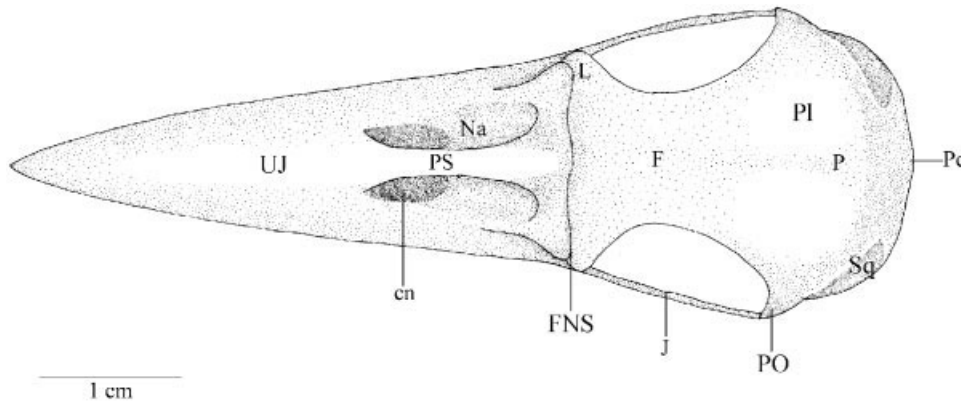


Fig. 2. Dorsal view of skull in *Electron carinatum*. cn, concavity of the nostril; F, frontal region; FNS, frontonasal suture; J, jugal arch; L, lacrimal region; Na, external naris; P, parietal region; Pc, *Prominentia cerebellaris*; Pl, parietal lobes; PO, *Proc. postorbitalis*; PS, *Pila supranasalis*; Sq, squamosal region; UJ, upper jaw.

the orbital depression (od, Figs. 4, 5, 8), which is shallow in all Momotidae.

Laterally, the parietal region is about 2.7 times broader than the frontal region in *Baryphthengus ruficapillus*, *Momotus mexicanus* (Fig. 1), *Electron platyrhynchum*, *E. carinatum* (Fig. 2), *Eumomota superciliosa* and *Aspatha gularis*; about twice as broad in *B. martii* and *M. momota*; and about four times as broad in *Hylomanes momotula* (Fig. 3), giving the skull a triangular appearance.

The temporal fossa (*Fossa temporalis*, FT, Figs. 4–10) is bounded dorsally by the superior temporal crest and ventrally by the inferior temporal crest (itc, Figs. 4, 6), except in *Electron platyrhynchum* (Fig. 5), *E. carinatum*, *Eumomota superciliosa*, *Aspatha gularis*, and *Hylomanes momotula*, where ventrally it is partially fused with the transverse nuchal crest (CrNT, Figs. 4, 5). These crests are separate in *Baryphthengus ruficapillus* (Fig. 4), *B. martii*, *Momotus momota*, and *M. mexicanus*. The temporal fossa is longer than it is broad in all the species studied. It is shallow in all species except *E. platyrhynchum* (Fig. 5), *E. carinatum*, and *H. momotula*.

The subtemporal fossa (*Fossa subtemporalis*, FST, Figs. 4–10) is shallow and short due to the prominence of the temporal fossa. It is delimited rostrally

by part of the inferior temporal crest, caudally by the transverse nuchal crest, and ventrally by another crest (cS, Figs. 6, 7), which is prolonged by the zygomatic process and contributes to the formation of the dorsal surface of the external acoustic meatus. The suprameatic process (*Proc. suprameaticus*) is not highly developed in Momotidae.

The zygomatic process (*Proc. zygomaticus*, Z, Figs. 5–11) is well developed in Momotidae, occupying roughly half of the distance from its origin in the squamosal region to the jugal arch. The distal portion has a slightly tapering apex, except in *Aspatha gularis* (Fig. 9) which has a flattened zygomatic process with a truncated apex. The process receives contributions from prolongation of the anterior temporal crest (atc, Figs. 4–7, 10) and from the crest of the squamosal (cS), defining the rostral, caudal, and medial surfaces.

The postorbital process (*Proc. postorbitalis*, PO, Figs. 1–10) extends ventrally toward the jugal arch, except in *Momotus mexicanus*, *Aspatha gularis* (Fig. 9), and *Hylomanes momotula* (Fig. 10), where its orientation is rostroventral. It is laminar in shape, with a rounded distal extremity in most species. The exceptions are *Electron platyrhynchum* (Fig. 7), *E. carinatum*, *Eumomota superciliosa* (Fig. 8), and *H. momotula* (Fig. 10), where the extremity tapers, and

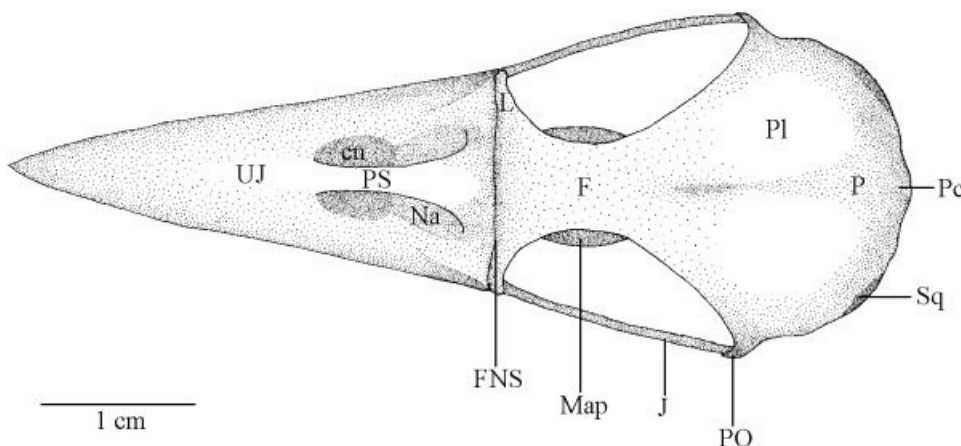


Fig. 3. Dorsal view of skull in *Hylomanes momotula*. cn, concavity of the nostril; F, frontal region; FNS, frontonasal suture; J, jugal arch; L, lacrimal region; Map, maxillary process of the palatine bone; Na, external naris; P, parietal region; Pc, *Prominentia cerebellaris*; Pl, parietal lobes; PO, *Proc. postorbitalis*; PS, *Pila supranasalis*; Sq, squamosal region; UJ, upper jaw.

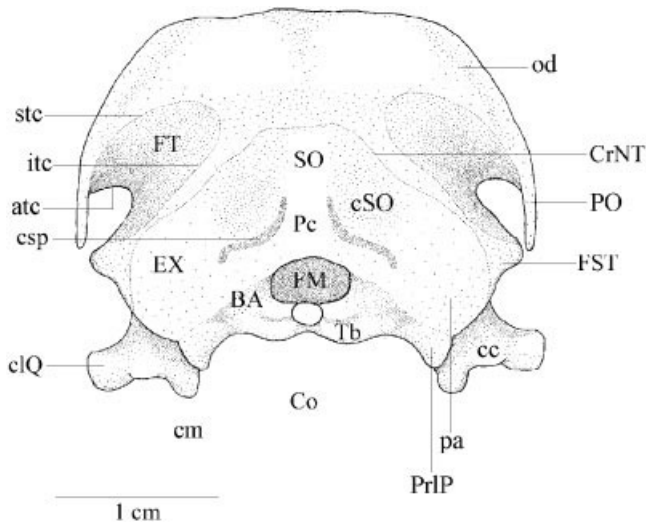


Fig. 4. Caudal view of skull in *Baryphthengus ruficapillus*. atc, anterior temporal crest; BA, basioccipital region; cc, caudal condyle of the quadrate; clQ, *Condylus lateralis of the quadrate*; cm, *Condylus medialis*; Co, *Condylus occipitalis*; CrNT, *Crista nuchalis transversa*; cSO, concavity of the supraoccipital region; csp, *Canalis semicircularis posterior*; EX, exoccipital region; FM, foramen magnum; FST, *Fossa subtemporalis*; FT, *Fossa temporalis*; itc, inferior temporal crest; od, orbital depression; pa, paroccipital process; Pc, *Prominentia cerebellaris*; PO, *Proc. postorbitalis*; PrIP, *Proc. lateralis parasphenoidalis*; SO, supraoccipital region; stc, superior temporal crest; Tb, *Tuberculum basilare*.

A. gularis, where it is truncated (Fig. 9). In *Baryphthengus ruficapillus* (Fig. 6), *B. martii*, *M. momota*, *M. mexicanus*, *E. carinatum*, *E. superciliosa* (Fig. 8), *A. gularis* (Fig. 9), and *H. momotula* (Fig. 10), the postorbital process is long, occupying roughly half the distance between its base in the cranium and the jugal arch, while in *E. platyrhynchum* (Figs. 5, 7) it is shorter, occupying about one-third of this distance.

The parasphenoid region fuses caudally with the basisphenoid region (*Os basisphenoidale*, BS, Figs. 11–13) and extends laterally from the parasphenoid rostrum to the parasphenoid ala. Rostrally it articulates to the pterygoid bone (Pt, Figs. 6–13) through the articular surface of the pterygoid (*Facies articularis pterygoidea*) and the articular surface of the caudal portion of the palatine (*Facies articularis palatina*). Laterally it is bounded by the tympanic cavity and caudally by the basioccipital region (BA, Fig. 11).

The parasphenoid rostrum (*Rostrum parasphenoidale*, RP, Figs. 11–13) is situated on the same horizontal plane as the pterygoid. In the caudolateral portion of the parasphenoid rostrum, the basipterygoid process (*Proc. basipterygoideus*, bp) is small in *Momotus mexicanus* (bp, Fig. 11), *Electron platyrhynchum*, *E. carinatum*, *Eumomota superciliosa* (bp, Fig. 12), *Aspatha gularis*, and *Hylomanes momotula* (bp, Fig. 13). The process is absent in all other species of Momotidae.

The projection of *Basis rostri parasphenoidalis* (Brp, Figs. 11–13) is developed in all the species studied. Ventrally there is a *Tuba auditiva communis* and laterocaudally a shallow concavity (cP) only in *Baryphthengus ruficapillus*, *B. martii*, *Momotus mexicanus* (cP, Fig. 11), and *Aspatha gularis*. The region is flat in all other species.

The lateral process of the parasphenoid (*Proc. lateralis parasphenoidalis*, PrIP, Figs. 4, 5) projects ventrally. It was impossible to compare this process in *Hylomanes momotula* since it was damaged in the only specimen studied.

Medially to the lateral process of the parasphenoid is the parabasal fossa (*Fossa parabasalis*, FPa, Figs. 11–13), with the cranial nerve channels, cerebral carotid, and external ophthalmic arteries opening into it.

The basioccipital region (*Os basioccipitale*, BA, Fig. 11), formed by the odd basioccipital bone, contains the occipital condyle (*Condylus occipitalis*, Co, Figs. 4, 5, 11–13); caudally to the latter is the foramen magnum (*Foramen magnum*, FM, Figs. 4, 5, 11–13). The subcondylar fossa (*Fossa subcondylaris*, Fsc, Figs. 11–13) is bounded laterorostrally by the basal tubercle (Tb, Figs. 4, 5, 11–13). The depth of this fossa varies in different individuals and species.

The basal tubercle (*Tuberculum basilare*, Tb, Figs. 4, 5, 11–13) is well developed and globular in shape.

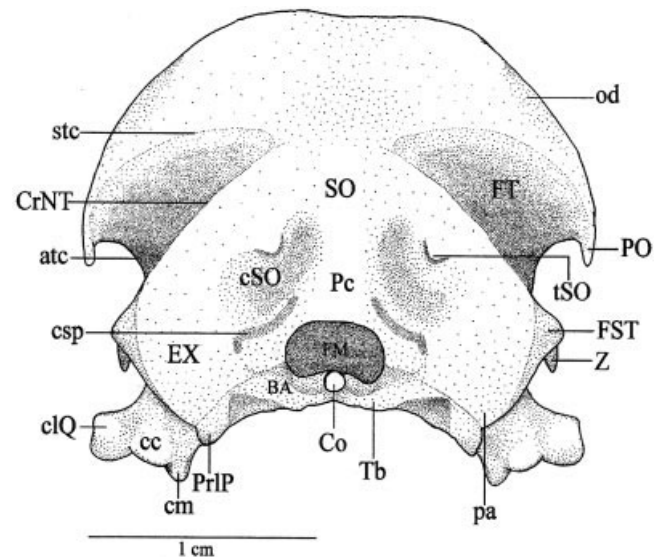


Fig. 5. Caudal view of skull in *Electron platyrhynchum*. atc, anterior temporal crest; BA, basioccipital region; cc, caudal condyle of the quadrate; clQ, *Condylus lateralis of the quadrate*; cm, *Condylus medialis*; Co, *Condylus occipitalis*; CrNT, *Crista nuchalis transversa*; cSO, concavity of the supraoccipital region; csp, *Canalis semicircularis posterior*; EX, exoccipital region; FM, foramen magnum; FST, *Fossa subtemporalis*; FT, *Fossa temporalis*; od, orbital depression; pa, paroccipital process; Pc, *Prominentia cerebellaris*; PO, *Proc. postorbitalis*; PrIP, *Proc. lateralis parasphenoidalis*; SO, supraoccipital region; stc, superior temporal crest; Tb, *Tuberculum basilare*; tSO, tuberosity of the supraoccipital region; Z, zygomatic process.

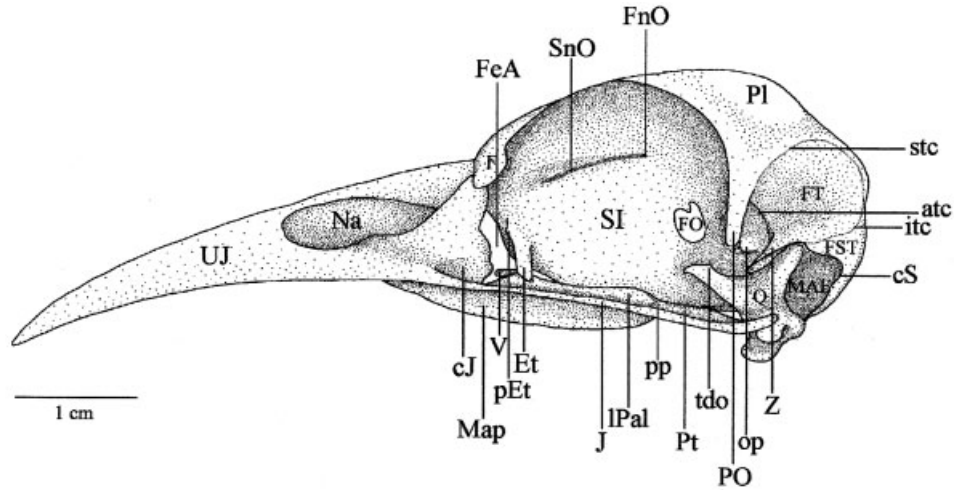


Fig. 6. Lateral view of skull in *Baryphthengus ruficapillus*. atc, anterior temporal crest; cJ, concavity of the jugal process of the maxillary; cS, crest of the squamosal; Et, ectethmoid; F, frontal region; FeA, *Fenestra antorbitalis*; FnO, *Foramen n. olfactorii*; FO, *Foramen opticum*; FST, *Fossa subtemporalis*; FT, *Fossa temporalis*; itc, inferior temporal crest; J, jugal arch; IPal, dorsal lamellae of the maxillary process of the palatine; MAE, *Meatus acusticus externus*; Map, maxillary process of the palatine bone; Na, external naris; op, orbitosphenoid process; pEt, dorsal projection of the ectethmoid; PI, parietal lobes; PO, *Proc. postorbitalis*; pp, *Pes pterygoidei*; Pt, pterygoid bone; Q, quadrate bone; SI, *septum interorbitale*; SnO, *Sulcus n. olfactorii*; stc, superior temporal crest; tdo, tuberosity of the orbital process; UJ, upper jaw; V, vomer; Z, zygomatic process.

Ventrally is the transverse basal crest (*Crista basilaris transversa*) placed lateromedially in all the specimens studied.

The exoccipital region (*Os exoccipitale*, EX, Figs. 4, 5, 11–13) is fused ventromedially with the basioccipital region; rostroventrally it touches the caudal surface of the lateral process of the parasphenoid process via an inconspicuous paroccipital process (*Proc. paroccipitalis*, pa, Figs. 4, 5), which projects ventrally. The lateral margin of this process contributes to the formation of the caudal surface of the external acoustic meatus (*Meatus acusticus externus*, MAE, Figs. 6–13). Dorsolaterally, the exoccipital region is bounded by the squamosal region via the transverse nuchal crest.

The medial portion of the supraoccipital region (*Os supraoccipitale*, SO, Figs. 4, 5) contains a cerebellar prominence (*Prominentia cerebellaris*, Pc, Figs. 1–5), an inconspicuous medial convexity situated dorsally to the foramen magnum. Laterally is a shallow concavity (cSO, Figs. 4, 5), bounded dorsally by the transverse nuchal crest and ventrally by the posterior semicircular canal. In *Electron platyrhynchum* (tSO, Fig. 5), *E. carinatum*, *Eumomota superciliosa*, *Aspatha gularis*, and *Hylomanes momotula*, there is a conspicuous tuberosity in the dorsomedial part of the concavity of the supraoccipital region. However, this tuberosity is an individual variation in *Baryphthengus martii* and it is absent in all other species of Momotidae.

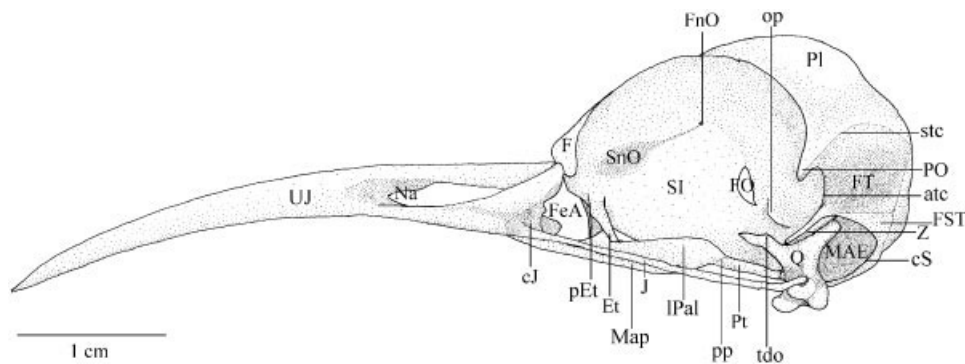


Fig. 7. Lateral view of skull in *Electron platyrhynchum*. atc, anterior temporal crest; cJ, concavity of the jugal process of the maxillary; cS, crest of the squamosal; Et, ectethmoid; F, frontal region; FeA, *Fenestra antorbitalis*; FnO, *Foramen n. olfactorii*; FO, *Foramen opticum*; FST, *Fossa subtemporalis*; FT, *Fossa temporalis*; J, jugal arch; IPal, dorsal lamellae of the maxillary process of the palatine; MAE, *Meatus acusticus externus*; Map, maxillary process of the palatine bone; Na, external naris; op, orbitosphenoid process; pEt, dorsal projection of the ectethmoid; PI, parietal lobes; PO, *Proc. postorbitalis*; pp, *Pes pterygoidei*; Pt, pterygoid bone; Q, quadrate bone; SI, *septum interorbitale*; SnO, *Sulcus n. olfactorii*; stc, superior temporal crest; tdo, tuberosity of the orbital process; UJ, upper jaw; Z, zygomatic process.

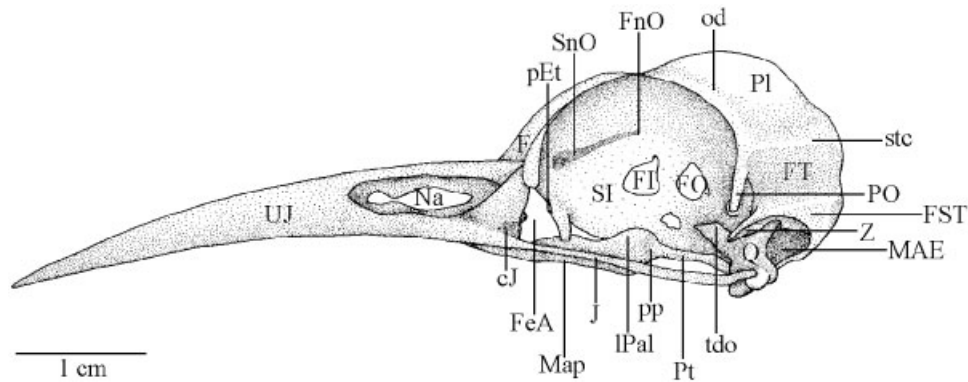


Fig. 8. Lateral view of skull in *Eumomota superciliosa*. cJ, concavity of the jugal process of the maxillary; F, frontal region; FeA, Fenestra antorbitalis; FI, Fonticuli interorbitales; FnO, Foramen n. olfactorii; FO, Foramen opticum; FST, Fossa subtemporalis; FT, Fossa temporalis; J, jugal arch; IPal, dorsal lamellae of the maxillary process of the palatine; MAE, Meatus acusticus externus; Map, maxillary process of the palatine bone; Na, external naris; od, orbital depression; pEt, dorsal projection of the ectethmoid; PI, parietal lobes; PO, Proc. postorbitalis; pp, Pes pterygoidei; Pt, pterygoid bone; Q, quadrate bone; SI, septum interorbitale; SnO, Sulcus n. olfactorii; stc, superior temporal crest; tdo, tuberosity of the orbital process; UJ, upper jaw; Z, zygomatic process.

The conspicuous posterior semicircular canal (*Canalis semicircularis posterior*, csp, Figs. 4, 5) is placed lateromedially, extending from the ventrolateral region of the cerebellar prominence to the dorsolateral portion of the foramen magnum.

Orbit

The rostral portion of the orbit contains the ectethmoid region, which fuses medially with the interorbital septum. Rostromedially the ectethmoid fuses with the mesethmoid (*Os mesethmoidale*) and rostradorsolaterally with the frontal and lacrimal, contributing to the formation of the rostral surface of the orbit. The ectethmoid (*Os ectethmoidale*, Et, Figs. 6, 7, 9, 10, 12), a long, narrow, laminar bone process with a straight distal extremity, projects lateroventrally from the mesethmoid. The ectethmoid occupies roughly half the distance from its

origin in the mesethmoid region to the jugal arch. The rostradorsal surface of the ectethmoid contains a dorsal projection of the ectethmoid (pEt, Figs. 6–10). This projection is small and varies from individual to individual. It is absent in *Momotus mexicanus*. The ectethmoid and mesethmoid regions are not fused to the caudal portion of the nasal bone. There is a space between the two regions in this area, known as the antorbital fenestra (*Fenestra antorbitalis*, FeA, Figs. 6–10). This fenestra is bounded rostrally by the nasal process of the maxillary bone and the maxillary process of the nasal bone, and laterally by the jugal arch. In these species the lacrimal does not participate in the formation of the antorbital fenestra because of its small size and fusion with the frontal.

The interorbital septum (*Septum interorbitale*, SI, Figs. 6–10) is a thin laminar bone that separates the two lateral portions of the orbit. In *Hylomanes mo-*

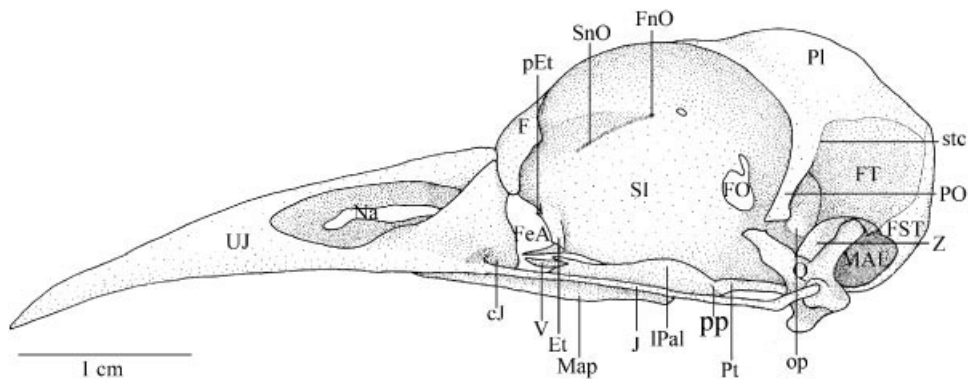


Fig. 9. Lateral view of skull in *Aspatha gularis*. cJ, concavity of the jugal process of the maxillary; Et, ectethmoid; F, frontal region; FeA, Fenestra antorbitalis; FnO, Foramen n. olfactorii; FO, Foramen opticum; FST, Fossa subtemporalis; FT, Fossa temporalis; J, jugal arch; IPal, dorsal lamellae of the maxillary process of the palatine; MAE, Meatus acusticus externus; Map, maxillary process of the palatine bone; Na, external naris; op, orbitosphenoid process; pEt, dorsal projection of the ectethmoid; PI, parietal lobes; PO, Proc. postorbitalis; pp, Pes pterygoidei; Pt, pterygoid bone; Q, quadrate bone; SI, septum interorbitale; SnO, Sulcus n. olfactorii; stc, superior temporal crest; UJ, upper jaw; V, vomer; Z, zygomatic process.

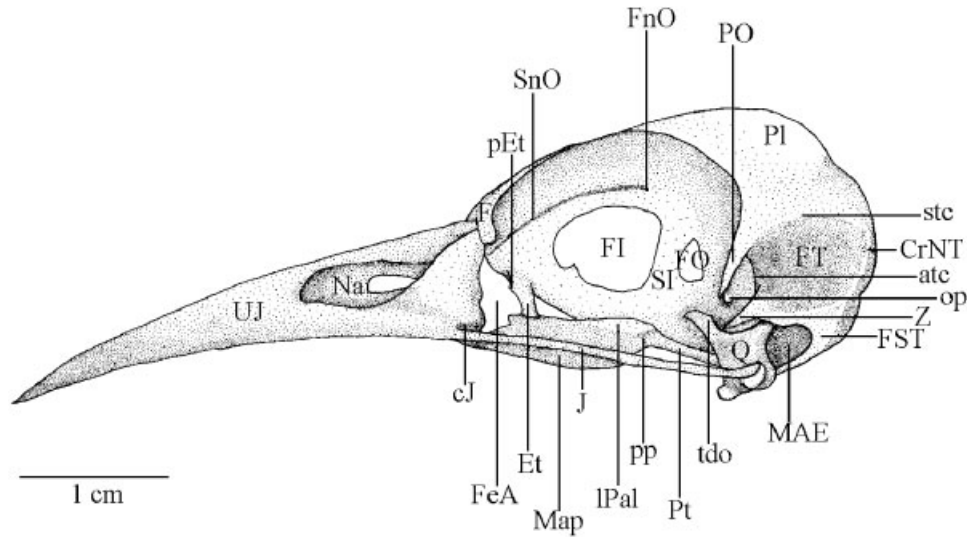


Fig. 10. Lateral view of skull in *Hylomanes momotula*. atc, anterior temporal crest; cJ, concavity of the jugal process of the maxillary; CrNT, *Crista nuchalis transversa*; Et, ectethmoid; F, frontal region; FeA, *Fenestra antorbitalis*; FI, *Fonticuli interorbitales*; FnO, *Foramen n. olfactorii*; FO, *Foramen opticum*; FST, *Fossa subtemporalis*; FT, *Fossa temporalis*; J, jugal arch; IPal, dorsal lamellae of the maxillary process of the palatine; MAE, *Meatus acusticus externus*; Map, maxillary process of the palatine bone; Na, external naris; op, orbitosphenoid process; pEt, dorsal projection of the ectethmoid; PI, parietal lobes; PO, *Proc. postorbitalis*; pp, *Pes pterygoidei*; Pt, pterygoid bone; Q, quadrate bone; SI, *septum interorbitale*; SnO, *Sulcus n. olfactorii*; stc, superior temporal crest; tdo, tuberosity of the orbital process; UJ, upper jaw; Z, zygomatic process.

motula (Fig. 10), it is not highly ossified. In *Electron carinatum* and *Eumomota superciliosa* (Fig. 8), the degree of ossification is intermediate between *H. momotula* and the other species. Among the latter, the *Fonticuli interorbitales* is well developed in *H. momotula* (FI, Fig. 10) and inconspicuous in *E. cari-*

natum and *E. superciliosa* (FI, Fig. 8). In *Momotus mexicanus* the interorbital septum is partially damaged. Rostr dorsally the interorbital septum is fused with the frontal region, rostrally with the mesethmoid and ectethmoid, caudally with the laterosphenoid (La, Figs. 11–13), and ventrally with the para-

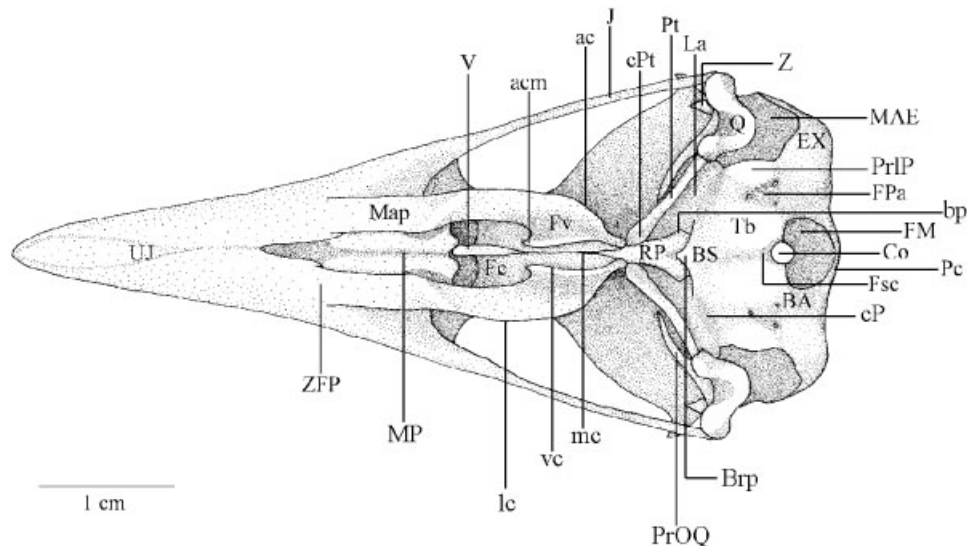


Fig. 11. Ventral view of skull in *Momotus mexicanus*. ac, *Angulus caudolateralis*; acm, *Angulus caudomedialis*; BA, basioccipital region; bp, basipterygoid process; Brp, *Basis rostri parasphenoidalis*; BS, basisphenoid region; Co, *Condylus occipitalis*; cP, concavity of the parasphenoid region; cPt, concavity of the pterygoid; EX, exoccipital region; Fc, *Fossa choanalis*; FM, foramen magnum; FPa, *Fossa parabasalis*; Fsc, *Fossa subcondylaris*; Fv, *Fossa ventralis*; J, jugal arch; La, laterosphenoid region; lc, lateral palatine crest; MAE, *Meatus acusticus externus*; Map, maxillary process of the palatine bone; mc, medial palatine crest; MP, maxillopalatine process; Pc, *Prominentia cerebellaris*; PrlP, *Proc. lateralis parasphenoidalis*; PrOQ, *Proc. orbitalis* of the quadrate; Pt, pterygoid bone; Q, quadrate bone; RP, *Rostrum parasphenoidale*; Tb, *Tuberculum basilare*; UJ, upper jaw; V, vomer; vc, ventral palatine crest; Z, zygomatic process; ZFP, *Zona flexoria palatina*.

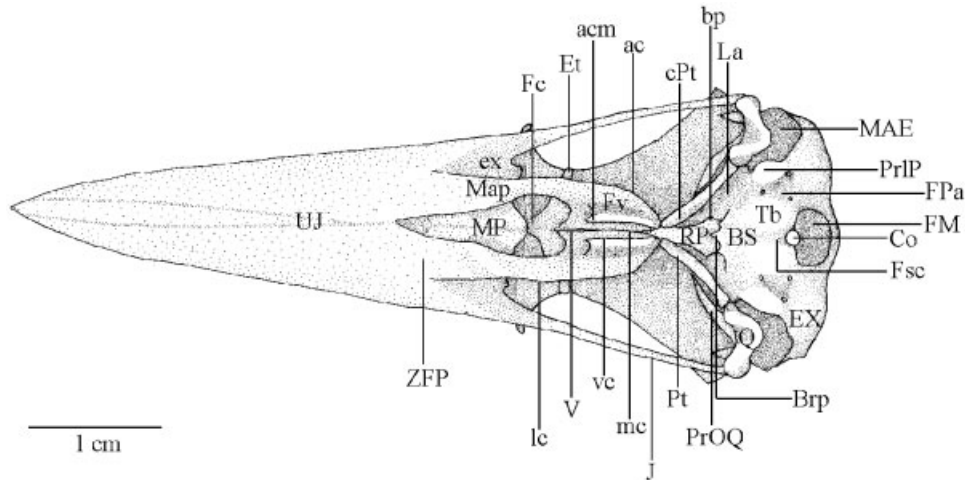


Fig. 12. Ventral view of skull in *Eumomota superciliosa*. ac, *Angulus caudolateralis*; acm, *Angulus caudomedialis*; bp, basipterygoid process; Brp, *Basis rostri parasphenoidalis*; BS, basisphenoid region; Co, *Condylus occipitalis*; cPt, concavity of the pterygoid; Et, ectethmoid; EX, exoccipital region; Fc, *Fossa choanalis*; FM, foramen magnum; FPa, *Fossa parabasalis*; Fsc, *Fossa subcondylaris*; Fv, *Fossa ventralis*; J, jugal arch; La, laterosphenoid region; lc, lateral palatine crest; MAE, *Meatus acusticus externus*; Map, maxillary process of the palatine bone; mc, medial palatine crest; MP, maxillopalatine process; PrIP, *Proc. lateralis parasphenoidalis*; PrOQ, *Proc. orbitalis* of the quadrate; Pt, pterygoid bone; Q, quadrate bone; RP, *Rostrum parasphenoidale*; Tb, *Tuberculum basilare*; UJ, upper jaw; V, vomer; vc, ventral palatine crest; ZFP, *Zona flexoria palatina*.

sphenoid rostrum. Moreover, it is articulated ventrally with the palatine through the dorsal lamellae of the maxillary process of the palatine (IPal, Figs. 6–10). The dorsal region contains the olfactory nerve sulcus (*Sulcus n. olfactorii*, SnO, Figs. 6–10), placed rostrocaudally with regard to the orbit and narrow along its entire length. The caudal portion of the olfactory sulcus contains the *Foramen n. olfactorii* (FnO, Figs. 6–10), which has an external aperture with individual and specific variations.

The caudal portion of the interorbital septum contains the optic foramen (*Foramen opticum*, FO, Figs. 6–10), which is circular in shape.

The laterosphenoid (*Os laterosphenoidale*, La, Figs. 11–13) makes up most of the caudal part of the orbit, extending caudolaterally from the interorbital septum. Ventromedially it fuses with the dorsal portion of the parasphenoid. The *Area muscularis aspera* lies rostrally. It is globular in shape and prominent in all species analyzed. Its ventrolateral

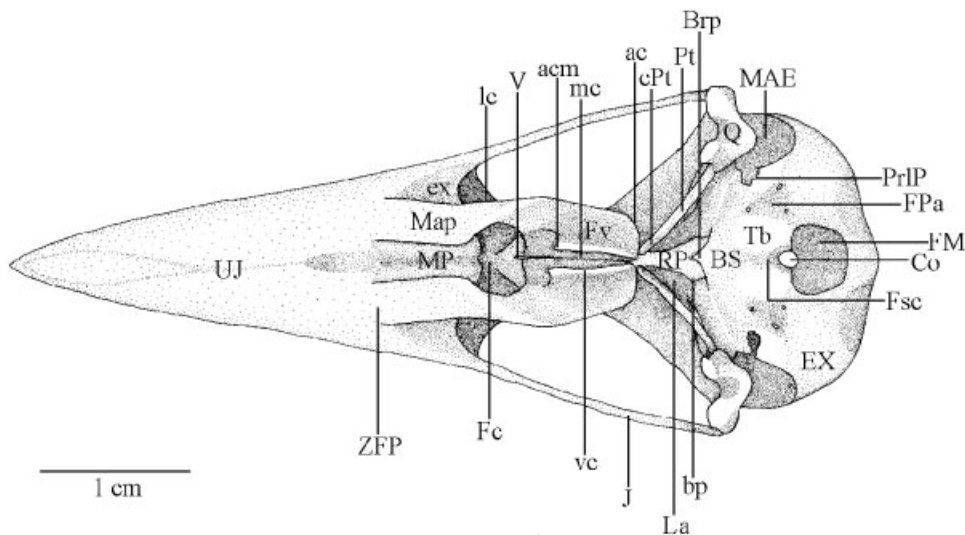


Fig. 13. Ventral view of skull in *Hylomanes momotula*. ac, *Angulus caudolateralis*; acm, *Angulus caudomedialis*; bp, basipterygoid process; Brp, *Basis rostri parasphenoidalis*; BS, basisphenoid region; Co, *Condylus occipitalis*; cPt, concavity of the pterygoid; EX, exoccipital region; ex, extension of the jugal process of the maxillary; Fc, *Fossa choanalis*; FM, foramen magnum; FPa, *Fossa parabasalis*; Fsc, *Fossa subcondylaris*; Fv, *Fossa ventralis*; J, jugal arch; La, laterosphenoid region; lc, lateral palatine crest; MAE, *Meatus acusticus externus*; Map, maxillary process of the palatine bone; mc, medial palatine crest; MP, maxillopalatine process; PrIP, *Proc. lateralis parasphenoidalis*; Pt, pterygoid bone; Q, quadrate bone; RP, *Rostrum parasphenoidale*; Tb, *Tuberculum basilare*; UJ, upper jaw; V, vomer; vc, ventral palatine crest; ZFP, *Zona flexoria palatina*.

portion contains the *Foramen n. maxillomandibularis*, a conspicuous structure covered by the quadrate bone.

Dorsal of the *Area muscularis aspera* is a broad, shallow, oval fossa. This fossa is inconspicuous in *Aspatha gularis*. The crests delimiting the fossa meet ventrally, forming the characteristic orbitosphenoid process, which is highly developed in *Baryphthengus ruficapillus* (op, Fig. 6), *B. martii*, *Momotus momota*, and *M. mexicanus*, but much less prominent in *Electron platyrhynchum* (op, Fig. 7), *E. carinatum*, *A. gularis* (op, Fig. 9), and *Hylomanes momotula* (op, Fig. 10), and of intermediate size in *Eumomota superciliosa*.

Ossa Faciei

Ossa maxillae. The upper jaw (UJ, Figs. 1–3, 6–13) corresponds to about 60% of the total length of the skull in *Baryphthengus ruficapillus*, *B. martii*, *Momotus momota*, *M. mexicanus*, *Electron platyrhynchum*, *E. carinatum*, *Eumomota superciliosa*, and *Aspatha gularis*; in *Hylomanes momotula* (Fig. 3) it corresponds to about 50%. The upper jaw is narrow and tall in the species studied, with the exception of *E. platyrhynchum* and *E. carinatum* (UJ, Fig. 2), in which it is broad and flattened dorsoventrally in the caudal region. In *E. superciliosa* (UJ, Fig. 8) its characteristics are intermediate between *E. platyrhynchum*, *E. carinatum*, and the other species. The rostral apex tapers with a slight ventral curvature in all species analyzed.

The caudolateral portion of the upper jaw contains the nostril (*Apertura nasi ossea*, Na, Figs. 1–3, 6–10), which is long and oval. The rostral portion is broader than the caudal portion in *Baryphthengus ruficapillus*, *B. martii*, *Momotus momota*, *M. mexicanus* (Fig. 1), *Aspatha gularis*, and *Hylomanes momotula* (Fig. 3). In *Electron platyrhynchum*, *E. carinatum* (Fig. 2), and *Eumomota superciliosa*, this aperture is located in the dorsocaudal region and the rostral portion is narrower than the caudal portion.

The external nasal aperture occupies about 33% of the total length of the upper jaw in *Baryphthengus ruficapillus*, *B. martii*, *Electron platyrhynchum*, *E. carinatum* (Fig. 2), *Eumomota superciliosa*, and *Hylomanes momotula* (Fig. 3), while in *Momotus momota* it corresponds to 25% and in *Aspatha gularis* and in *M. mexicanus* (Fig. 1) to about 38%. The rostroventral portion of the nostril contains an oval concavity (cn, Figs. 1–3). This concavity is shallow in *B. ruficapillus* and *B. martii*, comprising 50% of the length of the external nasal aperture. In the other species studied it is deep, corresponding to about 66% of the aperture in *M. momota*, 50% in *E. platyrhynchum*, 55% in *M. mexicanus* and *E. superciliosa*, and 60% in *A. gularis* and *H. momotula*. In *E. carinatum* (Fig. 2) the concavity is extremely deep, occupying about 50% of the nostril.

The external nares are separated medially by the nasal septum (*Septum nasi osseum*) and are therefore holorrhinal. The nasal septum is laminar and thin in the species analyzed, with individual and specific variations in the degree of ossification. It is absent or hardly ossified at all in *Electron platyrhynchum* (Na, Fig. 7) and *E. carinatum*.

In *Baryphthengus ruficapillus*, *B. martii*, *Electron platyrhynchum*, *E. carinatum*, *Eumomota superciliosa*, *Aspatha gularis*, and *Hylomanes momotula*, the external nasal aperture is caudally fused with the postnasal foramen (*Foramina neurovascularia*) so that there is no distinction between them. In *Momotus momota* and *M. mexicanus* (l, Fig. 1), a thin dorsoventrally placed lamina separates the two cavities; this is more visible in *M. mexicanus*. Rostrolaterally to the postnasal foramen or the region of the fusion with the upper jaw is the neurovascular canal (*Canalis neurovascularis maxillae*); this is shallow and confined to the caudal portion of the nasal cavity in *B. ruficapillus*, *B. martii*, *M. momota*, *M. mexicanus*, *A. gularis*, and *H. momotula*.

The caudoventromedial portion of the upper jaw contains the maxillopalatine process (*Proc. maxillopalatinus*, MP, Figs. 11–13), which is medially fused but incompletely so, as evidenced by the presence of a shallow sulcus placed rostrocaudally in the ventromedial region. Dorsally it is fused with the caudal portion of the maxillary bone. In *Baryphthengus ruficapillus*, *B. martii*, *Momotus momota*, *M. mexicanus* (Fig. 11), *Aspatha gularis*, and *Hylomanes momotula* (Fig. 13), the caudomedial extremity of the maxillopalatine process protrudes caudally and is slightly bilobate, an additional indication of incomplete fusion. In *Electron platyrhynchum*, *E. carinatum*, and *Eumomota superciliosa* (Fig. 12), the caudal protrusion is medially fused and the ventromedial sulcus is not as deep as in the other species. Laterally to the ventromedial sulcus there is a large concavity whose depth varies individually and specifically. This concavity extends under a rostral portion of the maxillary process of the palatine as far as the rostromedial region of the jugal process of the maxillary bone.

The *Pila supranasalis* (PS, Figs. 1–3) is conspicuous and convex in the species analyzed. It is especially conspicuous as well as narrower in *Electron platyrhynchum* and *E. carinatum* because the upper jaw is flattened. In *Eumomota superciliosa* its characteristics are intermediate between those of *E. platyrhynchum* and *E. carinatum* and the other species.

Palati. The maxillary process of the palatine (*Proc. maxillaris Os palatinum*, Map, Figs. 3, 11–13) is a thin, long, rostrocaudally placed lamina. It is broad in *Baryphthengus ruficapillus*, *B. martii*, *Momotus momota*, and *M. mexicanus* (Fig. 11) and narrow in *Electron platyrhynchum*, *Eumomota superciliosa* (Fig. 12), and *Aspatha gularis*. In *E. carinatum* the rostral portion is broader than in *E. platyrhynchum*.

chum, *E. superciliosa*, and *A. gularis*. In *Hylomanes momotula* (Fig. 13) it is broader than in all other species. The rostral portion of the maxillary process of the palatine is superimposed on the maxillopalatine, fusing with the upper jaw and forming a bending zone (*Zona flexoria palatina*, ZFP, Figs. 11–13). The maxillary process of the palatine is articulated dorsally to the parasphenoid rostrum and caudally to the pterygoid (*Os pterygoideum*, Pt, Figs. 6–13) by the *Facies articularis parasphenoidalis* and *Facies articularis pterygoidea*, respectively.

In Momotidae the *Facies articularis parasphenoidalis* is a dorsal extension of the palatine, which forms a dorsal lamella (*Lamella dorsalis*, lPal, Figs. 6–10) along the lateral surface of the parasphenoid rostrum, which articulates these two regions. Caudally the dorsal lamella of the palatine is fused with the rostral surface of the base of the pterygoid (*Pes pterygoidei*, pp, Figs. 6–10) and its dorsal extremity forms the dorsolateral crest (*Crista dorsolateralis*).

The choanal fossa (*Fossa choanalis*, Fc, Figs. 11–13) is bounded dorsomedially by the medial palatine crests (*Crista medialis*, mc, Figs. 11–13) and ventrolaterally by the ventral palatine crests (vc, Figs. 11–13). The latter are situated far apart in the rostromedial portion, forming the lateral wall of the choanal fossa. The choanal fossa is a broad deep cavity in all species analyzed, communicating rostrally with the oropharynx. The *Pars lateralis* contains the ventral fossa (*Fossa ventralis*, Fv), which is broad and deep in *Baryphthengus ruficapillus*, *B. martii*, *Momotus momota*, *M. mexicanus* (Fv, Fig. 11), *Electron carinatum*, and *Hylomanes momotula* (Fv, Fig. 13), and narrow and deep in *E. platyrhynchum*, *Eumomota superciliosa* (Fv, Fig. 12), and *Aspatha gularis*. It is bounded by the ventral and lateral palatine crests (*Crista lateralis*, lc, Figs. 11–13). The ventral palatine crest is well developed and projects ventrally. The ventral, medial, and lateral palatine crests become confluent caudally in the region of articulation with the pterygoid bone. The caudal portion of the maxillary process of the palatine is relatively elongated in *B. ruficapillus*, *B. martii*, *M. momota*, *M. mexicanus* (Fig. 11), and shorter in *E. platyrhynchum*, *E. carinatum*, *E. superciliosa* (Fig. 12), *A. gularis*, and *H. momotula* (Fig. 13).

The caudolateral portion of the *Pars choanalis* narrows near the rostral region of the articulation with the pterygoid, forming the caudolateral angle (*Angulus caudolateralis*, ac, Figs. 11–13), which is rounded with an angle of $\sim 60^\circ$ in *Baryphthengus ruficapillus*, *B. martii*, *Momotus momota*, *M. mexicanus* (Fig. 11), *Electron carinatum*, *Eumomota superciliosa* (Fig. 12), and *Aspatha gularis*, $\sim 45^\circ$ in *E. platyrhynchum*, and $\sim 10^\circ$ in *Hylomanes momotula* (Fig. 13). There is no transpalatine process in Momotidae. The caudomedial angle (*Angulus caudomedialis*, acm, Figs. 11–13) is well developed in all Momotidae.

The vomer (*Vomer*, V, Figs. 6, 9, 11–13) is a single medial bone structure formed by fusion of the two portions. It is thick and short in Momotidae, with a slightly rounded rostral region except in *Electron platyrhynchum*, *Eumomota superciliosa* (Fig. 12), and *Hylomanes momotula* (Fig. 13), where it is thin, lateromedially flattened, and smaller than in the other species. It is rostrocaudally oriented toward the caudomedial portion of the maxillopalatine process. In *Baryphthengus ruficapillus*, *B. martii*, *Momotus momota*, and *M. mexicanus* the vomer lightly touches the caudomedial portion of the maxillopalatine process, while in other species there is no contact. Dorsocaudally the vomer is articulated to the parasphenoid rostrum by the *Facies articularis parasphenoidalis*. In *E. carinatum* the vomer is absent or broken, so that comparison of this species with the rest is impossible in this respect.

The pterygoid bone is articulated rostrally with the caudal portion of the palatine by the *Facies articularis palatina* and with the rostral surface of the parasphenoid rostrum. The rostral extremity of the pterygoid is relatively small in *Baryphthengus ruficapillus*, *B. martii*, *Electron platyrhynchum*, *E. carinatum*, *Eumomota superciliosa*, *Aspatha gularis*, and *Hylomanes momotula*, while in *Momotus momota* and *M. mexicanus* it is flat and relatively large laterally, reducing the breadth and depth of the medial concavity of the pterygoid (cPt, Figs. 11–13). This extremity forms the base of the pterygoid (pp, Figs. 6–10), which defines the articulatory surfaces for the caudal portion of the palatine and parasphenoid rostrum.

The dorsocaudal region of the pterygoid contains a small dorsal muscular process (*Proc. dorsalis Os pterygoideum*), which is especially conspicuous in *Hylomanes momotula*. The pterygoid is slightly rounded caudally and flattened dorsally. The surface that articulates with the quadrate (*Facies articularis quadratica*) has a shallow cotyle.

The jugal arch (*Arcus jugalis*, J, Figs. 1–3, 6–13) is a long narrow bar formed by fusion of the jugal process of the maxillary bone (*Proc. jugalis Os maxillare*) with the jugal (*Os jugale*) and quadratojugal (*Os quadratojugale*), connecting the superior maxillary to the quadrate. The jugal process of the maxillary bone, where it fuses with the upper jaw, is a dorsoventrally flattened rostromedial extension (ex, Fig. 13). The dorsal surface of this extension contains the concavity of the jugal process of the maxillary bone (cJ, Figs. 6–10). This concavity is broad and rostrally protuberant in *Baryphthengus ruficapillus* and *B. martii*. In *Momotus momota*, *M. mexicanus*, *Electron platyrhynchum*, *E. carinatum*, *Eumomota superciliosa*, *Aspatha gularis*, and *Hylomanes momotula* it is rostrally less prominent. The caudal extremity of the jugal arch has a conspicuous dorsal curvature (J, Figs. 6–13). The caudomedial portion also contains the *Condylus qua-*

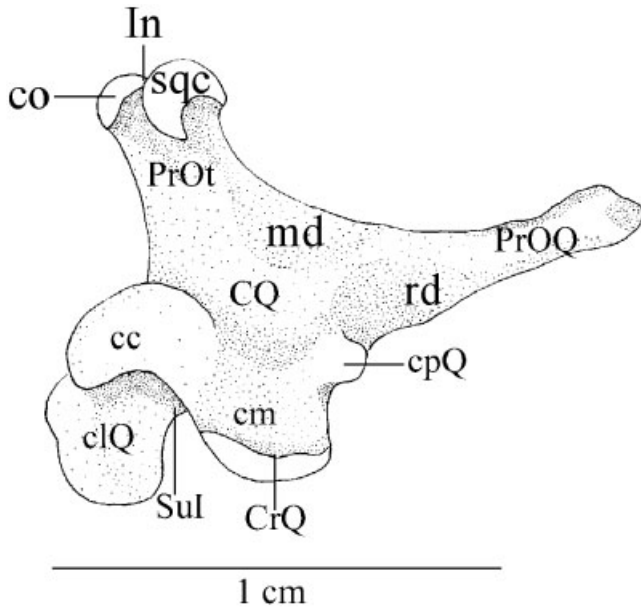


Fig. 14. Medial view of the left quadrate bone in *Baryphthenus ruficapillus*. cc, caudal condyle of the quadrate; clQ, *Condylus lateralis* of the quadrate; cm, *Condylus medialis*; co, *Capitulum oticum*; cpQ, *Condylus pterygoideus*; CQ, *Corpus ossis quadrati*; CrQ, crest of the quadrate; In, *Incisura intercapitularis*; md, medial depression of the body of the quadrate; PrOQ, *Proc. orbitalis* of the quadrate; PrOt, *Proc. oticus*; rd, rostromedial depression of the body of the quadrate; sqc, squamosal capitulum; Sul, *Sulcus intercondylaris*.

draticus, which is articulated to the cotyla of the quadrate bone.

The quadrate bone (*Os quadratum*, Q, Figs. 6–15) articulates the braincase with the mandible. It is basically formed by the robust body of the quadrate bone (*Corpus ossis quadrati*, CQ, Fig. 14), where three processes originate: mandibular, orbital, and otic. The medial surface (*Facies tympanica*) of the quadrate body has a shallow depression (md, Fig. 14). Dorsally to the pterygoid condyle there is a deep rostromedial depression (rd, Fig. 14) in all Momotidae.

The lateral surface of the quadrate body contains three depressions, which are similar in all the species analyzed: the laterocaudal depression (lcd, Fig. 15), which is shallow and narrow; the laterodorsal depression (ldd, Fig. 15), which is shallow and broad; and the lateroventral depression (lvd, Fig. 15), which is deep and broad.

The caudal condyle of the mandibular process of the quadrate (*Condylus caudalis*, cc, Figs. 4, 5, 14) is fused laterally with the lateral condyle and medially with the medial condyle. It is small and rounded, with a slightly pointed tip in all specimens examined.

The tip of the medial condyle of the mandibular process of the quadrate (*Condylus medialis*, cm, Figs. 4, 5, 14, 15) is rostroventrally oriented and oval with a crest (CrQ, Figs. 14, 15), delimiting the entire articulation region, present in all the species dis-

cussed here. The medial condyle is situated rostro-medially to the caudal condyle and protrudes farther ventrally than the lateral and caudal condyles. The intercondylar sulcus (*Sulcus intercondylaris*, Sul, Figs. 14, 15) is deep.

The lateral condyle of the mandibular process of the quadrate (*Condylus lateralis*, clQ, Figs. 4, 5, 14, 15) is the most developed of the three condyles in all Momotidae. It is rostromedially oriented and oval in shape. Laterodorsally it has a conspicuous quadratojugal cotyla (*Cotyla quadratojugal*, coq, Fig. 15), which is articulated to the *Condylus quadraticus* of the jugal arch.

The pterygoid condyle (*Condylus pterygoideus*, cpQ, Figs. 14, 15) is the smallest condyle; it is slightly rounded and articulated with the pterygoid bone by the *Facies articularis quadratica*.

The orbital process of the quadrate bone (*Proc. orbitalis*, PrOQ, Figs. 11, 12, 14, 15) is long, laminar, and narrow, with a rostromedial orientation from the quadrate body. The distal portion is thin and slightly curved ventrally. The dorsomedial portion of the process begins dorsally oriented and then diminishes abruptly, fusing with the central surface in all Momotidae. This dorsal projection forms the dorsal tuberosity of the orbital process (tdo, Figs. 6–8, 10), which is highly developed in *Baryphthenus ruficapillus* (Fig. 6) *B. martii*, *Momotus momota*, *M. mexicanus*, *Aspatha gularis*, and *Hylomanes momotula* and small in *Electron platyrhynchum* (Fig. 7), *E. carinatum*, and *Eumomota superciliosa* (Fig. 8).

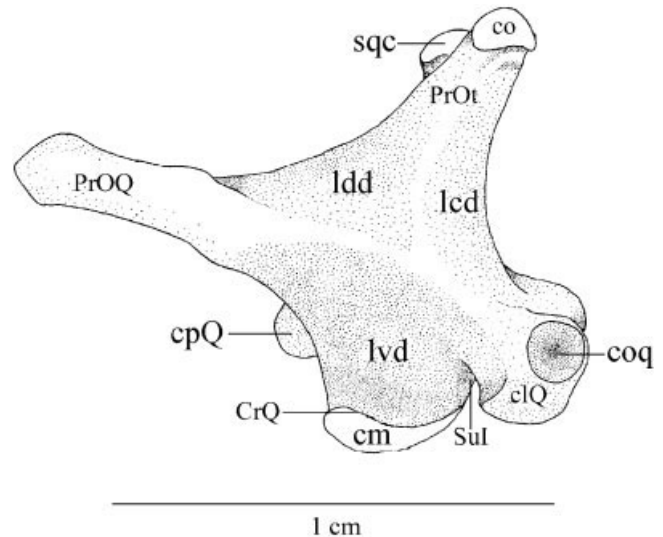
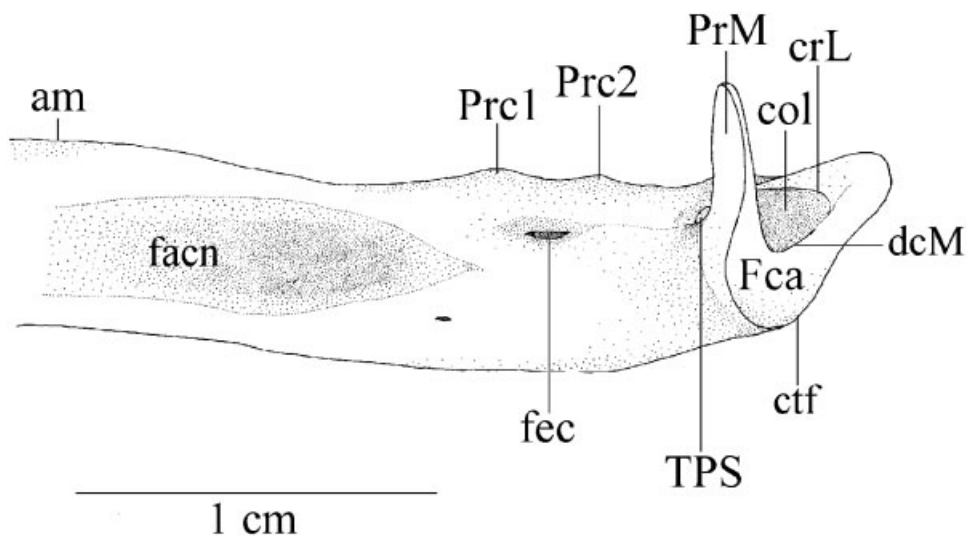


Fig. 15. Lateral view of the left quadrate bone in *Baryphthenus ruficapillus*. clQ, *Condylus lateralis* of the quadrate; cm, *Condylus medialis*; co, *Capitulum oticum*; coq, *Cotyla quadratojugal*; cpQ, *Condylus pterygoideus*; CrQ, crest of the quadrate; lcd, laterocaudal depression of the body of the quadrate; ldd, laterodorsal depression of the body of the quadrate; lvd, lateroventral depression of the body of the quadrate; PrOQ, *Proc. orbitalis* of the quadrate; PrOt, *Proc. oticus*; sqc, squamosal capitulum; Sul, *Sulcus intercondylaris*.

Fig. 16. Medial view of right mandible in *Baryphthengus ruficapillus*. am, *Angulus mandibulae*; col, *Cotyla lateralis*; crL, crest of the *Cotyla lateralis*; ctf, *Crista transversa fossae*; dcM, dorsal crest of the mandible; facn, *Fossa aditus canalis neurovascularis*, Fca, *Fossa caudalis*; fec, *Fenestra caudalis mandibulae*; Prc1, *Proc. coronoideus 1*; Prc2, *Proc. coronoideus 2*; PrM, *Proc. medialis mandibulae*; TPS, *Tuberculum pseudo-temporale*.



The otic process of the quadrate bone (*Proc. oticus*, PrOt, Figs. 14, 15) is long and thick in all species. It is articulated to the skull through two capitula, one medial and the other lateral: the otic capitulum and the squamosal capitulum, respectively.

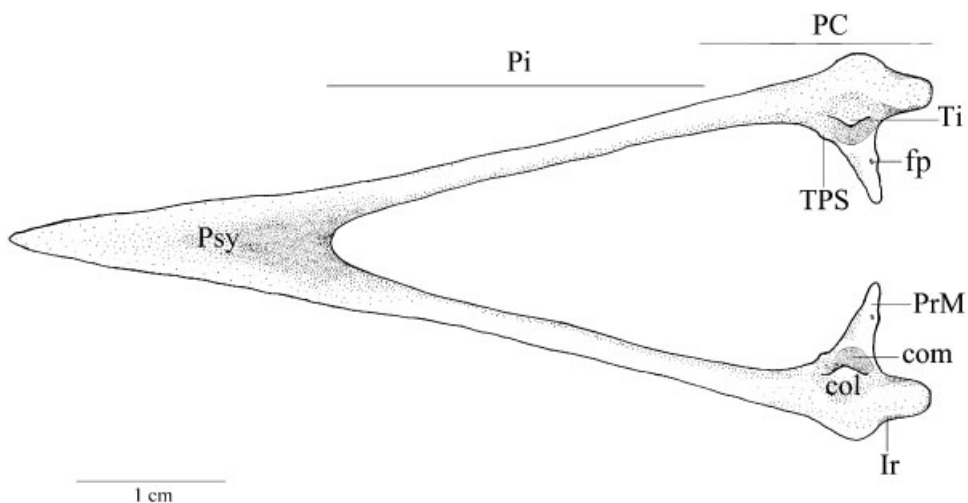
The otic capitulum (*Capitulum oticum*, co, Figs. 14, 15) in *Baryphthengus ruficapillus* is moderately more developed than the squamosal capitulum and is crescent-shaped. It is articulated to the *Pila otica* by the otic cotyla of the quadrate bone (*Cotyla quadratica otici*) and separated from the squamosal capitulum by a shallow intercapitular incisure (*Incisura intercapitularis*, In, Fig. 14).

In *Baryphthengus ruficapillus*, the squamosal capitulum (*Capitulum squamosum*, sqc, Figs. 14, 15) is articulated to the squamosal region by the squamosal cotyla of the quadrate bone (*Cotyla quadratica squamosi*) and situated caudomedially to the zygomatic process.

Ossa Mandibulae

The mandibular symphysis (*Pars symphysialis*, Psy, Figs. 17, 18) is thick, narrow, and dorsoventrally flattened, with a shallow dorsal concavity in *Baryphthengus ruficapillus*, *B. martii*, *Momotus momota* (Fig. 17), *M. mexicanus*, *Aspatha gularis* and *Hylomanes momotula*. In *Electron platyrhynchum* it is thin and extremely broad for its entire length, with a deep dorsal concavity. In *E. carinatum* and *Eumomota superciliosa* (Fig. 18) the breadth and depth of the dorsal concavity are intermediate. The mandibular symphysis accounts for about 30% of the total length of the mandible in *B. ruficapillus*, *B. martii*, and *E. platyrhynchum*; about 35% in *M. momota* and *M. mexicanus*; and about 40% in *E. carinatum*, *E. superciliosa*, *A. gularis*, and *H. momotula*. The rostral extremity tapers and flattens out dorsoventrally, becoming broader in the caudal direction. From the caudal region of the *Rostrum mandibulae*,

Fig. 17. Dorsal view of mandible in *Momotus momota*. col, *Cotyla lateralis*; com, *Cotyla medialis*; fp, *Foramen pneumaticum articulare*; Ir, *Incisura retroarticularis*; PC, *Pars caudalis*; Pi, *Pars intermedia*; PrM, *Proc. medialis mandibulae*; Psy, *Pars symphysialis*; Ti, *Tuberculum intercotylare*; TPS, *Tuberculum pseudotemporale*.



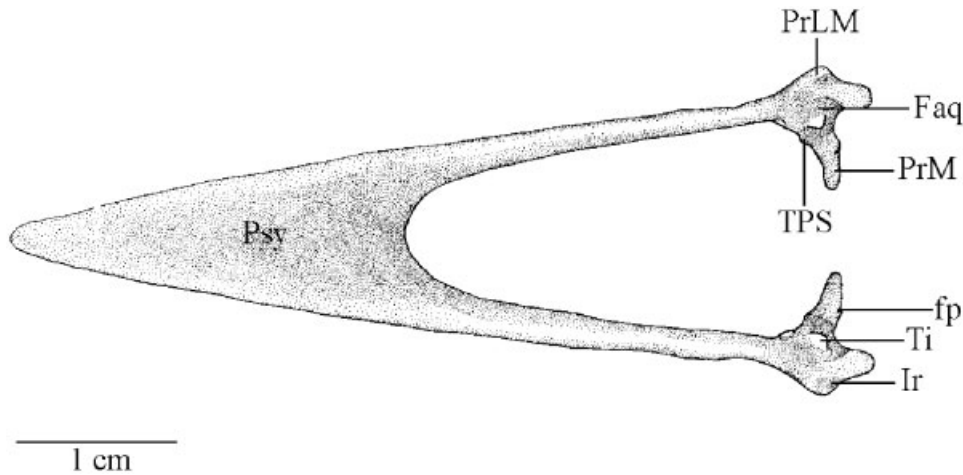


Fig. 18. Dorsal view of mandible in *Eumomota superciliosa*. fp, *Foramen pneumaticum articulare*; Ir, *Incisura retroarticularis*; Faq, *Fossa articularis quadratica*; PrLM, *Proc. lateralis mandibulae*; PrM, *Proc. medialis mandibulae*; Psy, *Pars symphysialis*; Ti, *Tuberculum intercotylare*; TPS, *Tuberculum pseudotemporale*.

this part of the mandible becomes lateromedially flattened as far as the caudal portion of the *Pars caudalis*, which expands irregularly.

The intermediate part of the ramus (*Pars intermedia*, Pi, Fig. 17) is lateromedially flattened throughout its length except in *Electron platyrhynchum*, where the rostradorsal region expands medially, and in *E. carinatum* and *Eumomota superciliosa* (Fig. 18), where an intermediate condition is seen between the mandibular symphysis and the posterior part of the mandible. Its medial surface contains a medial fossa (*Fossa aditus canalis neurovascularis*, facn, Fig. 16), which is shallow, broad, and long in all Momotidae except *E. platyrhynchum* and *E. carinatum*, where it is shallow and narrow owing to the greater rostromedial expansion of the intermediate part. The *Fenestra caudalis mandibulae* (fec, Fig. 16) is small and narrow, and covered by a lamina formed by the supraangular bone. The mandibular angle (*Angulus mandibulae*, am, Figs. 16, 19) is feebly developed, giving the mandible a slight ventral curvature.

The lateral surface of the intermediate part contains the lateral fossa (*Fossa lateralis mandibulae*), comprising two parts in all species examined: rostral (flmr, Fig. 19) and caudal (flmc, Fig. 19). The rostral fossa is deeper and narrower than the caudal fossa in all Momotidae.

The rostradorsal surface of the posterior part (*Pars caudalis*, PC, Fig. 17) contains coronoid processes 1 and 2 (*Proc. coronoideus*, Prc1 e Prc2, Figs. 16, 19). Coronoid process 1 is more developed than coronoid process 2. In *Electron platyrhynchum* both processes are dorsolaterally placed, whereas in all other species their placement is on the dorsal margin of the mandible. In *E. carinatum* they are inconspicuous and their respective positions cannot be defined. The medial surface of the posterior part contains a small pseudotemporal tubercle (*Tuberculum pseudotemporale*, TPS, Figs. 16–18), situated rostrolaterally to the medial process of the mandible.

The caudal extremity of the *Pars caudalis* is irregularly shaped. Medially is the medial process of the mandible (*Proc. medialis mandibulae*, PrM, Figs. 16–20), which is dorsomedially oriented. This process is long and narrow, with a moderately tapering distal extremity. The transverse crest (ctf, Figs. 16–20) and dorsal crest (dcM, Figs. 16–20) delimit the rostral, caudal, and ventral surfaces of the medial process. The medial region of the dorsal surface of this process contains a conspicuous pneumatic foramen (*Foramen pneumaticum articulare*, fp, Figs. 17, 18).

The retroarticular process of the mandible is absent in Momotidae.

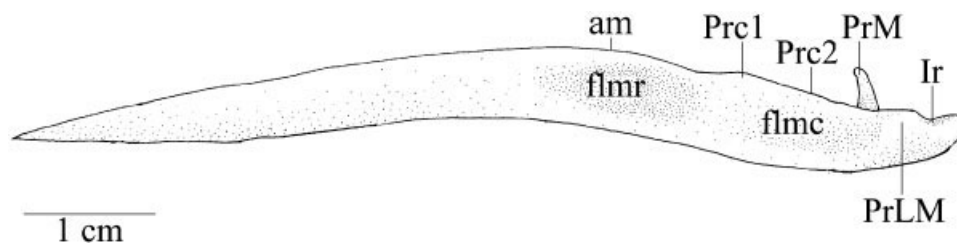


Fig. 19. Lateral view of left mandible in *Baryphthengus martii*. am, *Angulus mandibulae*; flmc, caudal part of the *Fossa lateralis mandibulae*; flmr, rostral part of the *Fossa lateralis mandibulae*; Ir, *Incisura retroarticularis*; Prc1, *Proc. coronoideus* 1; Prc2, *Proc. coronoideus* 2; PrLM, *Proc. lateralis mandibulae*; PrM, *Proc. medialis mandibulae*.

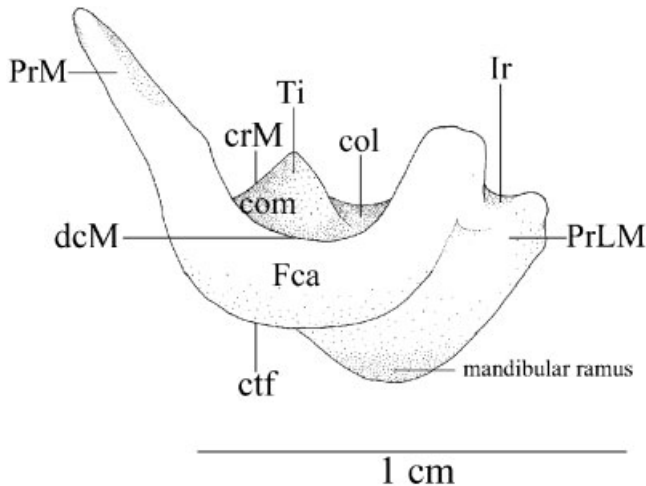


Fig. 20. Caudal view of right mandible in *Baryphthengus ruficapillus*. col, *Cotyla lateralis*; com, *Cotyla medialis*; crM, crest of the mandible; ctf, *Crista transversa fossae*; dcM, dorsal crest of the mandible; Fca, *Fossa caudalis*; Ir, *Incisura retroarticularis*; PrLM, *Proc. lateralis mandibulae*; PrM, *Proc. medialis mandibulae*; Ti, *Tuberculum intercotylare*.

The lateral process of the mandible (*Proc. lateralis mandibulae*, PrLM, Figs. 17–20) is small. Dorsomedially lies the retroarticular incisure (*Incisura retroarticularis*, Ir, Figs. 17–20), which borders on the lateral cotyla.

The shallow quadratic articular fossa (*Fossa articularis quadratica*, Faq, Fig. 18) is responsible for articulation with the condyles of mandibular process of the quadrate bone. The quadratic articular fossa contains the lateral and medial cotylae. The medial cotyla is deeper than the lateral cotyla in all the species examined. The medial cotyla (*Cotyla medialis*, com, Figs. 17, 20) is situated laterally to the medial process of the mandible and borders rostrolaterally on a conspicuous medial crest (crM, Fig. 20). The lateral cotyla (*Cotyla lateralis*, col, Figs. 16, 17, 20) is shallow except caudally, in the region containing a lateral crest (crL, Fig. 16). The conspicuous medial and lateral cotylae are separated by an extremely pronounced intercotylar tubercle (*Tuberculum intercotylare*, Ti, Figs. 17, 18, 20).

The caudoventral portion of the mandible contains a postarticular surface, the caudal fossa (*Fossa caudalis*, Fca, Figs. 16, 20). This fossa is shallow, long, and narrow in all species examined. It is bounded by the pronounced transverse crest (*Crista transversa fossae*, ctf, Figs. 16, 20). The ventral surface of the caudal portion of the mandible is flat (Fig. 20), so that the angular bone has no vertex in Momotidae.

DISCUSSION

Skull

The fusion between the frontal and lacrimal bones in Momotidae also occurs in other families of Coraciiformes, i.e., Upupidae and Phoeniculidae, and in

other families of Aves, such as Columbidae (Andrela and Donatelli, 1995) and Picidae (Donatelli, 1996). All other Coraciiformes lack the fusion, however, and have separate frontal and lacrimal bones.

The ectethmoid is narrow and feebly developed in Momotidae, contrasting with those found in Meropidae, Trogonidae, Upupidae, and Todidae. On the other hand, it is similar in shape to the ectethmoid in Coraciidae, Brachypteraciidae, and Leptosomatidae and in Dendrocolaptidae (Passeriformes) according to Donatelli (1997), although it differs from the latter in the degree of development. It is also similar in shape to the ectethmoid in Cuculiformes, particularly species of the genus *Crotophaga*, as described by Posso and Donatelli (2001), and in Musophagiformes as described by Marceliano (1996).

The size of the parietal region in Momotidae is roughly twice as wide as that of the frontal region, except in *Hylomanes momotula*, where the parietal region is about four times the size of the frontal region. According to Burton (1984), this narrowing in the region of the orbits may be associated with a broader field of vision, especially in birds that forage with an open bill or that perch, such as Phoeniculidae (Coraciiformes).

According to Baumel et al. (1993), the temporal fossa is bounded by the temporal crest and the transverse nuchal crest. Flausing et al. (1999) describe the temporal fossa as being bounded by three subdivisions of the temporal crest: the inferior temporal crest situated caudally, the superior temporal crest situated dorsorostrally, and the anterior temporal crest situated laterally. The same overall arrangement is found in this study, but two distinct patterns of boundaries for the temporal fossa were observed in Momotidae: in *Electron platyrhynchum*, *E. carinatum*, *Eumomota superciliosa*, *Aspatha gularis*, and *Hylomanes momotula* the inferior temporal crest is partially fused with the transverse nuchal crest, while in *Baryphthengus ruficapillus*, *B. martii*, *Momotus momota*, and *M. mexicanus* they remain separate and the temporal fossa is bounded only by the temporal crest, so that the transverse nuchal crest does not make contact with the temporal crest in these species.

The temporal fossa is shallow in all species of Momotidae analyzed except *Electron platyrhynchum*, *E. carinatum*, and *Eumomota superciliosa*, where it is deeper. In all species the medial portion is shallower than the lateral. This characteristic relates to the development of the external mandibular adductor system, as noted in Flausing et al. (1999), whose description of cranial myology in *Momotus momota* showed atypical development of the first bundle of *M. adductor mandibulae externus superficialis*, which originates in and occupies the entire temporal fossa. The second bundle of the same muscle is feebly developed and originates in the medial portion of the temporal fossa, which is shallow.

Electron platyrhynchum, *E. carinatum*, *Eumomota superciliosa*, *Aspatha gularis*, and *Hylomanes momotula* have a protuberance in the supraoccipital region, while in *Baryphthengus martii* this structure varies from one individual to another, and in other species is absent. However, a study of cranial anatomy in Coraciiformes and Piciformes by Burton (1984) makes no mention of this characteristic for Momotidae, nor are there references in the literature to this structure in other families of Aves.

The two portions of the maxillopalatine are fused medially with each other and dorsally with the nasal septum. There is only one concavity on the median line. According to Burton (1984), despite its desmognathous palate, the median line of fusion of the maxillopalatines in *Momotus momota* is incomplete. This was also observed in *M. momota* by Flausino et al. (1999) and in the other species of Momotidae analyzed in this study. Burton (1984) argues that the presence of a desmognathous palate provides a support against the stress of catching and biting prey and is also directly associated with the development of the *M. pterygoideus dorsalis*, which originates in the maxillopalatine.

The maxillary process of the palatine is broad and long in *Baryphthengus ruficapillus*, *B. martii*, *Momotus momota*, and *M. mexicanus*, contrasting with that of *Electron platyrhynchum*, *E. carinatum*, *Eumomota superciliosa*, and *Aspatha gularis*, in which it is narrower. In *Hylomanes momotula* the process is even broader and shorter than in all other species; this may be associated with its feeding habits, which have not been studied in detail.

According to Sibley and Ahlquist (1990), the basipterygoid process is absent in Coraciiformes or, when it exists, it is rudimentary. Bock (1964) argues that in most birds this process is vestigial — very small, not articulated to the pterygoid, or completely absent. Among Momotidae the process is observed in *Momotus mexicanus*, *Electron platyrhynchum*, *E. carinatum*, *Eumomota superciliosa*, *Aspatha gularis*, and *Hylomanes momotula*, where it is very small. According to Bock (1964), the only function performed by the basipterygoid process seems to be to limit the movements of the pterygoid, diminishing cranial kinesis. This process has certainly lost its functional importance in cranial kinesis, acquiring other functions among the various patterns observed in the different taxa of Aves that have preserved it. Its function remains obscure, however (Bock, 1964).

The pterygoid is situated between the quadrate and palatine bones, forming a connection between the palate and quadrate that in some species is associated with the vomer and prevents the palatine and quadrate from breaking and/or dislocating from the ventral surface of the braincase (Bühler, 1981). The pterygoid exhibits the *Pes pterygoidei*, a rostral extension toward the palatine. Donatelli (1996) observed this structure in Picidae, naming it rostral

extension of the pterygoid. It differs from that found in Momotidae, however, by extending only in a rostradorsal direction, while in Momotidae it extends both rostradorsally and rostroventrally, according to Baumel et al. (1993). The dorsal muscular process of the pterygoid is small in Momotidae, contrasting with that found in Picidae (Donatelli, 1996), in which it is highly developed. Bock (1964) argues that the development of the dorsal muscular process of the pterygoid is related to the development of the *M. protractor pterygoidei*, particularly in Picidae, where both the protractor muscle of the pterygoid and the dorsal muscular process of the pterygoid are highly developed, as ratified by Donatelli (1996). Flausino et al. (1999) observed that in *Momotus momota* the *M. protractor pterygoidei* is inserted in the aponeurosis X, which in turn is inserted in the dorsocaudomedial surface of the pterygoid, particularly the pterygoid protractor tubercle, corresponding to the dorsal muscular process of the pterygoid described for Momotidae.

The jugal arch plays an important role in transmitting muscular strength from the quadrate bone to the caudoventral region of the upper jaw (Bühler, 1981). The caudal extremity of the jugal arch in Momotidae has a dorsal curvature. In this respect they differ from Alcedinidae (Burton, 1984) and Picidae (Donatelli, 1996), but resemble *Dendrocolaptes certhia* (Dendrocolaptidae [Donatelli, 1997]) and New World Cuculiformes (Posso and Donatelli, 2001), in which the dorsal curvature is less pronounced.

The interorbital septum in Momotidae is totally fused except in *Hylomanes momotula*, *Eumomota superciliosa*, and *Electron carinatum*, where the degree of ossification is low due to the presence of the *Fonticuli interorbitales*, also well developed in *H. momotula*. The *Fonticuli interorbitales* is weak in *E. superciliosa* and *E. carinatum*, and absent in other species. Verheyen (1955) described the interorbital septum in Momotidae as lacking an aperture, which corresponds to the *Fonticuli interorbitales* described for Momotidae, except *E. superciliosa*. In the present study, however, this fonticuli was also found in *H. momotula* and *E. carinatum*. According to Baumel et al. (1993), the presence of the *Fonticuli interorbitales* reflects an unusual deficiency in the interorbital septum.

Among the Momotidae examined, *Electron platyrhynchum*, *E. carinatum*, and *Eumomota superciliosa* differ from the other species in the dorsal flattening of the upper jaw, which is caudally very broad, with its breadth exceeding its height. However, with the exception of *Hylomanes momotula*, in which the upper jaw occupies about 50% of the total skull length, in the other species examined the upper jaw occupies roughly 60%. Burton (1984) says the flattened shape of the bill in *E. platyrhynchum* remains enigmatic and can be explained only if more is known about its feeding habits. This argument is

supported by Remsen et al. (1993), where it is also assumed that the flat bill in *E. platyrhynchum* may be associated with feeding habits. For Burton (1984) and Bühler (1981), cranial morphology is influenced by a wide variety of factors such as feeding and nest building, and this applies particularly to the upper jaw. Bock (1966) argues that because many forces exert pressure on the upper jaw, the acquisition of a stronger structure is an advantage.

Burton (1984) points out that the skull is subjected to a number of forces during feeding and nest building, arguing that such forces must profoundly influence morphology. Thus, bird species that exhibit this behavior have developed certain osteological and arthrological features of an adaptive nature, minimizing the movements of the jaw apparatus and palate and enabling them to withstand the forces caused by interaction with prey or objects in the environment. The orbital process of the quadrate bone plays an important role in reducing protractive movement of the mandible when it touches the caudal surface of the orbit or the laterosphenoid region. Burton (1984) also notes that some birds, such as Bucerotidae, have an intumescence in the orbitosphenoid region that may reflect repeated contact between the orbital process of the quadrate bone and the orbitosphenoid region. The intumescence described by Burton (1984) is termed *Area muscular aspera* in Momotidae, where it is well developed. Donatelli (1996, 1997) described this structure in Picidae and Dendrocolaptidae as an intumescence of the orbitosphenoid region. It is also well developed in these families. However, the development of the *Area muscular aspera* in both Momotidae and Picidae would appear to corroborate the doubts raised by Burton (1984), especially in light of the fact that these two families have similar feeding and nest-building habits.

The orbital process of the quadrate bone in Momotidae is similar to the development of the process in Picidae described by Donatelli (1996). The main difference is the absence of a dorsal tuberosity in Picidae. In describing *Campylorhamphus procurvoides* (Dendrocolaptidae), Donatelli (1997) mentions a feature similar to the distal extremity of the orbital process of the quadrate bone, but refers to two distinct parts, the rostral and caudal. According to the same author, the distal extremity of the orbital process of the quadrate bone is the origin of the *M. pseudotemporalis profundus*. This is corroborated by Flausino et al. (1999).

According to Zusi (1967), the quadrate condyles play an important role in coordinating the movements of the upper jaw and, in association with the postorbital ligament, increase coordination in keeping the surfaces of the joint in close contact while the mandible is depressed. In Momotidae the lateral condyle is the most developed condyle in the mandibular process of the quadrate bone, projecting farther in a ventral direction than the lateral and cau-

dal condyles. Burton (1984) says this condyle performs a key additional function in preventing dislocation of the mandible.

Mandible

The movements made by the mandible are not only determined by muscular insertion into the mandibular rami or by the participation of ligaments and the morphology of the quadrate-mandible articulation, but also by the exceptional mobility of the quadrate bone in association with the jugal arch, palate, and braincase. The presence or absence of articular zones in the region of the mandible also contributes (Bühler, 1981).

Bock and Kummer (1968) argue that the strongest pressure is exerted on the dorsal and ventral portions of the mandible, and that little action takes place in the central region of the mandible. Moreover, the mandible is more rigid in the dorsoventral direction, where it is supported by a thicker bone structure than in the lateromedial plane, where the bone is less thick and affords greater flexibility. This can be seen in the intermediate part of the mandible, which is lateromedially flattened, making the mandible thin and broad in the dorsoventral direction and far more flexible lateromedially.

The mandible is relatively straight in Momotidae, with no ventral curvature. This feature is heightened by the development of the mandibular angle, which is small in the taxa examined here.

With the exception of *Electron platyrhynchum*, *E. carinatum*, and *Eumomota superciliosa*, where the mandibular symphysis is extremely broad and deep, in the other species this portion of the mandible is narrow and tapers rostrally, forming a shallow dorsal concavity. According to Bock (1964), the shape and development of the mandible are directly associated with feeding habits in all birds.

According to Bock and Kummer (1968), the quadrate bone is not the only support for the mandible. Besides the cranial muscles and ligaments that are inserted into the mandible, the medial process of the mandible functions as a secondary articulation with the skull. Burton (1984) agrees with Bock and Kummer (1968), highlighting the importance of this process in dislocation of the mandible.

The development of the medial process of the mandible in Momotidae resembles those of certain New World Cuculiformes (Posso and Donatelli, 2001), as well as Galbulidae, except *Jacamerops aurea* (Donatelli, 1992), while also appearing similar to that of *Columbina squammata* (Andrela and Donatelli, 1995) in both development and shape. Burton (1984) named the medial process "the medial arm," observing it in an advanced stage of development in Alcedinidae, Momotidae, and Coraciidae, feeble development in Meropidae, Todidae, and Upupidae, and absence in Leptosomatidae, Phoeniculidae, Bucerotidae, and Piciformes (Galbulidae,

Bucconidae, Capitonidae, Indicatoridae, Ramphastidae, Picidae).

The medial fossa of the mandible is the site of insertion for the muscles of the internal mandibular adductor system, particularly the *Musculus pseudotemporalis superficialis* and *pseudotemporalis profundus* (Donatelli, 1992; Flausino et al., 1999). The lateral fossa of the mandible in Momotidae is subdivided into two portions, rostral and caudal. However, Burton (1984) does not mention the existence of this subdivision in Coraciiformes and Piciformes.

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