

# Phylogeny and classification of the Bucconidae (Aves, Galbuliformes) based on osteological characters

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**Abstract.** The puffbirds (Bucconidae) are relatively poorly studied birds whose intrafamilial relationships have not yet been explored within a phylogenetic framework in a published study. Here, we performed a parsimony analysis of osteological data obtained following the examination of all the genera and 32 out of the 36 species recognized in Bucconidae currently. The analysis yielded eight equally parsimonious trees (426 minimum steps). Ambiguous relationships were observed only in *Notharcus ordii*, *Malacoptila fusca*, and *Nonnula rubecula*. Notably, *Bucco* was polyphyletic, leading to the resurrection of *Cyphos* and *Tamatia*. In addition, the osteological data provided a well-resolved phylogeny (topological dichotomies) and the support indices indicated that most of the nodes were robust at all hierarchical levels. We thus propose the first revised classification of the Bucconidae.

**Key-Words.** Puffbirds; Morphology; Systematics.

## INTRODUCTION

The Bucconidae (puffbirds) comprises 10 genera and 36 species (Remsen *et al.*, 2020) endemic to the Neotropics, with the highest diversity in the Amazon Basin. They are mostly silent and secretive birds, perching motionless for long periods (Rasmussen & Collar, 2002), which makes it challenging to study them in the Neotropical forests. Therefore, the behavior, breeding, morphology, and systematics of these arboreal, colorful, and insectivorous birds are poorly understood.

Some studies have been conducted on puffbirds, Steinbacher (1937) published the first anatomical description of some species of the Bucconidae, while Höfling & Alvarenga (2001) compared the shoulder girdle of this family with those of other birds, and Ladeira & Höfling (2007) described the cranial osteology of seven genera in the Bucconidae. However, both of the latter studies did not entail systematics analyses. The first analysis of phylogenetic interrelationships among the Bucconidae was performed by Witt (2004) to estimate the mitochondrial DNA evolution rates for application in Neotropical avian biogeography studies, while Duarte (2015) performed a phylogenetic analysis including *Nystalus* based on molecular datasets. However, the findings of both

studies remain unpublished. Ferreira, Aleixo, Ribas & Santos (2016) performed a phylogenetic analysis to infer biogeography patterns of puffbirds in South America; however, they restricted themselves to the genus *Malacoptila*. In addition, no studies on within-family relationships based on modern analytical methods have been published (Remsen *et al.*, 2020).

Consequently, this study presents: a) a phylogenetic hypothesis for the Bucconidae based on osteological data and b) a formal classification that reflects relationships inferred from the hypothesis, for the first time, in these Neotropical birds.

## MATERIAL AND METHODS

The present study compared 200 complete skeletons belonging to 44 species. We studied 123 main skeletons belonging to 32 Bucconidae species. The study encompasses almost all the *Bucconidae* species, excluding *Bucco noanamae* Hellmayr, 1909; *Nonnula amaurocephala* Chapman, 1921 and *Notharcus pectoralis* (Gray, 1846). Further, our sample of the *Nystalus striolatus* complex (from Peru and Bolivia) actually refers to the recently splitted *Nystalus obamai* Whitney, Piacentini, Schunck, Aleixo, Sousa, Silveira & Rêgo,

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2013. Galbulidae was selected as the out-group based on 77 specimens from 7 genera and 12 species. All specimens had been prepared previously (dried structures) and belong to collections in Brazil and USA (Table 1).

The comparative osteology examinations were carried out under stereomicroscopes (9.6x–60x). Some bone structures (characters 2, 6, 11, 15, 38, 40, 45, 59, 74, 75, 80, 89, 92, 100, 101, 103, 105, 109, 112, 115, 120, 123, 131, and 133, Appendix 1) were measured with a Mitutoyo digital caliper with a 0.01-mm accuracy. We adopted the averages of three measurements and the relative sizes

(percentages) of each structure were compared with the relative sizes of other structures to avoid misunderstandings about different body sizes within the Bucconidae/Galbulidae species (Figs. 1-5).

The anatomical nomenclature was according to the proposal in *Nomina Anatomica Avium* (Baumel & Witmer, 1993) and was supplemented by recent suggestions by Posso & Donatelli (2005).

Characters for which information was unavailable were coded as missing (?) and multistate characters that were considered binary characters were treated

**Table 1.** List of the specimens (alphabetical order). FMNH = Field Museum of Natural History; LSU, USA = Louisiana States University, USA; MZUSP = Museu de Zoologia Universidade de São Paulo, Brazil; USNM = United States National Museum, USA; MPEG = Museu Paraense Emilio Goeldi, Brazil.

Species	Museum and number of collection
<b>Bucconidae</b>	
<i>Bucco capensis</i> Linnaeus, 1766	LSU 111183, 118362, 118363; MZUSP 87231, USNM 621739, FMNH 330305, 318888.
<i>Chelidoptera tenebrosa</i> (Pallas, 1782)	LSU 111187, 101291, 101290; MPEG 1029, 1030.
<i>Cyphos macrodactylus</i> (Spix, 1824)	LSU 93946, 74869, 62751, 65001; FMNH 321004, 321000, 315414, 321005.
<i>Hapaloptila castanea</i> (Verreaux, 1866)	LSU 1815, 92014.
<i>Hypnelus ruficollis</i> (Wagler, 1829)	FMNH 339641, 372629.
<i>Malacoptila fulvogularis</i> Sclater, 1854	LSU 107094, 95365; FMNH 291778, 291779, 321035, 321036.
<i>M. fusca</i> (Gmelin, 1788)	LSU 111184, 111185, 107093, 107092, 165799.
<i>M. mystacalis</i> (Lafresnaye, 1850)	FMNH 376707.
<i>M. panamensis</i> Lafresnaye, 1847	LSU 108757, 108758, 108759.
<i>M. rufa</i> (Spix, 1824)	MZUSP 88209; LSU 118364, 118367, 118365, 118366, 553364, 562213; MPEG 2707, 2708.
<i>M. semicincta</i> Todd, 1925	LSU 52694, 70217, 131478; MZUSP 89415.
<i>M. striata</i> (Spix, 1824)	MZUSP 89408, 89409, 89410, 89411, 89412, 89413, 89414.
<i>Micromonacha lanceolata</i> (Deville, 1849)	LSU 118368, 171211.
<i>Monasa atra</i> (Boddaert, 1783)	MZUSP 87231; LSU 68991; FMNH 317350, 317351, 317352.
<i>M. flavirostris</i> Strickland, 1850	LSU 111186, 121041.
<i>M. morphoeus</i> (Hahn & Küster, 1823)	MZUSP 88279; LSU 48581, 62749, 62750, 93947, 101289, 153957; FMNH 290502.
<i>M. nigrifrons</i> (Spix, 1824)	LSU 73066, 118568, 70218, 13215, 48775, 52695, 125757, 136722; MZUSP 88139, MPEG 94.
<i>Nonnulla brunnea</i> Sclater, 1881	LSU 48776.
<i>N. frontalis</i> (Sclater, 1854)	LSU 108760, 108761, 108762, 108763.
<i>N. ruficapilla</i> (Tschudi, 1844)	LSU 99592; FMNH 290247.
<i>N. rubecula</i> (Spix, 1824)	LSU 118369; MZUSP 87232.
<i>N. sclateri</i> Hellmayr, 1907	LSU 50771.
<i>Notharcus hyperhynchus</i> (Sclater, 1856)	FMNH 330301; USNM 500432; LSU 108748.
<i>N. macrorhynchus</i> (Gmelin, 1788)	LSU 93945; USNM 623128.
<i>N. ordii</i> (Cassin, 1851)	FMNH 318882.
<i>N. swainsoni</i> (Gray, 1846)	MZUSP 89416.
<i>N. tectus</i> (Boddaert, 1783)	LSU 136721, 165798; USNM 610217.
<i>Nystalus chacuru</i> (Vieillot, 1816)	LSU 125759, 151641; MZUSP 89417, 89418, 89419, 89420; MPEG 19, 252.
<i>N. maculatus</i> (Gmelin, 1788)	FMNH 334413; LSU 153898, 125758.
<i>N. radiatus</i> (Sclater, 1854)	LSU 108756.
<i>N. striolatus</i> (Pelzeln, 1856) or <i>N. obamai</i> Whitney et al., 2013	LSU 131477; FMNH 291777.
<i>Tamatia tamatia</i> (Gmelin, 1788)	USNM 622256; LSU 151640; FMNH 05547.
<b>Galbulidae</b>	
<i>Brachygalba lugubris</i> (Swainson, 1838)	LSU 136720; USNM 345911, 345912, 559511, 622889, 637212, 428703; FMNH 317347, 330287.
<i>B. salmoni</i> (Spix, 1824)	LSU 108755; USNM 430945, 432631.
<i>Caucalias leucogastra</i> (Vieillot, 1817)	LSU 93944; USNM 345910; FMNH 330295.
<i>Galbalcyrhynchus leucotis</i> Des Murs, 1845	LSU 118567, 118353.
<i>G. purusianus</i> Goeldi, 1904	LSU 48773.
<i>Galbina ruficauda</i> (Cuvier, 1816)	LSU 31900, 101288; USNM 555700, 612055, 612056, 612057, 15989, 322980, 289820, 344108, 344109, 345907, 345909, 612066, 345908; FMNH 313424, 313425, 330293, 334410, 335024, 337030.
<i>Galbula albirostris</i> Latham, 1790	LSU 50918, 111180, 118355, 118356; USNM 621409, 621976; FMNH 317348, 317349, 318877, 318878, 343795.
<i>G. cianicollis</i> Cassi, 1851	USNM 492312, 492329; FMNH 330290.
<i>G. cyanescens</i> Deville, 1849	LSU 107091, 48774; FMNH 289330, 289331, 289332, 320995, 320996, 320997, 320998, 320999, 433242.
<i>G. galbula</i> Linnaeus, 1766	USNM 500436.
<i>Jacamerops aureus</i> (Muller, 1776)	LSU 87600, 118361; USNM 429779, 430890, 492873, 637205, 430943; FMNH 397899.
<i>Urogalba dea</i> (Linnaeus, 1758)	LSU 131476, 165796; USNM 492280, FMNH 330299, 376705, 376706.

as not comparable (-) to avoid character duplication. Equal weights were assigned to the characters and all multistate characters were treated as unordered (Appendices 1 and 2).

The phylogenetic relationships were obtained using TNT software (Goloboff *et al.*, 2008). Heuristic searches algorithm was selected to identify the best scored trees, and MAXTREES was set at 1000 trees. Random additive sequence analysis and tree-bisection-reconnection branch swapping algorithms were also adopted, saving 10 trees per replicate (MulTrees). Bootstrap (500 pseudoreplicates) and ratchet-minimized support (Bremer) indices were calculated to assess the nodes support.

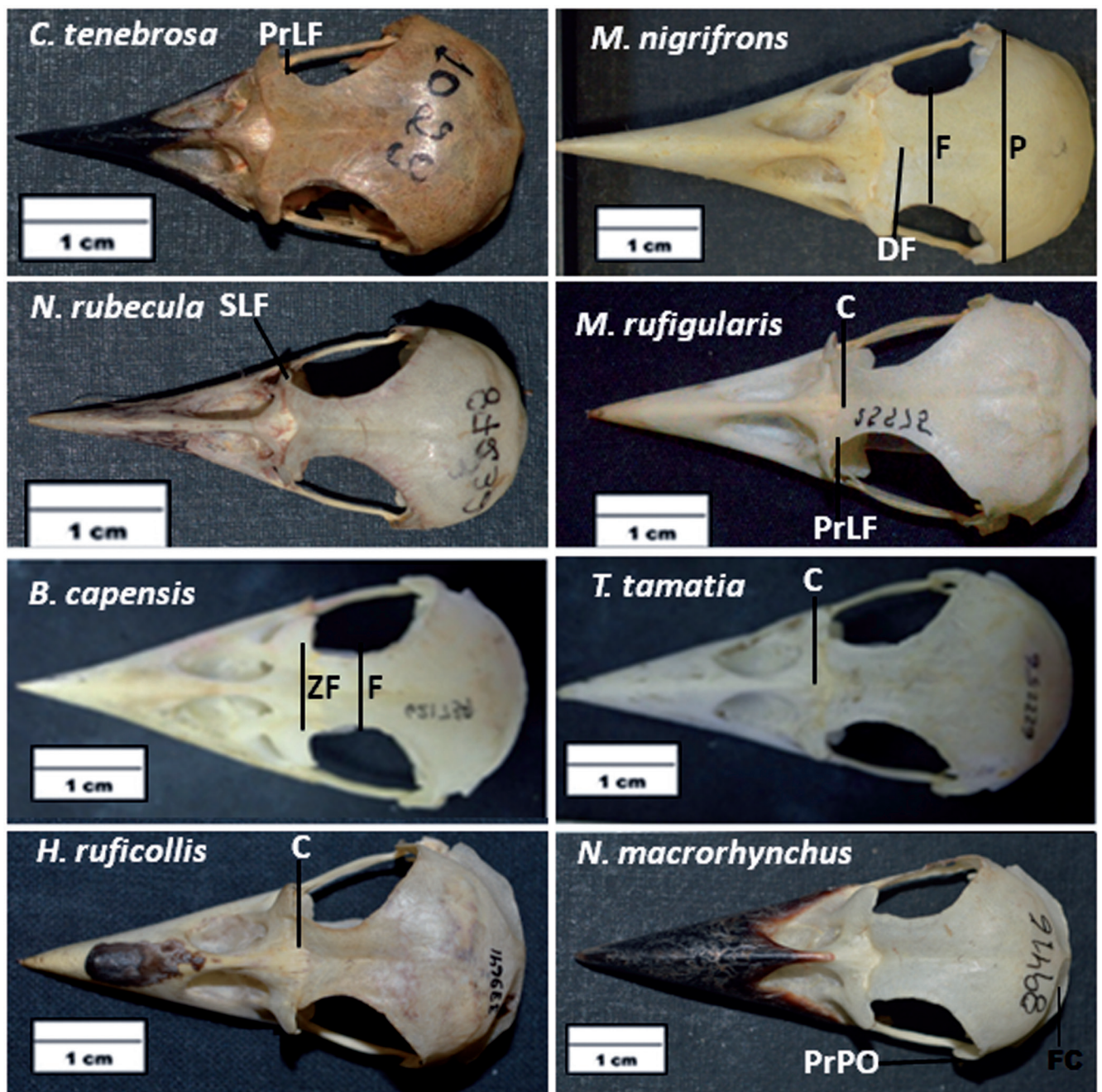
The species nomenclature and classification were according to Remsen *et al.* (2020). Changes in nomencla-

ture are proposed in line with the International Code of Zoological Nomenclature (ICZN, 1999).

### RESULTS AND DISCUSSION

Different states from 135 characters (87 cranial and 48 postcranial) were selected (Appendix 1) and distributed among 33 taxa to reconstruct puffbird phylogeny. The matrix is available in Appendix 2.

The synapomorphies uniting the major clades are mentioned below and also they are shown in the Figs. 1 to 5. However, the synapomorphies among the species in each genus, the number of steps, consistency indices, and polarizations of each character are presented in Appendix 3.

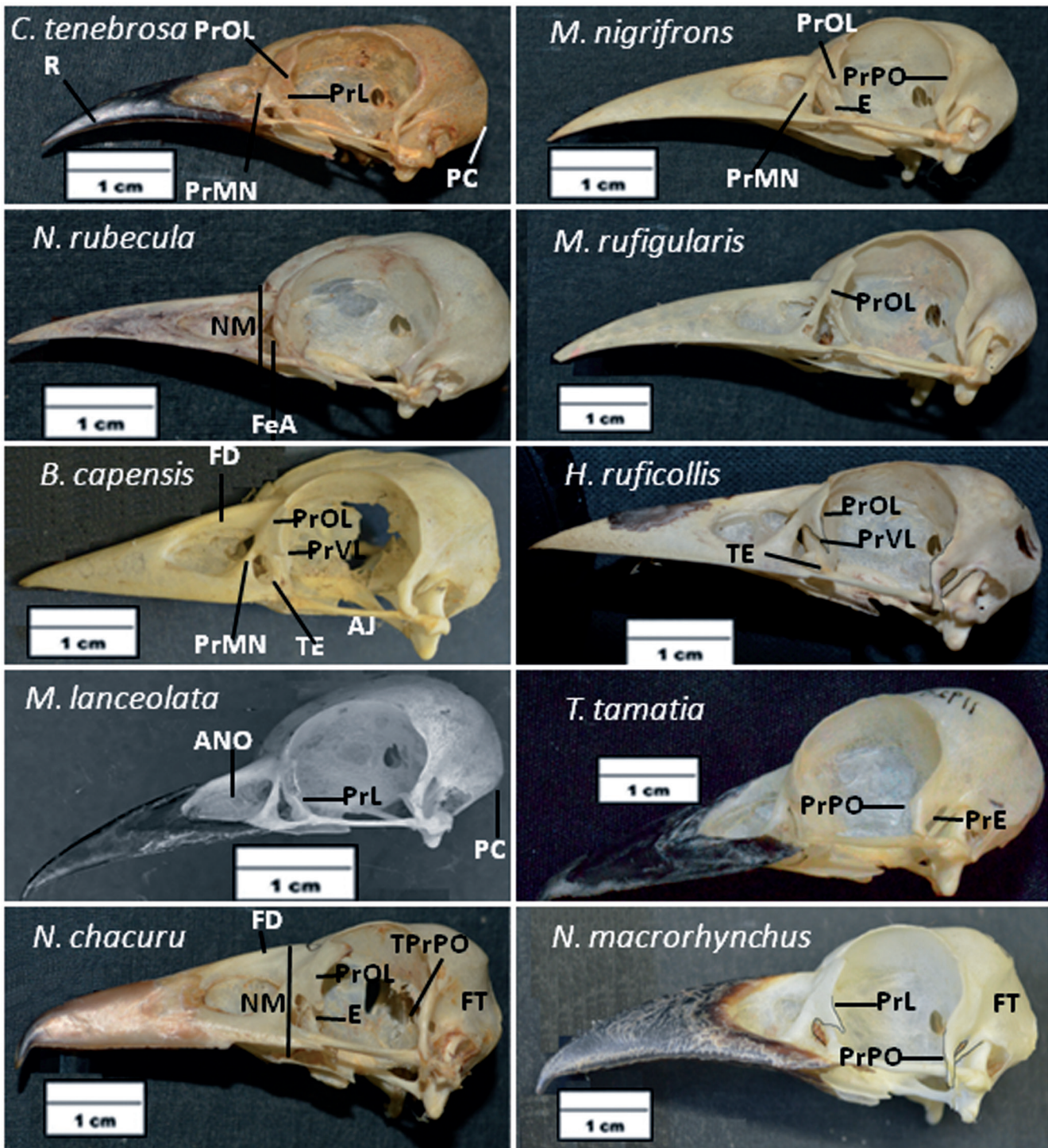


**Figure 1.** Dorsal view of the skull. C = concavity in the *fissura zona flexoria craniofacialis*; DF = *depressio frontalis*; F = *os frontale*; FC = *fossa caudalis*; P = *os parietale*; PrFL = *proc. lacrimalis os frontale*; PrPO = *proc. postorbitalis*; SFL = *suture between os frontale and os lacrimalis*; ZF = *zona flexoria craniofacialis*.

The analysis recovered eight equally parsimonious trees, each with 426 steps. Fig. 6 presents the strict consensus tree. The analysis revealed that most of the genus within Buccconidae recognized currently is valid, with numerous apomorphies observed on the basal stem of each clade.

According to Rasmussen & Collar (2002), Galbulidae and Buccconidae are similar in terms of behavior, external morphology, and anatomy, excluding the shape of the spinal cord and the number of ribs. Höfling & Alvarenga

(2001) also observed five exclusive similarities between them on the shoulder girdle. However, the present study revealed major osteological differences between the two families: 56 from the skull/mandible and 24 from the post-cranial skeleton. Although they are considered to belong to the same order, the osteological modifications suggest they diverged from one another early. The present study also reveals polymorphism in *os lacrimalis*, *fossa temporalis*, and *os palatinum* within the Buccconidae, as

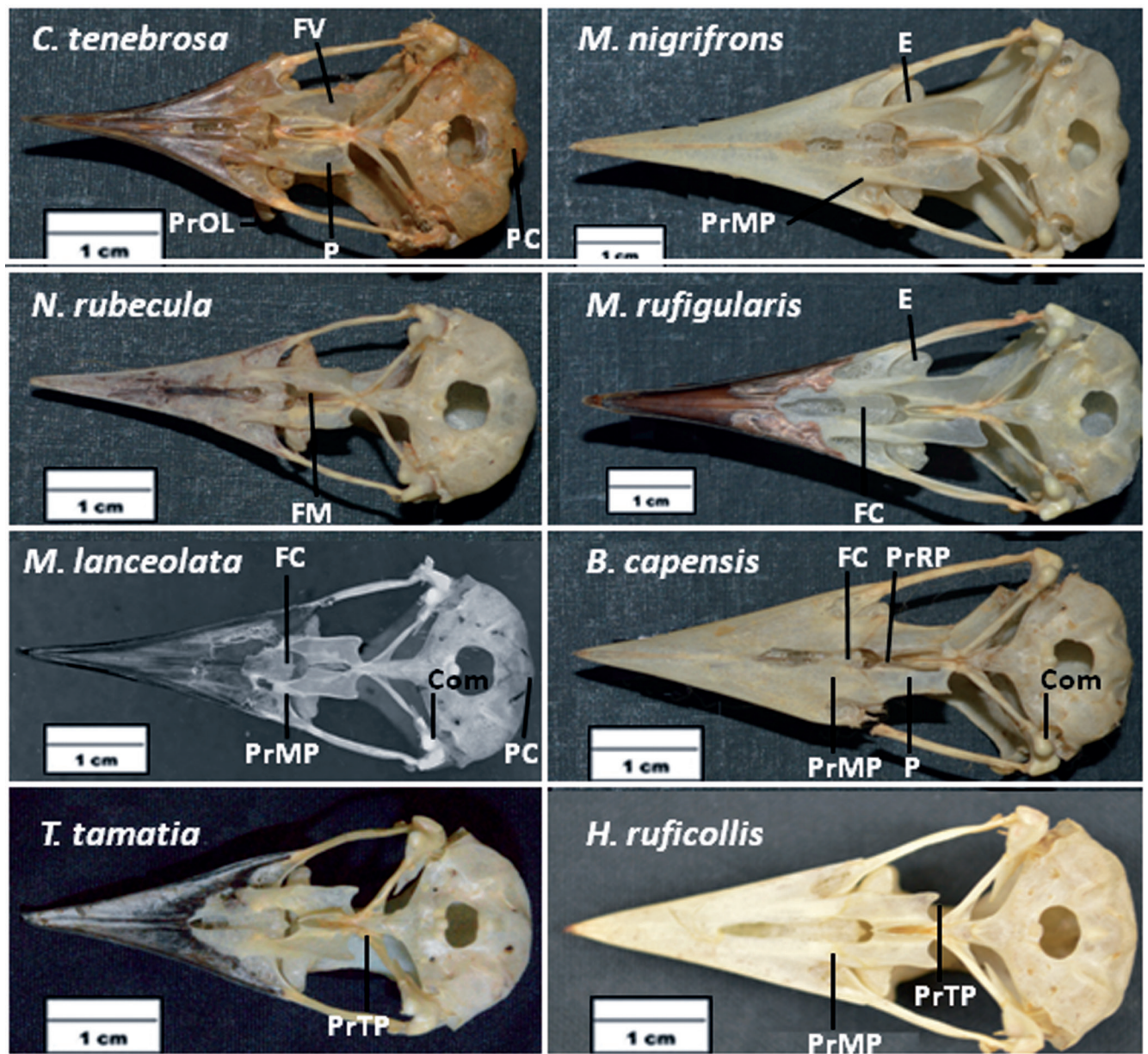


**Figure 2.** Lateral view of the skull. AJ = arcus jugalis; ANO = apertura nasi ossea; CrD = crista dorsalis os pterigoideus; CrV = crista ventralis os palatinum; E = os ectethmoidale; FD = facies dorsalis of the maxilla (upper jaw); FeA = fenestra anteorbitalis; FT = fossa temporalis; NM = nasal/maxillary height; PC = proeminentia cerebellaris; PRE = proc. esquamalis; PrL = proc. lacrimalis; PrMN = proc. maxillaris os nasale; PrOL = proc. orbitalis os lacrimale; PrPO = proc. postorbitalis; PrTP = proc. transplatinum os palatinum; PrVL = proc. ventralis os lacrimale; TE = tuberculum os ectethmoidale; TPrPO = tuberculum of the proc. postorbitalis.

described in Ladeira & Höfling (2007). However, the *proc. postorbitalis*, *os ectethmoidale*, *os quadratum*, the upper and lower jaws, the relative sizes of *tibiotarsus/tarsometatarsus/femur* and the *second/forth toes* and numerous features of the shoulder girdle and *pelvis* are also highly variable and, therefore, would facilitate the establishment of primary homologies.

Most of the primary homologies established in Ladeira & Höfling (2007), which were listed in support of *Monasa/Malacoptila/Nonnula/Chelidoptera*, were recovered as symplesiomorphies in our analysis. This is particularly notable in the case of *Chelidoptera tenebrosa* (Pallas, 1782) as it emerges as an isolated lineage from (sister-group of) the other *Bucconidae*. *Chelidoptera tenebrosa* exhibits major osteological variations in comparison with the other *Bucconidae* species, particularly in the skull structures. Consequently, the apomorphies that support the *C. ten-*

*ebrosa* clade (*Chelidopterinae*) are as follows: the *proc. lacrimalis os frontale* is laterally large (Fig. 1, character 3, series of transformation 0-2); the *proeminentia cerebellaris* is tubercular and laterally large (Figs. 2 and 3, 12, 1-2); *proc. lacrimalis* is thick with medial curvature and large with lateral concavity (Fig. 2, 24, 1-3); the *proc. orbitalis os lacrimale* is lateromedially large with medial curvature (Figs. 2 and 3, 2, 28, 1-2); the *proc. maxillaris os nasale* is narrow (bar-shaped) and laterally large (Fig. 2, 42, 1-3); the *fossa ventralis os palatinum* is deep, long and large (Fig. 3, 58, 2-4); the caudal portion *os palatinum* is larger than the rostral portion (Fig. 3, 59, 0-2); the *fossa caudalis mandible* is narrow and shallow (Fig. 4, 87, 1-2); the *proc. dorsalis terminalis ischii* broads 5% of the *synsacrum* (Fig. 5, 102, 0-1) and the apex of the *ramphotheca* has a long curvature (Fig. 2, 134, 1-2). Puffbirds are forest and sit-and-wait hunters; however, *C. tenebrosa* lives in more open coun-



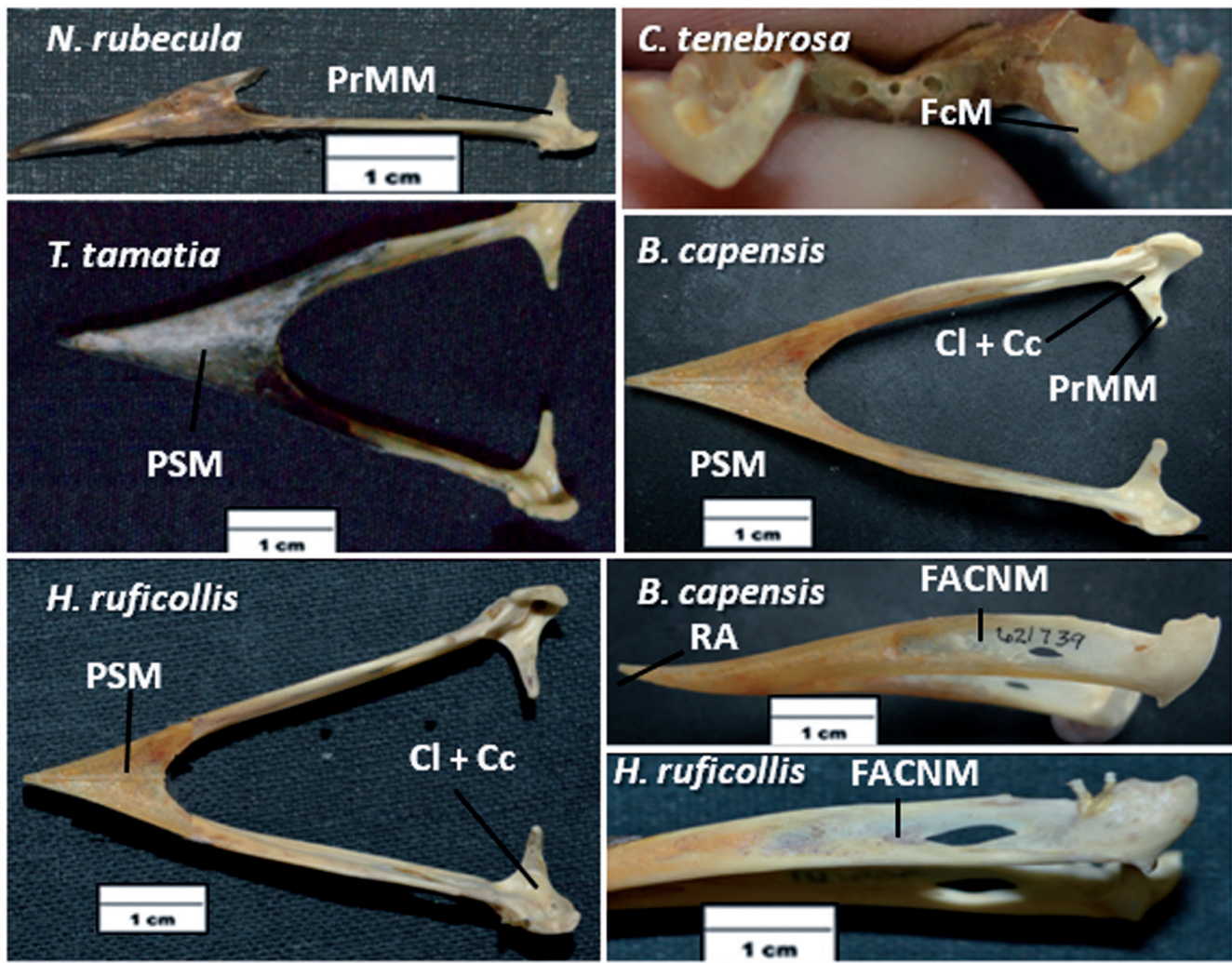
**Figure 3.** Ventral view of the skull. Com = *condylus medialis os quadratum* is longer and larger; E = *os ectethmoidale*; FC = *fossa choanalis*; FM = *fossa medialis*; FV = *fossa ventralis*; P = *os palatinum*; PC = *proeminentia cerebellaris*; PrOL = *proc. orbitalis os lacrimale*; PrMP = *proc. maxillaris os palatinum*; PrPP = *proc. pterigoideus os palatinum*; PrRP = *proc. rostradorsalis os palatinum*; PrTP = *proc. transpalatinum os palatinum*; PrVL = *proc. ventralis os lacrimale*.

try and captures insects from open perches, in addition to exhibiting distinctive external morphology, particularly a dark plumage and a short beak, and it is a unique swallow-winged puffbird (Sick, 1997; Rasmussen & Collar, 2002). For the reasons above, we placed *C. tenebrosa* in a monotypic and new sub-family, Chelidopterinae, as opposed to a nominate subfamily, Bucconinae.

The synapomorphies of the sub-family Bucconinae are as follows: the *proc. postorbitalis* is large and long, close to *arcus jugalis* (Fig. 2, 15, 0-1); the tuberculum in the rostroventral portion of the *proc. postorbitalis* is short (Fig. 2, 16, 0-1); the ventral portion of the *proc. orbitalis os lacrimale* is long, narrow, but sharp in its extremity (Fig. 2, 31, 0-2); the *os ectethmoidale* is thick (Figs. 2 and 3, 32, 0-1); the *foramem orbitonasalis lateralis* is large (36, 0-1); the *proc. transpalatinus os palatinum* is long (Fig. 3, 56, 0-1); the *fonticuli lateralis* of *ala preacetabularis* is short (91, 1-2); the caudal tuberculum in the lateral surface of *ala preacetabularis* is prominent (Fig. 5, 96, 0-1); the tuberculum on the dorsal surface *sulcus articularis* with *os coracoideum* is vestigial (Fig. 5, 104, 0-1); the *proc. craniolateralis* is long (20% of the total length *os sternum*) (Fig. 5, 109, 0-1); the *sulcus intercnemialis* is narrow and

shallow (Fig. 5, 130, 0-1); the *facies gastrocnemialis os tibiotarsus* is large and deep (Fig. 5, 132, 0-1) and the total length *os tarsometatarsus* reaches 90% the total length *os femoris* (Fig. 5, 133, 0-1).

Within the Bucconinae, *Monasa* Vieillot, 1816, is the sister-group to the remaining species with robust node support and the highest number of synapomorphies (see above). The findings justified maintaining *Monasa* in the same subfamily as the other Bucconinae. *Monasa* is monophyletic, supported by six synapomorphies with high support indices. The clade of the genus is supported by the *depression frontalis* shallow (Fig. 1, 1, 2-1); the *os frontale* reaches 50% of the *os parietale* (Fig. 1, 2, 1-0); the *os ectethmoidale* is short, sharp and long (Figs. 2 and 3, 33, 2-1); the tuberculum *os ectethmoidale* is prominent (Fig. 2, 35, 1-2); *proc. maxillaris os nasale* is bar-shaped (Fig. 2, 42, 1-2) and the *os tibiotarsus* is 40% longer than the *os femoris* (Fig. 5, 131, 1-0). Its monophyly has never been questioned. The *Monasa* species are quite similar to each other based on their plumage and they are the most vocal puffbird species, with a large repertoire of calls and songs, and they often give very loud shouts (Rasmussen & Collar, 2002). In addition, they

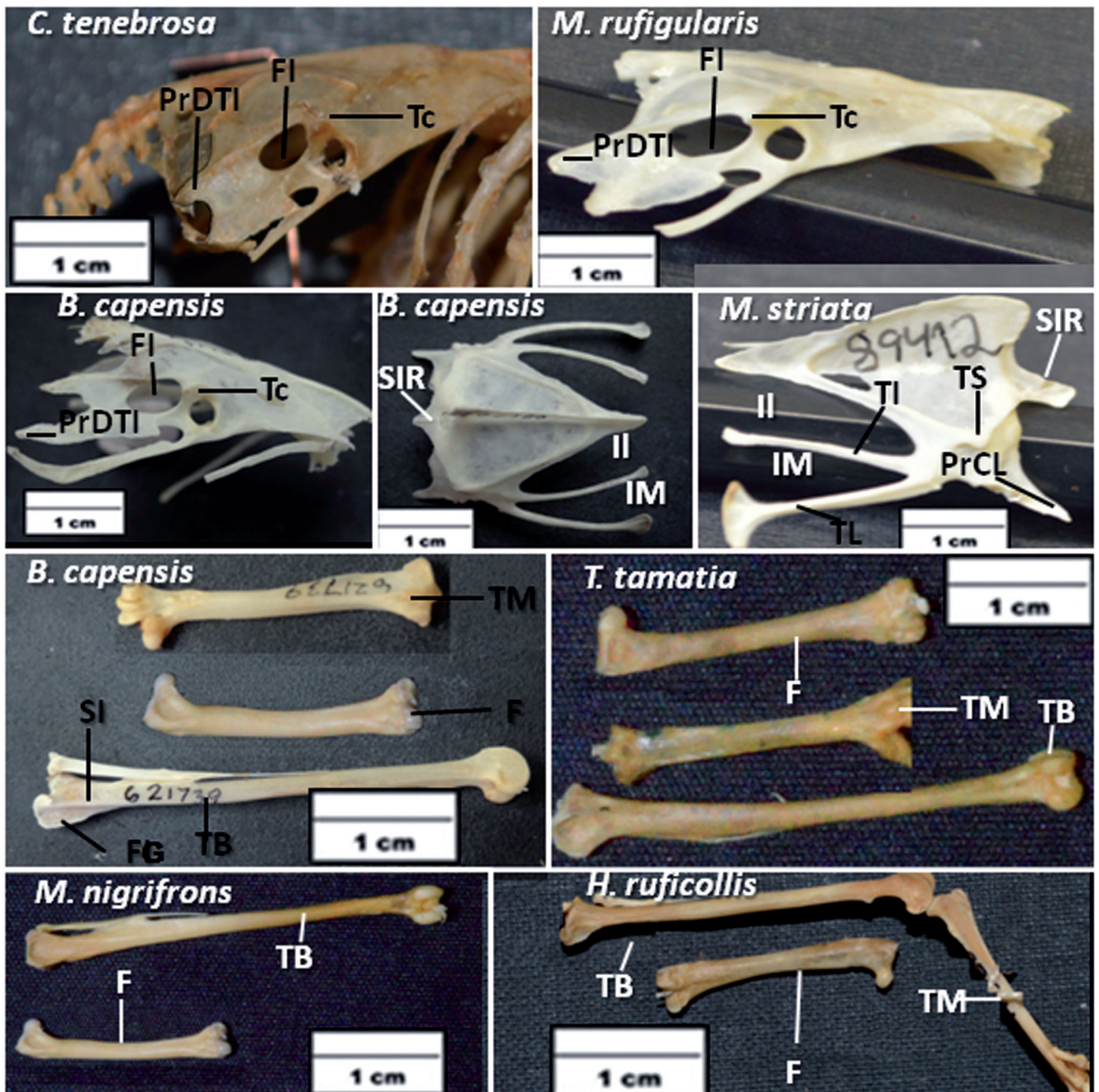


**Figure 4.** Mandible: Dorsal view of *N. rubecula*, *T. tamatia*, *B. capensis* and *H. ruficollis*; caudal view of *C. tenebrosa* and lateral view of *B. capensis* and *H. ruficollis*. Cl + Cc = cotyla lateralis and cotyla caudalis; FACNM = fossa aditus canalis neurovascularis mandible; FcM = fossa caudalis mandibulae; PrMM = Proc. medialis mandibulae; PSM = Pars simpliciis mandibulae; RA = rostral apex of the mandible.

are more gregarious and are found in flocks (Sick, 1997). In our view, the characteristics justify the placement of *Monasa* within a new tribe of its own, Monasini, within the Bucconinae. The internal arrangement of the *Monasa* species based on the osteological analysis is dichotomous: (*Monasa atra* [Boddaert, 1783]/*Monasa morphoeus* [Hahn & Küster, 1823]) and (*Monasa flavirostris* Strickland, 1850/*Monasa nigrifrons* [Spix, 1824]). *Monasa flavirostris* and *M. nigrifrons* were grouped together based on five synapomorphies and had higher support indices; however, the *M. atra*/*M. morphoeus* branch had low support indices, and it was supported by four synapomorphies.

*Monasa flavirostris* has plumage that is similar with that of *M. atra*, and it is thought to be related closely to *M. atra* and *M. morphoeus* (Rasmussen & Collar, 2002). Although the similarities seem plesiomorphic, further systematics analyses should be carried out within *Monasa* based on other characters as sources of data.

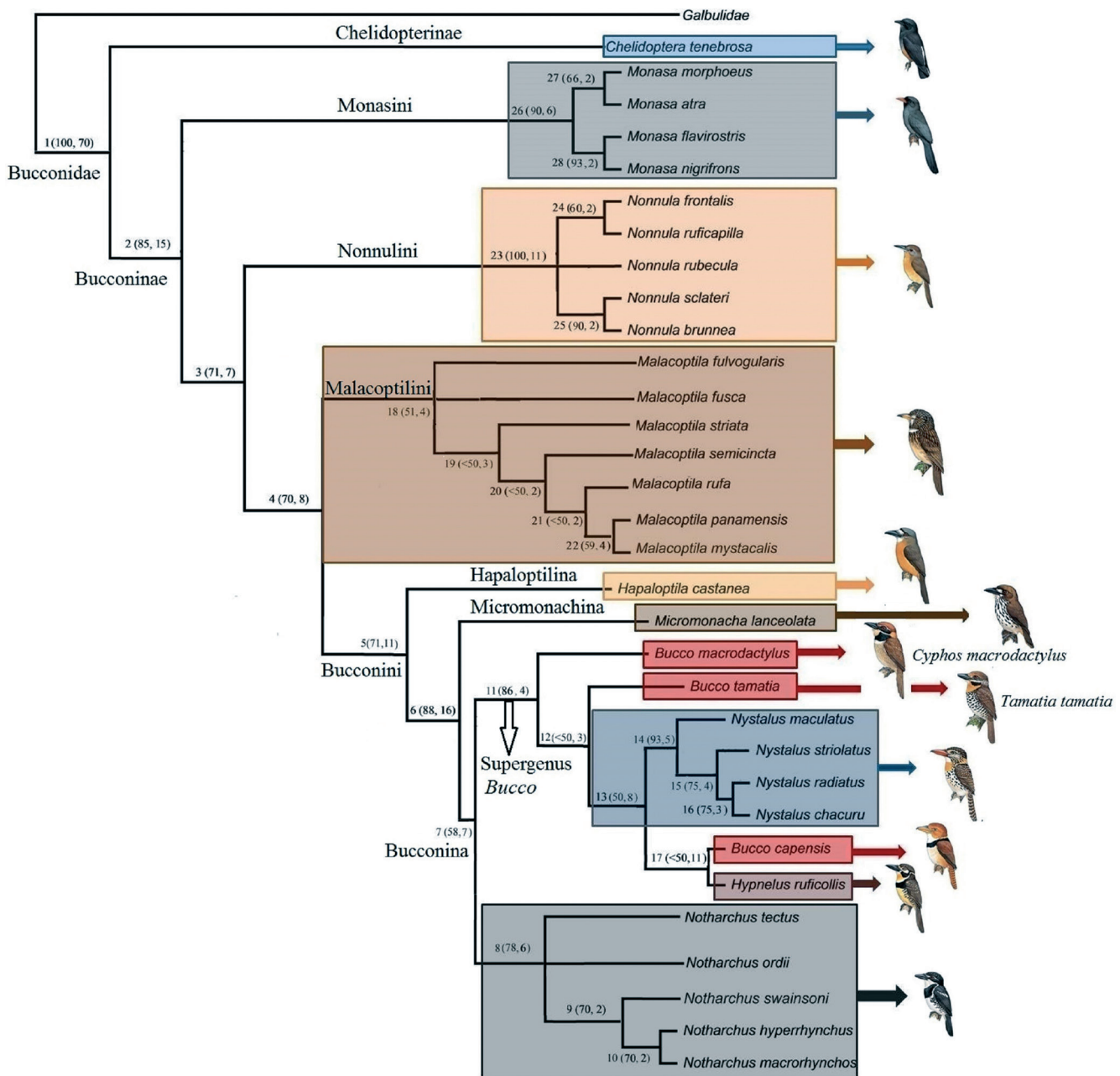
The following node (3, Fig. 6) places *Nonnula* Sclater, 1854 as a sister-group of the other Bucconinae, excluding *Monasa*, with high support indices and eight synapomorphies: the suture between *os frontale* and *os lacrimalis* is short (Fig. 1, 23, 0-1); the *fenestra anteorbitalis* is triangular (Fig. 2, 37, 0-1); the caudal portion of the



**Figure 5.** Lateral view of the pelvic region of *C. tenebrosa*, *M. ruficularis* and *B. capensis*; dorsal view of the *os sternum* of *B. capensis* and lateral view of the *os sternum* of *M. striata*; lateral view of *os tibiotarsus*, *tarsometatarsus* and *os femoris* of *B. capensis*, *T. tamatia*, *M. nigrifrons* and *H. ruficollis*. F = *os femoris*; FG = *facies gastrocnemialis os tibiotarsus*; FI = *foramen ilioschiadicum*; IL = *Incisura lateralis* or *fenestra lateralis*; IM = *incisura medialis* or *fenestra medialis*; PrCL = *proc. craniolateralis*; PrDTI = *proc. dorsalis terminalis ischii*; SI = *suclus intercnemialis*; SIR = *spina interna rostri*; TB = *os tibiotarsus*; Tc = *caudal tuberculum* in the lateral surface of *ala preacetabularis*; TI = *trabecula intermedia*; TL = *trabecula lateralis*; TM = *os tarsometatarsus*; TS = *tuberculum sulcus articularis*.

upper jaw (*os nasale* and *os maxillare*) (NM) is dorsally large (about 70% of the narrow caudoventral portion of the upper jaw) (Fig. 2, 40, 2-1); the *fossa medialis os palatinum* is large (Fig. 3, 53, 0-1); the *foramen ilioschiadicum* is 50% of the total length of the *synsacrum* (Fig. 5, 92, 2-0); the *trabecula intermedia* of the *os sternum* is 60% of the total length *os sternum* (Fig. 5, 112, 1-0); the tuberculum on the dorsal surface *os metacarpale* is prominent (Fig. 5, 126, 2-1); 4<sup>th</sup> toes is longer than 2<sup>th</sup> toes (*ossa digitorum pedis*) (135, 0-1). The node grouping all *Nonnula* species is robust and supported by 12 synapomorphies: the *os frontale* reaches 20% of the *os parietale* (Fig. 1, 2, 1-2); the *proc. suprameaticus* is long (Fig. 2, 11, 0-1); the *proeminentia cerebellaris* is tubercular and laterally large (12, 1-2); the *proc. postorbitalis* is short (reduced)

(15, 1-0); the *proc. orbitalis os lacrimale* is reduced and triangular-shaped (28, 1-3); the *proc. transpalatinus* is long and sharp (Fig. 3, 56, 1-2); the tuberculum of the *proc. opticus os quadratum* is absent (72, 1-0); the *proc. medialis mandible* is short (8% mandible) (Fig. 4, 80, 2-1); the *fossa caudalis mandible* is narrow and shallow (Fig. 4, 87, 1-2); the caudal tuberculum of the *ala preacetabularis* is prominent and large (Fig. 5, 96, 1-2); the *trabecula lateralis os sternum* reaches 70% of the *os sternum* (Fig. 5, 111, 0-1) and the *os tarsometatarsus* is longer than the *os femoris* (Fig. 5, 133, 1-2). Therefore, the osteological data and the small body size (12-14 cm) support the recognition of *Nonnula*. In addition, the plumage has a reddish-brown pattern on the underparts and the wings and tails (underparts) are dark-brown, and they are usu-



**Figure 6.** Phylogenetic relationships for Bucconidae species based on osteological data (Maximum Parsimony; Strict Consensus; 426 minimum steps; CI = 0,50; RI = 0,72). Numbers (1-28) indicate the nodes (branches). Values at the nodes in parentheses represent Bootstrap and Bremer indices, respectively. Red squares show the *Bucco* polyphyly. Illustrations of the Bucconidae species belong to the Handbook of Birds of the World – volume 7 – Bucconidae chapter (Rasmussen & Collar, 2002).



ally found in the *second-growth* forest galleries (Sick, 1997; Rasmussen & Collar, 2002). Witt (2004) demonstrated that *Nonnula* is the most divergent genus of puffbirds based on molecular data and, therefore, the genus is the most basal in the Witt (2004) phylogeny. Considering the (subjective) degree of distinctness of *Nonnula* compared to *Monasa*, and the remaining Bucconinae, we opted to place *Nonnula* in the tribe Nonnolini. Although the position of *N. rubecula* is unclear, the results of the osteological analysis highly supported the arrangement (*Nonnula ruficapilla* [Tschudi, 1844]/*Nonnula frontalis* [Sclater, 1854]) (*Nonnula sclateri* Hellmayr, 1907/*Nonnula brunnea* Sclater, 1881). The topology corroborates the taxonomic history based on plumage similarity and distribution. Plumage is very similar among *N. sclateri*, *N. brunnea*, and *N. rubecula*. They are also sympatric in the southwest Amazon Basin and they have been historically considered closely related, whereas *N. sclateri* has been considered a race of *N. brunnea* (Rasmussen & Collar, 2002). Plumage is similar between the allopatric *N. ruficapilla* and *N. frontalis*, and they have at times also been treated as conspecific (Rasmussen & Collar, 2002). Although *N. amaurocephala* was not included in the present study, it is traditionally considered closely related to *N. ruficapilla* and *N. frontalis* (Rasmussen & Collar, 2002). Therefore, the latter three species are considered a superspecies in the classification proposed here.

High support indices (branch 4, Fig. 6) and 10 synapomorphies suggest a sister relationship between *Malacoptila* Gray, 1841 and the tribe Bucconini: the *proc. lacrimalis os frontale* is short (Fig. 1, 3, 0-1); the medial concavity in the *fissura zona flexoria craniofacialis* is deep (Fig. 1, 5, 0-1); the ventral portion of the *proc. orbitalis os lacrimale* is long, narrow, medially curved and reaching the *arcus jugalis* (Fig. 2, 31, 2-0); the ventral portion *os ectethmoidale* is triangular in shape (Fig. 3, 33, 2-3); the *foramem orbitonasalis lateralis* is vestigial (36, 1-0); the *fossa choanalis* is long (Fig. 3, 57, 1-0); the *proc. pterigoideus* of the *os palatinum* is short (Fig. 3, 61, 2-1); the *ala postacetabularis ilii* is large (Fig. 5, 88, 2-1); the *proc. dorsalis terminalis ischia* is medially large and the apex is sharp (Fig. 5, 103, 1-0) and the *proc. interclavicularis* is rounded (117, 2-1). Five synapomorphies grouped the species of *Malacoptila*: the ventral portion of the *proc. orbitalis os lacrimale* is long, narrow, but straight (Fig. 2, 31, 0-1); the *fossa ventralis os palatinum* is deep and long (58, 2-3); the *foramen ilioschium* is 60% of the total length of the *synsacrum* (Fig. 5, 92, 0-1); the *incisura lateralis* or *fenestra lateralis* with equal length to the *incisura medialis* or *fenestra medialis os sternum* (113, 0-1) and the tuberculum on the dorsal surface *os metacarpale* is vestigial (126, 1-0). They also exhibit major similarities with regard to plumage (white moustaches and the rear, flanks, and bellies are streaked) and DNA, and historically, there is no controversy about *Malacoptila* monophyly (Sick, 1997; Rasmussen & Collar, 2002; Ferreira et al., 2016). Therefore, the inclusion of *Malacoptila* in the tribe Malacoptilini is prudent. The osteological characters were not adequate for the elucidation of the relationship of *M. fusca* with the other species. However, according to Ferreira et al.

(2016), the species is most closely related to *Malacoptila semicinca* Todd, 1925 based on four concatenated genes (Bayesian Inference). Although the support indices have low values, the other species are grouped based on four synapomorphies (branch 19, Fig. 6). The hypothesis provides high resolution information for the other species of *Malacoptila*, but they have low support index values, excluding the *Malacoptila mystacalis* (Lafresnaye, 1850)/*Malacoptila panamensis* Lafresnaye, 1847 branch. Historically, the two species have been considered conspecific, since they exhibit similar plumage and behavior characteristics and they are sympatric in the Andes of Colombia with *Malacoptila fulvogularis* Sclater, 1854 (Rasmussen & Collar, 2002). *Malacoptila mystacalis* is missing in the molecular analysis of Ferreira et al. (2016) and they concluded that *M. panamensis* is a sister-group of all *Malacoptila* species, excluding *M. fulvogularis*. Such a topology was not observed in our analysis. However, both molecular (Ferreira et al., 2016) and osteological hypotheses demonstrated that *M. fulvogularis* is a sister taxon of the other *Malacoptila* species. Even more notable, *Malacoptila striata* (Spix, 1824), which is restricted to the Atlantic forest of Brazil, is related most closely with species distributed in the Amazon Basin based on both osteological and molecular data (Ferreira et al., 2016). Actually, the topology of *Malacoptila* presented herein is inconsistent with common distribution and historical taxonomy (excluding the cases of *M. mystacalis* and *M. panamensis*), with some inconsistency with molecular phylogeny (Ferreira et al., 2016) and most of the branches have low support indices and few synapomorphies. In most respects, the relationships within *Malacoptila* remain inconsistent with molecular data.

Node support (71, 11, branch 5, Fig. 6) and 14 synapomorphies unite the *Haploptila/Micromonacha/Notharchus/Bucco/Nystalus/Hypnellus* clade: the *fossa temporalis* is long (90% of the lateral portion of the skull and medially close to each other) (Fig. 2, 6, 0-1); the *proc. maxillaris os nasale* is narrow (bar-shaped) (Fig. 2, 42, 1-2); the *proc. maxillaris* of the *os palatinum* is laterally large (Fig. 3, 51, 1-0); the *proc. rostradorsalis os palatinum* is vestigial (55, 1-0); the *fossa choanalis* is vestigial (narrow) (Fig. 3, 57, 0-2); the *crista ventralis os palatinum* is prominent and large (Fig. 2, 62, 1-2); the *crista dorsalis os pterigoideus* is short and dorsally large (Fig. 2, 64, 1-2); the rostral apex of the *ossa mandibulae (os dentale)* is curved (Fig. 4, 73, 2-1); the *pars simphysialis mandibulae* is short (about 40% of the total length of the mandible) (Fig. 4, 75, 2-1); the *fonticuli lateralis* of *ala preacetabularis* is present (90, 1-0); the *crista spinosa synsacri* is narrow and short, but prominent (93, 1-2); the *proc. cranio-lateralis* is longer (25 to 30% of the total length of the *os sternum*) (Fig. 5, 109, 1-2); the width of the *crista deltopectoralis os humerus* is large (121, 2-1); the rostral apex of the rhamphotheca is ventrally and strongly curved (134, 1-2).

The Bucconini clade has high support indices (branch 7, Fig. 6) and there are eight synapomorphies: the lateral extension of the *zona flexoria craniofacialis* is equal to the lateral extension *os frontale* (Fig. 1, 4, 1-0); the medial concavity in the *fissura zona flexoria craniofacialis*

is deep and long (more caudally extended) (Fig. 1, 5, 1-2); the *proc. esquamosalis* is the longest among puffbirds (either 90% of this distance or reaching the *arcus jugalis*) (Fig. 2, 10, 0-1); the *proc. orbitalis os lacrimale* is laterally large with sharp projection in the laterodorsal extremity (Fig. 2, 29, 0-1); the lateral tuberculum on the caudal extremity of the *arcus jugalis* is prominent (Fig. 2, 67, 2-1); the *condylus medialis os quadratum* is longer and larger (Fig. 3, 70, 1-2); the *cotyla lateralis* and the *cotyla caudalis mandible* are fused to each other and shallow (Fig. 4, 82, 1-2); the caudal tuberculum in the lateral surface of *ala preacetabularis* is vestigial or absent (96, 1-0); the expansion *carinae* into *trabecula medialis* is short and crest in shape (114, 2-1). Ladeira & Höfling (2007) also observed numerous skull similarities among *Bucco/Notharchus/Nystalus* and they have strong and long beaks, in addition to large heads (Rasmussen & Collar, 2002). Therefore, we classified the group as tribe Bucconini.

*Hapaloptila* Sclater, 1881 and *Micromonacha* Sclater, 1881 are sister-groups of the subtribe Bucconina. All the arrangements above are robust based on the support indices (branches 5 and 6, Fig. 6) and high numbers of synapomorphies. *Hapaloptila castanea* (Verreaux, 1866) can be distinguished from the other puffbirds based on the following apomorphies: the *os frontale* reaches 50% of the width of *os parietale* (2, 1-0); the *proc. lacrimalis os frontale* is laterally large (3, 1-2); the *proc. orbitalis os lacrimale* is straight and large (Fig. 2, 31, 0-3); the *proc. pterigoideus* is vestigial (tubercular) (61, 1-2); the *proc. medialis mandible* is short (8% of the total length of the *mandible*) (80, 2-1); the *crista iliaca dorsalateralis* is prominent and long (95, 1-2); the caudal tuberculum of the *ala preacetabularis* is prominent and large (triangular shape) (96, 1-3); the *trabecula intermedia* of the *os sternum* reaches 50% of the total length of the *os sternum* (112, 0-1); the *proc. interclavicularis* is rounded, large and more prominent (117, 1-2); and in the *ossa digitorum pedis* the 4<sup>th</sup> toe is longer than the 2<sup>th</sup> (135, 1-0). In addition, *Hapaloptila castanea* (Verreaux, 1866) is the only puffbird known to live in highlands. It is also the largest puffbird (25 cm) and it has some unique features on its plumage: a black band across the forehead, the upper parts and the tail are dark-brownish grey and the under parts are orange-rufous (Rasmussen & Collar, 2002).

*Micromonacha lanceolata* (Deville, 1849) is the smallest puffbird (13 cm) and the puffbird with the shortest tail (Rasmussen & Collar, 2002). The species can be diagnosed based on the *proeminentia cerebellaris* tubercular but laterally large (Figs. 2 and 3, 12, 1-2), the *proc. lacrimalis* is filiform and long (Fig. 2, 24, 1-0), the *apertura nasi ossea* is long (20% of the upper jaw) (Fig. 2, 45, 2-1), the *proc. maxillaris os palatinum* is narrow (51, 0-1), the *angulus rostromedialis os palatinum* not fused to each other (54, 1-0), the *fossa choanalis* is short and rounded (Fig. 3, 57, 2-1), the *crista dorsalis os pterigoideus* is short (Fig. 2, 64, 2-1), the *fonticuli lateralis ala preacetabularis* is long and large (91, 2-1), the *foramen ilioschium* reaches 60% of the *synsacrum* (92, 0-1), the *crista spinosa synsacri* is narrow and short (93, 2-1), the *proc. ventralis terminalis ischii* reaches between 25% to 20% of the *synsacrum*

(100, 1-0), the *proc. dorsalis terminalis ischii* is large with its apex rounded (103, 0-4); the *spina interna rostri* reaches 20% of the total length of the *os sternum* (106, 1-2), the *crista deltopectoralis os humerus* is short (it reaches 20% of the total length of the *humerus*) (120, 1-0), the *crista deltopectoralis os humerus* is reduced (121, 1-0) and the apex of the ramphotheca is slightly curved (134, 2-1).

Therefore, the large sets of apomorphies (mentioned above) in addition to their phylogenetic positions and the unique characteristics in both *Hapaloptila* and *Micromonacha* indicate ancient cladogenesis. Therefore, they are both considered monotypic subtribes in the classification proposed here.

The supergenus *Bucco* is justified by high support indices (branch 11, Fig. 6) and six synapomorphies: the dorsal portion of the *os ectethmoidale* is long, but not in contact with the *os lacrimale* (34, 2-1); the *proc. maxillaris os nasale* is narrow (bar-shaped) (Fig. 2, 42, 3-2); the *facies dorsalis* of the *maxilla* (upper jaw) is prominent and rounded (Fig. 2, 43, 0-1); the *proc. transpalatinus os palatinum* is vestigial (Fig. 3, 56, 1-0); the *fonticuli lateralis* of *ala preacetabularis* is long and large (Fig. 5, 90, 0-1) and the length of the *incisura lateralis* or *fenestra lateralis* is equal to the length of the *incisura medialis* or *fenestra medialis* of the *os sternum* (113, 0-1).

Notably, the traditionally accepted *Bucco* (Remsen et al., 2020) is polyphyletic (branch 11, Fig. 6: red square), as well as in Rasmussen & Collar (2002) based on the findings of Witt (2004). Both *B. macrodactylus* Spix, 1824 and *B. tamatia* (Gmelin, 1788) appeared as the earliest diverging lineages within Bucconini (branches 12 and 13, respectively, Fig. 6) and *Bucco capensis* is closely related to *Nystalus* and *Hypnellus ruficollis* (branches 13 and 17, Fig. 6).

Although the bootstrap index is low, 12 synapomorphies support the relationship between *Bucco capensis* and *Hypnellus ruficollis* (branch 17, Fig. 3) strongly: the sharp projection of the *proc. ventralis os lacrimale* is not parallel to the *proc. ventralis os ectethmoidale* (Fig. 2, 26, 0-1); the ventral portion of the *proc. orbitalis os lacrimale* is long, narrow and straight (Fig. 2, 31, 0-1); the tuberculum in the rostroventral portion *os ectethmoidale* is long and dorsally larger (Fig. 2, 35, 2-3); the *proc. maxillaris* of the *os palatinum* is thick (Fig. 3, 51, 0-2); the *pars simpliciis mandible* is short (about 30% of the total length of the *mandible*) (Fig. 4, 75, 1-2); the *fossa aditus canalis neurovascularis mandible* is long and deep (Fig. 4, 78, 1-2); the caudal tuberculum in the lateral surface of *ala preacetabularis* is prominent and large (96, 1-2); the *spina interna rostri* is reduced (20% of the total length of *os sternum*) (Fig. 5, 106, 0-2) and narrow (laterally flattened) (Fig. 5, 107, 1-0); the *incisura lateralis* or *fenestra lateralis* is longer to the *incisura medialis* or *fenestra medialis os sternum* (Fig. 5, 113, 1-0); the *proc. interclavicularis* is rounded, large and more prominent (117, 1-2) and the *os tarsometatarsus* is longer than the *os femoris* (Fig. 5, 133, 1-2). *Bucco capensis* is closely related to *H. ruficollis*; however, we considered them distinct genera because of the high number of autapomorphies in their historical taxonomy. In addition, they vary from each other based on plumage, ecology, and behavior (Sick, 1997; Rasmussen & Collar, 2002).

*Bucco tamatia* is the sister-group of all Bucconini species (branch 12, Fig. 6) with high support indices and four synapomorphies: the concavity in the *fissura zona flexoria craniofacialis* deep and short (Fig. 1, 5, 2-1); the extension of the *proc. postorbitalis* in relation to the jugal bar is long, reaching the lateral portion of the *arcus jugalis* (Fig. 2, 15, 1-2); the *spina interna rostri* is large (Fig. 5, 107, 0-1) and its *crista dorsalis* is absent (108, 0-1).

The type species of *Bucco* is *B. capensis* Linnaeus, 1766, therefore, "*Bucco*" *macroductylus* (Spix, 1824) must be assigned to a different genus if we maintain *Nystalus* and *Hypnelus*. Two genus names are available for *macroductylus*, with *Cyphos* Spix, 1824 having priority over *Argicus* Cabanis & Heine, 1863. We, therefore, suggest the reinstatement of the original combination *Cyphos macroductylus* Spix, 1824. Subsequently, *Bucco tamatia* also needs to be considered as a distinct genus based on the topology and three apomorphies. Rasmussen & Collar (2002) have applied the genus *Nystactes* Gogler, 1827 to it, however, the name could be a synonym of *Capito*. Regardless, *Tamatia* Cuvier, 1817 (type species *Tamatia maculata* Cuvier = *Bucco tamatia* Gmelin) would have priority over *Nystactes* ("*Tamatia*" in Cuvier [1798] was not used in a generic sense; in Rafinesque [1815] it is a *nomen nudum*). Therefore, we suggest the combination *Tamatia tamatia* (Gmelin). "*Bucco*" *noanamae* was not included in the phylogenetic analyses presented herein but appears as a sister group of *T. tamatia* (Rasmussen & Collar, 2002). Therefore, we included it in *Tamatia* as well.

*Nystalus* is the sister group of *B. capensis/Hypnelus ruficollis* (Wagler, 1829) with high support nodes and 10 synapomorphies: the *fossa temporalis* is long and fused to each in the medial portion of the skull (Fig. 2, 6, 1-2); the *proc. orbitalis os lacrimale* is larger laterally but shorter dorsally (Fig. 2, 29, 1-0); the dorsal portion *os ectethmoidale* is short, not in contact with the *os lacrimale* (Fig. 2, 34, 1-0); the tuberculum in the rostroventral portion *os ectethmoidale* is long (more prominent) (Fig. 2, 35, 1-2); the caudal portion of the upper jaw (*os nasale* and *os maxillare*) is dorsally large (about 70% of the width of the upper jaw) (Fig. 2, 40, 0-1); the *proc. transpalatinus os palatinum* is long and sharp (Figs. 2 and 3, 56, 0-2); the rostral portion of the *os palatinum* is larger than its caudal portion (Fig. 3, 59, 0-3); the *ala postacetabularis ilii* is narrow (Fig. 5, 88, 1-0); the caudal tuberculum in the lateral surface of *ala preacetabularis* is prominent (Fig. 5, 96, 0-1) and the length of *spina interna rostri* is 10% of the total length of *os sternum* (Fig. 5, 106, 1-0).

*Nystalus* Cabanis & Heine, 1863 is a valid genus with high node support (93, 5, branch 14, Fig. 6) and six synapomorphies: the tuberculum in the rostroventral portion of the *proc. postorbitalis* is vestigial (Fig. 2, 16, 1-0); the *facies dorsalis* of the *maxilla* (upper jaw) is prominent and sharp (Fig. 2, 43, 1-2); the *fossa ventralis os palatinum* is deep and long and larger than other puffbirds (Fig. 3, 58, 2-4); the *proc. orbitalis os quadratum* is the narrowest and longest of all puffbirds (71, 2-3); the *proc. dorsalis terminalis ischii* is narrow in its all extension and the apex is pointed (Fig. 5, 103, 0-1) and the dorsoventral depth *carina sterni* is narrow (115, 0-1). Although *Nystalus mac-*

*ulatus* (Gmelin, 1788) is sympatric with *Nystalus chacuru* (Vieillot, 1816) in eastern South America, *N. maculatus* is a lineage isolated from other *Nystalus* species. *Nystalus striolatus* is historically closely related to *N. radiatus* (Rasmussen & Collar, 2002). However *N. chacuru* together with *Nystalus radiatus* (Sclater, 1854) are the sister group of the *Nystalus striolatus* complex based on the results of our osteological analyses with high support indices and a high number of synapomorphies. Whitney et al. (2013) have recently suggested the *N. striolatus* complex to be composed of three cryptic species, which has been adopted by Piacentini et al. (2015), and partially by Remsen et al. (2020). We include *N. obamai* and *N. striolatus* s.s. in our classification because they have been considered the most closely related species and they exhibit morphological, distributional, and behavioral similarities within the complex (Whitney et al., 2013).

*Notharchus* Cabanis & Heine, 1863 is the sister-group to other Bucconina and a monophyletic genus with high support indices (78, 6, branch 8, Fig. 6) and eight synapomorphies: the *fossa temporalis* is the longest (fused to each in the medial portion of the skull) of all puffbirds (Figs. 1 and 2, 6, 1-2); the *proc. postorbitalis* is caudally curved and wide (Figs. 1 and 2, 14, 1-2); the *proc. lacrimalis* is thick (Fig. 2, 24, 1-2); the *fossa ventralis os palatinum* is deep, long and larger than other puffbirds (58, 2-4); the *proc. dorsalis terminalis ischii* is narrow in its all extension and the apex is pointed (Fig. 5, 103, 0-1); the *proc. craniofacialis* is long (20% of the total length *os sternum*) (Fig. 5, 109, 2-1); the dorsoventral depth *carina sterni* is the narrowest (reduced) among all puffbirds (115, 0-2) and the total length *os tarsometatarsus* is 75% the total length *os femoris* (Fig. 5, 133, 1-0). The genus has been historically considered monophyletic. The plumage is primarily black and white with black masks, white heads, in addition to black caps and barred flanks. They also have the largest bodies among the puffbirds (except *H. castanea*) and they are sympatric in the northern portion of South America, excluding *Notharchus macrorhynchus* (Gmelin, 1788), and *N. swainsoni* (Gray, 1846) in the Atlantic forest (Sick, 1997; Rasmussen & Collar, 2002). *Notharchus tectus* (Boddaert, 1783) has distinct plumage (black cap with white speckles and scapular white patches) and a short beak, and has been considered to belong to *Bucco* in some cases (Rasmussen & Collar, 2002), so that the placement of *N. tectus* as the sister-taxon to the other *Notharchus* is consistent with such morphological divergence. Although the position of *N. ordii* remains unclear based on the results of the osteological analysis, the historical taxonomy and plumage similarity suggest proximity with *Notharchus swainsoni* and it has historically been considered closely related to *Notharchus pectoralis* (Rasmussen & Collar, 2002). The osteological data suggest the *Notharchus swainsoni/Notharchus macrorhynchus/Notharchus hyperrhynchus* (Sclater, 1856) grouping, although with low node support and three synapomorphies. In addition, together with *N. pectoralis* (not included in this analysis), the grouping is more consistent when plumage similarity and historical taxonomy are considered (Sick, 1997; Rasmussen & Collar,

2002). *Notharchus swainsoni* has often been considered conspecific with *N. hyperrhynchus*; however, Alvarenga et al. (2002) considered *N. swainsoni* a valid species, based on its distinct morphological characters including its smaller size, and it is a geographically disjunct species distributed in the Atlantic Forests of Brazil, Argentina, and Paraguay. The topology from the analysis presented herein corroborates the Alvarenga et al. (2002) hypothesis for *N. swainsoni*. Two synapomorphies support the *N. macrorhynchus*/*N. hyperrhynchus* clade, which corroborates the historical taxonomy, since they were considered conspecifics until recently (Rasmussen & Collar, 2002; Remsen et al., 2020). They were considered distinct species by Remsen et al. (2020) and they are allopatric in distribution with plumage differences between each other (Rasmussen & Collar, 2002). In addition, we observed six autapomorphies of *N. hyperrhynchus*, which corroborates its validity. Conversely, *N. macrorhynchus* was the unique species without a single autapomorphy amongst all the Bucconidae species. Therefore, *N. macrorhynchus* should be taxonomically investigated using other characters as sources of data.

Finally, here, we propose five novel diagnosed taxa in the family-group to integrate the phylogenetic information into a linear classification in the Bucconidae (Table 2).

**Chelidopterinae, new subfamily:** Type and only genus: *Chelidoptera* Gould, 1837

**Diagnosis:** This subfamily can be distinguished by the *proc. lacrimalis os frontale* laterally large; *proeminentia cerebellaris* tubercular, laterally large; *proc. lacrimalis* thick, medial curvature, large, lateral concavity; *proc. orbitalis os lacrimale* lateromedially large, medial curvature; *proc. maxillaris os nasale* narrow (bar-shaped), laterally large; *fossa ventralis os palatinum* deep, long, large; caudal portion *os palatinum* larger than rostral; *fossa caudalis mandible* narrow, shallow; *proc. dorsalis terminalis ischii* 5% *symsacrum*; apex ramphotheca long curvature.

**Monasini, new tribe:** Type and only genus: *Monasa* Vieillot, 1816

**Diagnosis:** This tribe can be distinguished by the *depressio frontalis* shallow; *os frontale* 50% *os parietale*; *os ectethmoidale* short/sharp/long; tuberculum *os ectethmoidale* prominent; *proc. maxillaris os nasale* bar-shaped; *os tibiotarsus* 40% longer *os femoris*.

**Nonnolini, new tribe:** Type and only genus: *Nonnula* Sclater, 1854

**Diagnosis:** This tribe can be distinguished by the *os frontale* 20% *os parietale*; *proc. supraceuticus* long; *proeminentia cerebellaris* tubercular, laterally large; *proc. postorbitalis* reduced, *proc. orbitalis os lacrimale* reduced, triangular-shaped; *proc. transpalatinus* long, sharp; tuberculum *proc. opticus* absent; *proc. medialis mandible* short (8% *mandible*); *fossa caudalis mandible* narrow, shallow; caudal tuberculum *ala preacetabularis* prominent, large;

**Table 2.** Phylogenetic classification of the Bucconidae Horsfield, 1821. The term *incertae sedis* indicates taxa that were part of a polytomy in the most parsimonious tree (Fig. 6).

**Family Bucconidae Horsfield, 1821**

Subfamily Chelidopterinae, new subfamily

Genus *Chelidoptera* Gould, 1837

*C. tenebrosa* (Pallas, 1782)

Subfamily Bucconinae Horsfield, 1821

Tribe Monasini, new tribe

Genus *Monasa* Vieillot, 1816

Superspecies *M. atra* (Boddaert, 1783); *M. morphoeus* (Hahn & Küster, 1823)

*M. nigrifrons* (Spix, 1824)

*M. flavirostris* Strickland, 1850

Tribe Nonnolini, new tribe

Genus *Nonnula* Sclater, 1854

Superspecies *N. ruficapilla* (Tschudi, 1844); *N. frontalis* (Sclater, 1854);

*N. amaurocephala* Chapman, 1921

Superspecies *N. sclateri* Hellmayr, 1907; *N. brunnea* Sclater, 1881

*N. rubecula* (Spix, 1824) *incertae sedis*

Tribe Malacoptilini Ridgway, 1914

Genus *Malacoptila* Gray, 1841

*M. fulvogularis* Sclater, 1854

*M. fusca* (Gmelin, 1788)

*M. semicincta* Todd, 1925

*M. striata* (Spix, 1824)

*M. rufa* (Spix, 1824)

*M. mystacalis* (Lafresnaye, 1850)

*M. panamensis* Lafresnaye, 1847

Tribe Bucconini Horsfield, 1821

Subtribe Hapaloptilina, new subtribe

Genus *Hapaloptila* Sclater, 1881

*H. castanea* (Verreaux, 1866)

Subtribe Micromonachina, new subtribe

Genus *Micromonacha* Sclater, 1881

*M. lanceolata* (Deville, 1849)

Subtribe Bucconina Horsfield, 1821

Genus *Notharchus* Cabanis & Heine, 1863

*Notharchus tectus* (Boddaert, 1783)

Superspecies *N. hyperrhynchus* (Sclater, 1856); *N. swainsoni* (Gray, 1846);

*N. macrorhynchus* (Gmelin, 1788); *N. pectoralis* (Gray, 1846)

*N. ordii* (Cassin, 1851) *incertae sedis*

Supergenus *Bucco*

Genus *Cyphos* Spix, 1824

*C. macrodactylus* Spix, 1824

Genus *Tamatia* Cuvier, 1817

*T. tamatia* (Gmelin, 1788); *T. noanamae* (Hellmayr, 1909)

Genus *Bucco* Brisson, 1760

*B. capensis* Linnaeus, 1766

Genus *Hypnelus* Cabanis & Heine, 1863

*H. ruficollis* (Wagler, 1829)

Genus *Nystalus* Cabanis & Heine, 1863

*N. maculatus* (Gmelin, 1788)

Superspecies *N. obamai* Whitney et al., 2013; *N. striolatus* (Pelzeln, 1856)

*N. radiatus* (Sclater, 1854)

*N. chacuru* (Vieillot, 1816)

*trabecula lateralis os sternum* 70% *os sternum*, *os tarsometatarsus* longer *os femoris*.

**Hapaloptilina, new subtribe:** Type and only genus: *Hapaloptila* Sclater, 1881

**Diagnosis:** This subtribe can be distinguished by the *os frontale* 50% *os parietale*; *proc. lacrimalis os frontale* lat-

erally large; *proc. orbitalis os lacrimale* straight/large; *proc. pterigoideus* vestigial/tubercular; *proc. medialis mandible* short (8% mandible); *crista iliaca dorsolateralis* prominent/long; caudal tuberculum *ala preacetabularis* prominent/large (triangular); *trabecula intermedia os sternum* 50% *os sternum*; *proc. interclavicularis* rounded/large/more prominent; *ossa digitorum pedis*: 4<sup>th</sup> longer 2<sup>th</sup>.

**Micromonachina, new subtribe:** Type and only genus: *Micromonacha* Sclater, 1881

**Diagnosis:** This subtribe can be distinguished by the *proeminentia cerebellaris* tubercular, large; *proc. lacrimalis* filiform/long; *apertura nasi ossea* long (20% upper jaw); *proc. maxillaris os palatinum* narrow; *angulus rostromedialis os palatinum* not fused to each other; *fossa choanalis* short; *crista dorsalis os pterigoideus* short; *fonticuli lateralis ala preacetabularis* long/large; *foramen ilioschium* 60% *synsacrum*; *crista spinosa synsacri* narrow/short; *proc. ventralis terminalis ischii* 25% to 20% *synsacrum*; *proc. dorsalis terminalis ischii* large/apex rounded; *spina interna rostri* 20% *os sternum*; *crista deltopectoralis os humerus* short (20% *humerus*); *crista deltopectoralis os humerus* reduced; apex ramphotheca slightly curved.

## CONCLUSION

The present analysis revealed a well-resolved and strongly supported phylogeny, with high terminal taxa resolutions (topological dichotomies) for all the Bucconidae species, save for the ambiguous relationships observed in *Notharcus ordii* (Cassin, 1851), *Malacoptila fusca* (Gmelin, 1788), and *Nonnula rubecula* (Spix, 1824). In addition, the present topology is hardly in conflict with existing literature.

The analysis also reveals high numbers of apomorphies, which indicate the validity of all genera currently recognized. However, the major arrangement reveals that *Bucco* Brisson, 1760 is a polyphyletic genus, so that *Tamatia* and *Cyphos* are revalidated. Consequently, the present study demonstrates that osteology is an adequate source of data for elucidating most of the relationships within the Bucconidae.

The major contribution of the present study is a proposal for classification based on a modern analysis for the first time of the genus Bucconidae based on osteological characters. The proposal could facilitate studies focusing on the taxonomy, paleontology, evolution, biogeography, and ecology of these poorly understood Neotropical birds.

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## APPENDIX 1

### List of the osteological characters (1-135) and their respective states of variations (multistates from 0 to 4).

1. *Depressio frontalis*: (0) vestigial; (1) shallow; (2) deep.
2. Lateral length *os frontale* (orbital portion): (0) 50% of the lateral length *os parietale*; (1) 30% of the lateral length *os parietale*; (2) 20% of the lateral length *os parietale*.
3. *Proc. lacrimalis os frontale*: (0) vestigial; (1) short; (2) large (laterally prominent).
4. Lateral extension of the *zona flexoria craniofacialis*: (0) equal to the lateral extension *os frontale*; (1) shorter than the lateral extension *os frontale*.
5. Medial concavity in the *fissura zona flexoria craniofacialis*: (0) shallow; (1) deep; (2) deep and long (more caudally extended).
6. *Fossa temporalis*: (0) short (60 to 70% of the lateral portion of the skull and medially distant to each other); (1) longer (90% of the lateral portion of the skull and medially close to each other); (2) longest (fused to each in the medial portion of the skull).
7. Ventral portion of the *fossa temporalis*: (0) short and shallow; (1) long and deep.
8. *Proc. paraoccipitalis*: (0) vestigial; (1) long and large.
9. *Proc. esquamosalis*: (0) vestigial; (1) long and narrow.
10. *Proc. esquamosalis*: (0) long (40 to 70% of the distance to the *arcus jugalis*); (1) longest (either 90% of this distance or reaching the *arcus jugalis*).
11. *Proc. suprameaticus*: (0) short (either tubercular or vestigial); (1) long.
12. *Proeminentia cerebellaris*: (0) large and prominent; (1) tubercular and narrow; (2) tubercular but laterally larger than 1.
13. Dorsomedial portion of the *proc. post orbitalis*: (0) narrow; (1) large.
14. Shape of the *proc. postorbitalis*: (0) narrow and straight; (1) wider laterally and curved caudally at its apex; (2) caudally curved and wider than 1<sup>st</sup> condition.
15. Extension of the *proc. postorbitalis* in relation to the jugal bar: (0) short; (1) longer, close to *arcus jugalis*; (2) longest, reaching the lateral portion of the *arcus jugalis*.
16. Tuberculum in the rostroventral portion of the *proc. post orbitalis*: (0) vestigial; (1) short; (2) long (more prominent).
17. *Fossa lateralis os parasphenoidale*: (0) present; (1) absent.
18. *Proc. lateralis os parasphenoidale*: (0) large and short; (1) reduced (tubercular form); (2) thick e long.
19. *Canalis semicircularis os parasphenoidale*: (0) narrow; (1) ventrally rounded and dorsally narrow.
20. Rostral projection *os parasphenoidale*: (0) long and narrow; (1) short and large.
21. *Crista medialis* of the *lamina parasphenoidale*: (0) present; (1) absent.
22. *Proc. basipterygoideus*: (0) absent; (1) present.
23. Suture between *os frontale* and *os lacrimalis*: (0) long; (1) short; (2) shortest.
24. *Proc. lacrimalis*: (0) filiform, dorsally reaching *arcus jugalis*; (1) idem 0, bar-shaped, reaching medially *arcus jugalis*; (2) thicker than 1; (3) thicker than 1, but medially curved and the *proc. lacrimalis* is even larger and it presents a lateral concavity.
25. *Proc. supraorbitalis os lacrimale*: (0) dorsally large and rostrally sharp; (1) dorsoventrally narrow (rectangular in shape) and it presents a short projection to the *zona flexoria craniofacialis*.
26. Sharp projection of the *proc. ventralis os lacrimale* parallel to the *proc. ventralis os ectethmoidale*: (0) present; (1) absent.
27. Ventral projection of the *proc. dorsalis os lacrimale*: (0) long and fused to the *arcus jugalis*; (1) short; (2) reduced (tubercular in shape).
28. *Proc. orbitalis os lacrimale*: (0) narrow and sharp; (1) lateromedially large; (2) larger and it presents a medially curvature close to *os frontale*; (3) reduced (triangular in shape); (4) laterally larger but dorsally short.
29. *Proc. orbitalis os lacrimale*: (0) larger laterally but short dorsally; (1) idem 1, but with sharp projection in the laterodorsal extremity.
30. Suture between *os nasale* and *os lacrimale*: (0) long; (1) short; (2) vestigial.
31. Ventral portion of the *proc. orbitalis os lacrimale*: (0) long, narrow, medially curved and reaching *arcus jugalis*; (1) long, narrow, but straight; (2) long, narrow, but sharp in its extremity; (3) straight and large.
32. *Os ectethmoidale*: (0) thin; (1) thick.
33. Ventral Portion *os ectethmoidale*: (0) short and sharp; (1) short and sharp, but longer (ventrally extending well beyond *arcus jugalis*); (2) idem 3, but narrower; (3) triangular in shape.
34. Dorsal portion *os ectethmoidale*: (0) short, not in contact with the *os lacrimale*; (1) longer than 0, but not in contact with the *os lacrimale*; (2) longest (in contact with *os lacrimale*) and large.
35. Tuberculum in the rostroventral portion *os ectethmoidale*: (0) vestigial; (1) prominent; (2) longer than 1<sup>st</sup> condition (more prominent); (3) longer than 1<sup>st</sup> condition but dorsally larger.
36. *Foramem orbitonasalis lateralis*: (0) vestigial; (1) large.
37. Shape of the *fenestra anteorbitalis* (lateral view): (0) rounded; (1) triangular.
38. Upper jaw: (0) short (about 50 to 60% of the total length of the skull); (1) long (about 70% or more of the total length of the skull).
39. *Rostrum maxillae* (rostral apex *os premaxillare*): (0) not curved or slightly curved; (1) curved; (2) strongly curved and long.
40. Caudal portion of the upper jaw (*os nasale* and *os maxillare*): (0) dorsally short (about 50% of the width of the upper jaw); (1) dorsally large (about 70% of the width of the upper jaw); (2) larger than 2<sup>nd</sup> condition (about 90% of the width of the upper jaw); (3) extremely short (about 40% of the width of the upper jaw).
41. *Proc. jugalis os maxillare*: (0) vestigial; (1) narrow and long.
42. *Proc. maxillaris os nasale*: (0) thick and dorsally large; (1) thick, but dorsally narrow; (2) narrow (bar-shaped); (3) thin and but laterally larger.
43. *Facies dorsalis* of the *maxilla* (upper jaw): (0) not prominent and rounded; (1) prominent and rounded; (2) prominent and sharp.
44. Shape of the *apertura nasi (nasalis) ossea*: (0) narrow and straight; (1) oval; (2) rounded.

45. Length of the *apertura nasi (nasalis) ossea*: (0) short (10 to 15% of the total length of the upper jaw); (1) long (20% of the total length of the upper jaw); (2) longer (30% or more of the total length of the upper jaw).
46. Crest in the ventral surface of the *apertura nasi (nasalis) ossea*: (0) not prominent and short; (1) prominent and long.
47. Tuberculum in the caudal portion of the *apertura nasi (nasalis) ossea*, close to *fenestra antorbitalis*: (0) vestigial; (1) prominent; (2) more prominent and sharp.
48. Concavity in the *apertura nasi (nasalis) ossea*: (0) shallow and narrow; (1) deep and rounded.
49. Caudal aperture between the nostril and *fenestra antorbitalis*: (0) narrow; (1) large.
50. *Septum nasi (nasale) osseum*: (0) completely ossified; (1) partially ossified (there is a small aperture in the dorsocaudal portion of the nostril); (2) partially ossified, but the aperture is larger.
51. *Proc. maxillaris* of the *os palatinum*: (0) laterally large; (1) laterally narrow; (2) laterally narrow, but dorsoventrally thick.
52. *Pars lateralis os palatinum*: (0) short; (1) long.
53. *Fossa medialis os palatinum*: (0) narrow; (1) large.
54. Fusion between the *angulus rostromedialis os palatinum*: (0) absent; (1) present.
55. *Proc. rostradorsalis os palatinum*: (0) vestigial; (1) short; (2) long.
56. *Proc. transpalatinus os palatinum*: (0) vestigial; (1) long; (2) long and sharp.
57. *Fossa choanalis*: (0) long; (1) short; (2) vestigial.
58. *Fossa ventralis os palatinum*: (0) shallow and short; (1) shallow and long; (2) deep and short; (3) deep and long; (4) deep and long, but larger.
59. Width of the caudal portion *os palatinum* in relation to the rostral portion: (0) caudal larger than rostral; (1) caudal equal to rostral; (2) caudal larger than rostral, but the portion caudal is larger (closer to *arcus jugalis*); (3) rostral larger than caudal.
60. *Pars choanalis*: (0) large and long; (1) narrow and short.
61. *Proc. pterigoideus* of the *os palatinum*: (0) long; (1) short; (2) vestigial (tubercular in shape).
62. *Crista ventralis os palatinum*: (0) vestigial; (1) prominent; (2) prominent, but even larger.
63. *Proc. basipterygoideus*: (0) medially in contact to each other (they are meeting in midline below); (1) there is no contact to each other.
64. *Crista dorsalis os pterigoideus*: (0) long; (1) short (restrict to the rostral portion of the *os pterigoideus*); (2) short and dorsally large; (3) short and dorsally large, but more prominent; (4) vestigial.
65. Dorsal protuberance on the medial region of *arcus jugalis* (in the contact area with the *os lacrimale* and the *os ectethmoidale*): (0) reduced (thin); (1) thick.
66. Ventral tuberculum on the caudal portion of the *arcus jugalis*: (0) present; (1) absent.
67. Lateral tuberculum on the caudal extremity of the *arcus jugalis*: (0) vestigial; (1) prominent; (2) larger and more prominent.
68. Fusion between the *condylus caudalis* and *condylus lateralis os quadratum*: (0) absent; (1) present.
69. *Condylus lateralis os quadratum*: (0) large and thick; (1) short and ventrally flattened.
70. *Condylus medialis os quadratum*: (0) short and laterally flattened; (1) long, more prominent and its ventral extremity is rounded; (2) longer and larger relative to condition n. 1; (3) longer and larger but thicker.
71. *Proc. orbitalis os quadratum*: (0) short; (1) short, but larger in its basal portion, sharp and more distant from *os pterigoideus*; (2) longer and narrower relative to condition n. 1; (3) narrowest and longest.
72. Tuberculum on the dorsal surface of the *proc. oticus os quadratum*: (0) absent; (1) present.
73. Rostral extremity *ossa mandibulae (os dentale)*: (0) slightly curved; (1) curved; (2) strongly curved.
74. Width of the caudal aperture of the mandible: (0) short (about 30% of the total length of the mandible); (1) large (about 50% of the total length of the mandible).
75. *Pars symphysialis mandible*: (0) long (about 50% of the total length of the mandible); (1) short (about 40% of the total length of the mandible); (2) shortest (about 30% of the total length of the mandible).
76. Caudovernal region of the *pars symphysialis mandibulae*: (0) long and large; (1) short.
77. *Fenestra caudalis mandibulae*: (0) small aperture or absent; (1) narrow; (2) large and long.
78. *Fossa aditus canalis neurovascularis mandibulae*: (0) short and shallow; (1) long and shallow; (2) long and deep.
79. *Proc. coronoideus* 1 (rostral): (0) prominent; (1) vestigial.
80. *Proc. medialis mandible*: (0) reduced (about 5% of the total length of the mandible); (1) short (about 8% of the total length of the mandible); (2) long (about 10 a 13% of the total length of the mandible).
81. *Cotyla medialis mandible*: (0) shallow and large; (1) deep and narrow.
82. *Cotyla lateralis* and the *cotyla caudalis mandible*: (0) not fused to each other and deep; (1) fused to each other and deep; (2) fused to each other and shallow.
83. *Proc. retroarticularis mandible*: (0) large and rounded; (1) vestigial.
84. Tuberculum on the dorsal crista of the *fossa caudalis mandible*: (0) large; (1) narrow; (2) narrower (filiform); (3) vestigial.
85. Tuberculum *intercotylaris mandible*: (0) large; (1) narrow (crest in shape); (2) vestigial.
86. *Fossa lateralis mandible*: (0) deep; (1) shallow.
87. *Fossa caudalis mandible*: (0) large and deep; (1) narrow and deep; (2) narrower and shallow.
88. *Ala postacetabularis ilii*: (0) narrow; (1) large; (2) larger than 1 (embracing all lateral region of the *pygostilum*).
89. *Os pubis*: (0) long (70% of the total length of *ala preacetabularis*); (1) short (50% of the total length of *ala preacetabularis*).
90. *Fonticuli lateralis of ala preacetabularis*: (0) present; (1) absent.
91. *Fonticuli lateralis of ala preacetabularis*: (0) long and narrow; (1) long and large; (2) short.
92. *Foramen ilioschiadicum*: (0) 50% of the total length of the *synsacrum*; (1) 60% of the total length of the *synsacrum*; (2) 40% of the total length of the *synsacrum*.
93. *Crista spinosa synsacri*: (0) large and more prominent only in its rostral portion; (1) narrow and short; (2) narrow and short, but more prominent.
94. *Ala preacetabularis*: (0) narrow; (1) large.

95. *Crista iliaca dorsolateralis*: (0) reduced and short; (1) long (extending, partially recovering, to *foramen ilioischadicum*); (2) longer and dorsally larger than n. 1.
96. Caudal tuberculum in the lateral surface of *ala preacetabularis*: (0) vestigial or absent; (1) prominent; (2) prominent and large; (3) prominent and large, but larger and in triangular shape.
97. *Foramen orbituratum*: (0) absent; (1) present.
98. *Lamina pygostyli*: (0) large; (1) large but even larger in its rostroventral portion.
99. *Discus pygostyli*: (0) narrow; (1) large.
100. Length of the *proc. ventralis terminalis ischii*: (0) 25% to 20% of the total length of the *synsacrum*; (1) 12% to 10% of the total length of the *synsacrum*.
101. Shape of the *proc. ventralis terminalis ischii*: (0) narrow and sharp; (1) large.
102. *Proc. dorsalis terminalis ischii*: (0) 10% of the total length of the *synsacrum*; (1) 5% of the total length of the *synsacrum*.
103. *Proc. dorsalis terminalis ischii*: (0) medially large and the apex is sharp; (1) narrow in it all extension and the apex is pointed; (2) narrow in it all extension and the apex is rounded; (3) narrow in it all extension and the apex is bifurcated; (4) medially large, but the apex is rounded.
104. Tuberculum on the dorsal surface *sulcus articularis* with *os coracoideum*: (0) prominent; (1) vestigial.
105. Bifurcation of the cranial apex of *spina interna rostri*: (0) absent; (1) present.
106. Length of *spina interna rostri*: (0) 10% of the total length of *os sternum*; (1) 15% of the total length of *os sternum*; (2) 20% of the total length of *os sternum*.
107. Shape of the *spina interna rostri*: (0) narrow (laterally flattened); (1) Large.
108. *Crista dorsalis* of the *spina externa rostri*: (0) present; (1) absent.
109. *Proc. craniolateralis*: (0) short (15% of the total length *os sternum*); (1) long (20% of the total length *os sternum*); (2) longer (25 to 30% of the total length *os sternum*).
110. *Margo cranialis carinae*: (0) perpendicular (straight); (1) semi-lunar in shape (curved).
111. *Trabecula lateralis* of the *os sternum*: (0) 50 to 60% of the total length *os sternum*; (1) 70% of the total length *os sternum*.
112. *Trabecula intermedia* of the *os sternum*: (0) 60% of the total length *os sternum*; (1) 50% of the total length *os sternum*.
113. *Incisura lateralis* or *fenestra lateralis* in relation to *incisura medialis* or *fenestra medialis os sternum*: (0) lateral longer than medial; (1) lateral with equal length to the medial.
114. Expansion *carinae* into *trabecula medialis*: (0) reduced or absent; (1) short and crest in shape; (2) long and dorsally large.
115. Dorsoventral depth *carina sterni*: (0) large; (1) narrow; (2) narrowest (reduced).
116. *Proc. acrocoracoideus clavicularae*: (0) vestigial; (1) prominent.
117. *Proc. interclavicularis*: (0) vestigial; (1) rounded; (2) rounded, but larger and more prominent; (3) narrow and filiform.
118. *Proc. acrocoracoideus os coracoideum*: (0) vestigial; (1) prominent.
119. *Proc. lateralis os coracoideum*: (0) long, apex truncated (both tuberculum are reduced); (1) long but both tuberculum are prominent; (2) both tuberculum are prominent but longer than n. 1.
120. Length *crista deltopectoralis os humerus*: (0) short (20% of the total length *os humerus*); (1) long (28% to 33% of the total length *os humerus*).
121. Width of the *crista deltopectoralis os humerus*: (0) reduced; (1) large; (2) idem 1, but larger and thick.
122. *Olecranon os ulna*: (0) long and thick; (1) short and thicker; (2) shorter than condition 1 (tubercular in shape).
123. Length of the *os radius*: (0) 25% to 33% longer than the length *os humerus*; (1) 10% longer than the length *os humerus*.
124. Tuberculum *ligamentum collaterale ventralis*: (0) vestigial; (1) prominent.
125. *Papillae remigiales ventralis et caudalis*: (0) prominent; (1) vestigial.
126. Tuberculum on the dorsal surface *os metacarpale*: (0) vestigial; (1) prominent; (2) more prominent.
127. Tuberculum of the caudal surface of the *phalanx proximalis digiti majoris*: (0) present; (1) absent.
128. *Sulcus patellaris*: (0) shallow; (1) deep.
129. *Crista trochanteris*: (0) vestigial; (1) prominent and large.
130. *Sulcus intercnemialis*: (0) large and deep; (1) narrow and shallow.
131. Total length *os tibiotarsus*: (0) 40% longer than the total length of the *os femoris*; (1) 50% longer than the total length of the *os femoris*; (2) 60% longer than the total length of the *os femoris*.
132. *Facies gastrocnemialis os tibiotarsus*: (0) narrow and shallow; (1) large and deep.
133. Total length *os tarsometatarsus*: (0) 75% the total length *os femoris*; (1) 90% the total length *os femoris*; (2) longer than the total length *os femoris*.
134. Rostral apex of the rhamphotheca: (0) slightly curved or not curved; (1) ventrally curved; (2) ventrally and strongly curved; (3) idem 2, but more curved (hooked in shape) and longer.
135. Relative size 4<sup>th</sup> and 2<sup>th</sup> toes (*ossa digitorum pedis*): (0) 4<sup>th</sup> longer than 2<sup>th</sup>; (1) 4<sup>th</sup> equal to 2<sup>th</sup>.









### APPENDIX 3

#### List of synapomorphies among species within the genera of *Bucconidae*. Consistency index (ci) and series of transformation for each character in parenthesis, respectively.

**Notharchus species:** **branch 9:** (1, 0  $\Rightarrow$  1); 122 (0.667, 2  $\Rightarrow$  0); 123 (0.333, 1  $\Rightarrow$  0) and **branch 10:** 16 (0.667, 1  $\Rightarrow$  2); 34 (0.5, 2  $\Rightarrow$  0). **Branch 12:** 5 (0.667, 2  $\Rightarrow$  1); 15 (0.286, 1  $\Rightarrow$  2); 107 (0.250, 0  $\Rightarrow$  1); 108 (0.25, 0  $\Rightarrow$  1).

**Nystalus species:** **branch 13:** 6 (0.4, 1  $\Rightarrow$  2); 29 (0.333, 1  $\Rightarrow$  0); 34 (0.5, 1  $\Rightarrow$  0); 35 (.333, 1  $\Rightarrow$  2); 40 (0.6, 0  $\Rightarrow$  1); 56 (0.286, 0  $\Rightarrow$  2); 59 (0.6, 0  $\Rightarrow$  3); 88 (0.5, 1  $\Rightarrow$  0); 96 (0.3, 0  $\Rightarrow$  1); 106 (0.25, 1  $\Rightarrow$  0). **Branch 14:** 16 (0.667, 1  $\Rightarrow$  0); 43 (1, 1  $\Rightarrow$  2); 58 (0.429, 2  $\Rightarrow$  4); 71 (1, 2  $\Rightarrow$  3); 103 (0.5, 0  $\Rightarrow$  1); 115 (0.222, 0  $\Rightarrow$  1). **Branch 15:** 12 (0.222, 1  $\Rightarrow$  0); 92 (0.182, 0  $\Rightarrow$  2); 100 (0.200, 1  $\Rightarrow$  0); 105 (0.333, 0  $\Rightarrow$  1); 115 (0.222, 1  $\Rightarrow$  2). **Branch 16:** 90 (0.2, 1  $\Rightarrow$  0); 106 (0.250, 0  $\Rightarrow$  1); 117 (0.5, 1  $\Rightarrow$  3).

**Malacoptila species:** **Branch 19:** 35 (0.333, 1  $\Rightarrow$  2); 59 (0.6, 0  $\Rightarrow$  1); 106 (0.25, 1  $\Rightarrow$  0); 115 (0.222, 0  $\Rightarrow$  1). **Branch 20:** 15 (0.286, 1  $\Rightarrow$  2); 59 (0.6, 1  $\Rightarrow$  2). **Branch 21:** 56 (0.286, 1  $\Rightarrow$  0); 90 (0.2, 1  $\Rightarrow$  0); 113 (0.2, 1  $\Rightarrow$  0). **Branch 22:** 31 (0.375, 1  $\Rightarrow$  2); 62 (0.5, 1  $\Rightarrow$  2); 92 (0.182, 1  $\Rightarrow$  0); 107 (0.25, 0  $\Rightarrow$  1); 115 (0.222, 1  $\Rightarrow$  0); 123 (0.333, 1  $\Rightarrow$  0).

**Nonnula species:** **Branch 24:** 21 (0.25, 1  $\Rightarrow$  0); 102 (0.5, 0  $\Rightarrow$  1); 111 (0.333, 1  $\Rightarrow$  0). **Branch 25:** 45 (0.333, 2  $\Rightarrow$  1); 106 (0.25, 1  $\Rightarrow$  2).

**Monasa species:** **Branch 27:** 24 (0.429, 1  $\Rightarrow$  2); 103 (0.5, 1  $\Rightarrow$  3); 133 (0.286, 1  $\Rightarrow$  0); 134 (0.375, 1  $\Rightarrow$  2). **Branch 28:** 45 (0.333, 2  $\Rightarrow$  1); 78 (0.667, 1  $\Rightarrow$  2).