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RESEARCH ARTICLE

Evolution of the jaw apparatus in true woodpeckers (Picidae: Picinae) in association with the available food sources and foraging habits

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ABSTRACT. The evolution of woodpecker behaviors in association with their morphological adaptations is not well understood. This investigation aimed to determine the relationship between the anatomy of the jaw apparatus, the type of food consumed and the foraging mode of these birds. We present detailed anatomical descriptions of all parts of the jaw apparatus of true woodpeckers. Their characteristics were mapped into a consensus phylogenetic tree to describe woodpecker evolution. When morphological analyses were associated with feeding/foraging behavior, distinct patterns emerged. The protractor quadrati and pterygoideus systems are more developed in species that adopt pecking/hammering behaviors, even as secondary habits. By comparing *Hemicircus* (frugivorous with a poorly developed jaw apparatus) with the last common ancestor of Picinae, the early evolution of the jaw apparatus was found to be related to the type of food consumed. However, it became more complex in the ancestral lineage of Picinae, which enabled these birds to catch insects by gleaning/probing. It is hypothesized that the jaw apparatus of Picinae has evolved in response to foraging tactics and not to the type of food consumed. Pecking/hammering, as a secondary behavior, has evolved independently in *Dryocopus*, *Celeus*, and *Dendropicus*. Moreover, it has become more complex in *Piculus* and the clade comprising *Blythipicus*/*Reinwardtipicus*/*Camphephilus*, as they utilize pecking/hammering as their primary behavior.

KEY WORDS. Adaptiveness, anatomy feeding habits, form and function.

INTRODUCTION

The jaw apparatus of many vertebrates moves using only one paired joint between the mandible and the brain case. Mechanical refinement in the jaw apparatus of birds, however, is highly developed, with a complex system of bony bars, joints, and flexion zones (Bühler 1981). Extensive studies on the role of skeletal structural elements and the functions of the jaw apparatus in birds were previously conducted by Bock (1960, 1964, 1966, 1999). Bock (1999) stated that "Woodpeckers are the first example of adaptive evolution by Natural Selection mentioned by Darwin who commented that their feet, tail, beak, and tongue are so admirably adapted to catch insects under the bark of trees". Throughout history, researchers have sought to correlate form and function to the feeding and foraging habits of woodpeckers. Burt (1930) investigated the relationship between woodpecker skull and spine osteology, the muscles that move their jaws and their means of feeding. This was one of the first attempts to correlate form and function with the foraging habits of woodpeckers. Scharnke (1930, 1931), Steinbacher (1934, 1935, 1955), and more recently, Leonard and Heath (2010) also analyzed the form and function of woodpeckers and associated their anatomy with their food sources and foraging habits.

Beyond the aforementioned research, the relationships among bird feeding habits, food consumption, and the jaw apparatus have not yet been investigated comprehensively by ornithologists. The skeletal elements in birds are highly complex, making morphological analyses challenging (Donatelli et al. 2014). The diversity in foraging behaviors and specializations described for woodpeckers (Short 1982) that are associated with foraging modes (Winkler et al. 1995) and types of food consumed (Winkler and Christie 2002) may or may not be directly correlated with the variations in their jaw apparatus. Although skull variations have been correlated with diet in a few species of woodpeckers (Burt 1930, Spring 1965, Leonard and Heath 2010), those studies lacked a broad phylogenetic context. Donatelli et al. (2014) investigated the relationships between the jaw apparatus and foraging strategies in Oriental woodpeckers and subdivided the jaw apparatus into three classes according to their development, feeding habits, and the types of food consumed. Their analysis directly considered the methods used by the woodpeckers to obtain food. However, their hypotheses need to be tested using a parsimony analysis that includes other woodpecker species.

We investigate (1) whether the foraging methods and the structure of the jaw apparatus are linked in any way among Picinae; (2) whether it is possible to establish form/function relationships based on the structural differences between the mandibular apparatus, the types of food consumed, and the methods used for foraging; (3) how such structures and behavior may have evolved.

MATERIAL AND METHODS

Complete and detailed anatomical descriptions of all parts of the jaw apparatus of true woodpeckers can be found in Donatelli (1996, 2012a, 2012b, 2013, 2014) and Donatelli et al. (2014). All genera of Picidae are represented, with most species distributed in the Americas, Eurasia, and Oriental Region. Terrestrial and arboreal woodpeckers, from sea level to higher altitudes, with distinct feeding and breeding behaviors, were included. The complete list of woodpecker species studied (cranial osteology and jaw musculature) can be found in Donatelli (1996, 2012a, 2012b, 2013, 2014) and Donatelli et al. (2014).

In the present study, only the most relevant anatomical landmarks that are correlated with foraging have been highlighted to avoid new descriptions and unnecessary repetition. In addition, the methods adopted by Picinae for obtaining food or foraging were gleaned from specialized literature, particularly the work of Short (1982), Winkler et al. (1995), and Winkler and Christie (2002). Table 1 summarizes the foraging strategies of true woodpeckers, the locations of their food items, and the type of food consumed by each species. The definitions of woodpecker foraging behaviors are presented in Winkler et al. (1995), with suggestions from Remsen and Robinson (1990). Generally, gleaning involves the simple act of picking or taking a food item without much effort and without beating; probing involves investigating with the beak and searching for food inside the cracks of trees; tapping (or pecking) is an exploratory strike of the substrate in an attempt to obtain information about a food item; excavating involves a more complex action of penetration, force, and agility, with more conspicuous and intense movements of the head; and tonguing is a simple projection of the tongue to capture food items that have already been discovered.

Species nomenclature follows Winkler (2015), but we adopted the following proposition of Manegold and Topfer (2013) as a definition of the true woodpecker: Picinae sensu stricto and Picinae sensu lato (a sister-group relationship between *Hemicircus* and all remaining true woodpeckers). Thus, where Picinae, or true woodpeckers, are mentioned in this study, we are referring to Picinae sensu stricto.

Part of the material examined in this study was preserved in ethyl alcohol (A) 70% v/v and is part of the collections of the Ditsong National Museum of Natural History (TMSA, formerly Transvaal Museum), Pretoria, South Africa; Museu Paraense Emílio Goeldi (MPEG), Belém, Pará, Brazil; and the Museum of Natural History of the Indonesian Institute of Sciences (LIPI), Indonesia. The other part consisted exclusively of osteological material from the National Museum of Natural History (USNM), Smithsonian Institution, Washington DC, USA. The following specimens were examined: *Reinwardtipicus validus* (Temminck, 1825): LIPI MZB.Skt 119 Rv1, MZB.Skt 120 Rv2; *Blythipicus rubiginosus* (Swainson, 1837): LIPI MZB.Skt 117 Br1, MZB.Skt 118 Br2, USNM 489267 ♀, USNM 559840 ♀; *Dinopium javanense* (Ljungh, 1797): LIPI MZB.Skt 115 Dij1, MZB.Skt 116 Dij2, USNM 318076 ♂, USNM 318075 ♂, USNM 562041 ♀; *Dinopium rafflesii* (Vigors and Horsfield, 1830): LIPI MZB.Skt 114 Dr1; *Chrysophlegma mentale* (Temminck, 1826): LIPI MZB.Skt 110 Pm1, MZB.Skt 110 Pm2; *Chrysophlegma miniaceum* (Pennant, 1769): LIPI MZB.Skt. 112 Pmi3; *Picus puniceus* Horsfield, 1821: LIPI MZB.Skt 113 Pp2; *Hemicircus concretus* (Temminck, 1821): LIPI MZB.Skt 125 Hc1, LIPI MZB.Skt 126 Hc2; *Meiglyptes tristis* (Horsfield, 1821): LIPI MZB.Skt 123 Mtr1, MZB.Skt 124 Mtr2, USNM292228 ♂; *Meiglyptes tukki* (Lesson, 1839): LIPI MZB.Skt 121 Mtu1, MZB.Skt 122 Mtk1, USNM 489269 ♀; *Dryocopus pulverulentus* (Temminck, 1826):

Table 1. Foraging strategies and food taken by woodpeckers. According to Short (1982), Winkler et al. (1995) and Winkler and Christie (2002).

Species	Gleaning	Probing	Tapping	Pecking	Hammering	Excavating	Tonguing	Local	Food
Piculus flavigula				■	■			Middle and high strata	ants
Celeus flavescens	■	■		□	□			Middle and high strata	ants and termites; also, fruits
Melanerpes cruentatus	■							Treetops	arthropods and fruits
Colaptes melanochloros	■	■						Middle, lower strata and ground	ants
Campephilus rubricollis	□			■	■				
Geocolaptes olivaceus		□					■	Ground	ants
Geocolaptes abingoni	■	■			□			Middle strata	insects and their larvae; ants
Dendropicos griseocephalus	□	□		□		□		All strata	insects and their larvae; ants
Dendropicos fuscescens		■		□				All strata	insects and their larvae; beetles
Dendropicos namaquus	○			■	■			All strata	insects and their larvae; beetles
Hemicircus concretus	■	○	□	□				Treetops	Fruits
Meiglyptes tristis	■	□	○	○				Treetops	ants and other insects
Meiglyptes tukki	■	□	□	□○				Middle, lower strata	ants and termites
Dryocopus pulverulentus	■	□	□	□	□	□		Tress	ants and beetle larvae
Chrysophlegma miniaceum	■	■	○					Tress	ants, eggs and larvae
Picus puniceus	■	■			□			Tress	ants, eggs and termites
Chrysophlegma mentale	■	■		○	○	○		Tress	ants, termites, beetles
Dinopium rafflesii	■			○				Tress	ants, termites, pupae
Dinopium javanense	■	■		○				Tress	ants, larvae, scorpions
Blythipicus rubiginosus					■	□		Tress	beetles, insect larvae
Reinwardtipicus validus				■	■	□		All strata	beetle larvae, ants, termites

(■) Primary or main action, (□) secondary action, (○) eventual action.

LIPIMZB.Skt 127Mp1, MZB.Skt 128 Mp2, USNM 19201 ♀, USNM 562042 ♀; *Campephilus rubricollis* (Boddaert, 1783): MPEG A4320; *Melanerpes cruentatus* (Boddaert, 1783): MPEG A6019; *Colaptes melanochloros* (Gmelin, 1788): MPEG A6044; *Geocolaptes olivaceus* (Gmelin, 1788): TMSA 61.770; *Geocolaptes abingoni* (Smith, 1836): TMSA 60.943, TMSA 33.120, TMSA 33.121; *Dendropicos griseocephalus* (Boddaert, 1783): TMSA 38.218; *Dendropicos fuscescens* Vieillot, 1818): TMSA 40.813, TMSA 33.122, TMSA 33.123; *Dendropicos namaquus* (Lichtenstein, 1793): TMSA 39.077, TMSA 60.132; *Piculus flavigula* (Boddaert, 1783): USNM 621983 ♀; *Celeus flavescens* (Gmelin, 1788): USNM 562765 ♀.

Anatomical data were assessed by considering how food was obtained by the different species. The function of the jaw apparatus was the focus of this study, that is, the relationship between the structure of the jaw apparatus of a species and its characteristic method for obtaining food.

We chose the following characteristics and their respective states of variation (see Donatelli et al. 2014): 1) jaw apparatus complexity (low in *Hemicircus*, intermediate in the vast majority of Picinae, and high in *Piculus*, *Blythipicus*, *Reinwardtipicus*, and *Campephilus*); 2) food source (frugivorous in *Hemicircus* and insectivorous in Picinae); and 3) foraging method (fruits on treetops in *Hemicircus,* gleaning/probing in Picinae, gleaning/probing but with pecking/hammering as secondary behaviors in *Dryocopus*, *Celeus*, and *Dendropicus*, and pecking/hammering as the primary behaviors in *Piculus, Blythipicus*, *Reinwardtipicus*, and *Campephilus*). These characteristics were mapped in a consensus phylogenetic tree using data from the literature (Shakya et al. 2017) to describe their evolution. All characteristics were treated as unordered. Thus, we reconstructed the ancestral state by adopting the maximum parsimony method using Mesquite 3.2 (Maddison and Maddison 2023). The heuristic search algorithm was selected to identify the most parsimonious hypothesis for each characteristic in the tree of Shakya et al. (2017). The DELTRAN algorithm was adopted to optimize characters on the tree, and the MAXTREES was set to 1000 trees.

Intraspecific variations occur for several reasons and can be characterized by geographic and latitudinal, behavioral, morphological, vocalization, sexual, and age variations. Such variations cannot be characterized in a character polarity analysis, as they vary among individuals of the same species and should not be considered in a phylogenetic analysis. Such variations are discarded because they do not correspond to a character that is standard for the species or genus and that could be considered in a phylogenetic polarity analysis. With respect to cranial osteology and musculature, individual variations can be seen in the size of a bone structure, such as in a process or even in the development of a muscle (Costa and Donatelli 2009, Pascotto et al. 2006), which are not considered in an analysis of evolutionary history between taxa as was carried out in this work. Therefore, the species pattern is always considered for such analyzes and variations (whether due to any cause) are discarded in a phylogenetic analysis.

In addition, we compared the cladograms for the reconstruction of the ancestral states of the foraging mode and the feeding habit cladogram to the jaw apparatus to observe the topological correspondence between the evolution of form and function in woodpeckers.

RESULTS

Osteological aspects of the jaw apparatus in Picinae

In addition to the structural differences in the components of the cranial osteology of Picinae, as described by Donatelli (1996, 2012a, 2014) and Donatelli et al. (2014), a number of key characteristics involved in the operation of the jaw apparatus are relevant to foraging strategies: 1) the parietal/frontal diameter ratio; 2) the presence of a frontal overhang in many distinct species; 3) Fossa temporalis; 4) the postorbital process; 5) the zygomatic process; 6) the dorsal process of the pterygoid; 7) the depth of the ventral palatine fossa; 8) the pes pterygoidei, a well-developed structure; and 9) the orbital process of the quadrate bone.

The parietal/frontal diameter ratio is typical and relatively large in smaller woodpeckers. In general, the postorbital process is relatively standard in all Picinae (~1/3), but there are some exceptions – e.g., *Campephilus rubricollis* (Boddaert, 1783), 1/2, and *C. lucidus*, Scopoli, 1786, 4/5). Frontal overhangs are present in *Piculus flavigula* and Picumninae (Donatelli 1996), and are generally associated with smaller woodpeckers. The frontal overhang in specialized drilling woodpeckers provides a bony stop that prevents excessive abduction of the upper jaw during nonimpact periods while drilling into trees (Bock 1999). The zygomatic process is thick and long in *Mulleripicus* spp. and in *C. rubricollis*, *Celeus flavescens*, and *Dendropicos namaquus*; in other species, this process is comparatively less developed. The suprameatic process is conspicuous in *Mulleripicus* spp. and all Neotropical and Afrotropical true woodpeckers, but it is relatively less developed in Picini. The pes pterygoidei is relatively large in almost all Picinae, especially in *Mulleripicus* spp., whereas it is relatively small, thin, and narrow in *Meiglyptes* spp. and inconspicuous in *H. concretus* (Hemicircini). The ventral palatine fossa is relatively deeper in *Meiglyptes tristis* (but not in *M. tukki*), Campephilini (*Blythipicus fuliginosus* and C. rubricollis), Melanerpini (*D. fuscescens*, *D. namaquus*, and *D. griseocephalus*), and some Picini (*Colaptes melanochoros*, *Geocolaptes olivaceus*, *G. abingoni*, and *Dinopium javanense*), but less pronounced in *Mulleripicus* spp. and shallower in *Hemicircus concretus*. The orbital process of the quadrate is larger in *Blythipicus rubiginosus* than in other species. In general, there are clear distinctions between *Chrysophlegma* spp. and *Picus puniceus*, and the other Picini that do not have general cranial bone structures. In true woodpeckers, the fossa temporalis is wider than that in most other species, but there are many exceptions. For example, in *D. namaquus*, *Reinwardtipicus validus* (Campephilini), *C. lucidus*, *Dinopium javanense*, and *P. viridis* (Picini), the fossa temporalis is longer than it is wide. The dorsal process of the pterygoid bone is clearly conspicuous in almost all species of true woodpeckers, except for piculets, as reported by Donatelli (1996), and is an important insertion site for the aponeurosis of the *M. protractor pterygoidei* muscle, a powerful upper jaw retractor. The orbital process of the quadrate bone varies considerably among woodpeckers, but generally, it extends approximately 2/3 of the length of the pterygoid bone. The orbital process of the quadrate bone is the place of origin of the aponeurosis and the fleshy fibers of *M. pseudotemporalis profundus*, which is an important mandibular adductor and retractor of the maxilla. The development of this process, in association with this muscle unique to true woodpeckers.

Musculature aspects of the jaw apparatus in the Picinae

In addition to the structural differences in the components of the mandibular musculature of Picinae, as described by Donatelli (1996, 2012b, 2013) and Donatelli et al. (2014), there are a number of key characteristics involved in the operation of the jaw apparatus that are relevant to woodpecker foraging strategies: 1) Four components of the external mandibular adductor system are widespread and well developed: the adductor mandibulae externus rostralis medialis, lateralis, caudalis lateralis, and ventralis; 2) the muscles of the internal mandible are generally not well developed; 3) the protractor system is relatively variable in development, size, and structure, although woodpeckers show a clear distinction between the two different muscles in the protractor system; and 4) the pterygoideus system showed a relatively large degree of structural diversity and a clear pattern of well-developed components.

Form and function

The most complete study of a system (structure and shape, development, and complexity) in the Picinae involved the external mandibular adductor system. The muscles of this jaw adduction system are well developed in all true woodpeckers. The elements that comprise this system may compensate for other undeveloped adductors in some species, such as *M. pseudotemporalis profundus* (internal mandibular adductor) in *B. rubiginosus* (Fig. 1). Particularly in *B. rubiginosus*, the poorly developed M. pseudotemporalis profundus seems to be associated with the increased complexity of the muscles of the external mandibular adductor system and pterygoideus complex, which act secondarily as an auxiliary in the mandibular adduction. Associated with this, the orbital processes of the quadrate and ventral palatal fossa are relatively more developed in this species. This species excavates and hammers the tree trunk to obtain food. Other species that engage in excavating and hammering, such as *R. validus*, *Dendropicos griseocephalus,* and *Dryocopus pulverulentus* also have developed the external mandibular adductor system and the pterygoideus complex, including the internal adductor system, formed by the pseudotemporalis superficialis and pseudotemporalis profundus muscles.

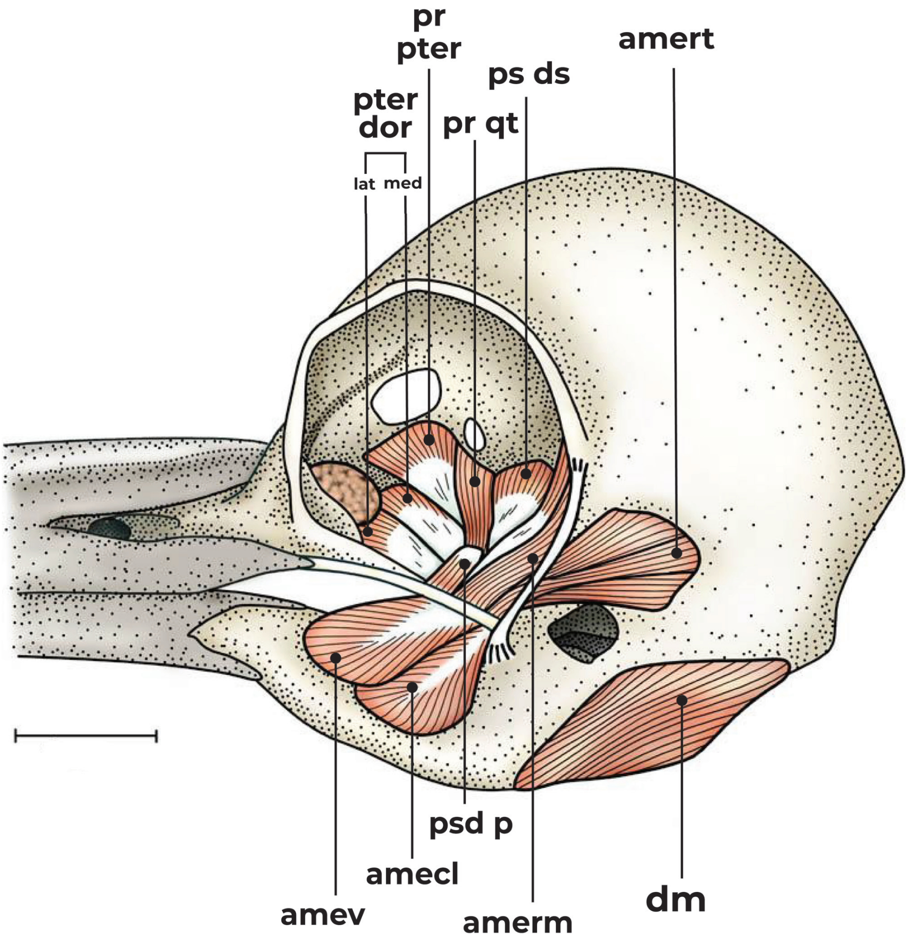

Figure 1. The jaw apparatus of *Blythipicus fuliginosus* as a representative of species that utilize the hammering method to obtain food. Of note is the development of the quadrate-pterygoid complex. (amecl) Adductor mandibulae externus caudalis lateralis; (amerm) adductor mandibulae externus rostralis medialis; (amert) adductor mandibulae externus rostralis temporalis; (amev) adductor mandibulae externus ventralis; (dm) depressor mandibulae; (pr qt) protractor quadrati; (psd p) pseudotemporalis profundus; (pter dor lat) pterygoideus dorsalis lateralis; (pter dor med) pterygoideus dorsalis medialis. Scale bar: 1 cm.

Conversely, in species that engage in gleaning and/or probing, we found that there was little development (structure, shape, size, and complexity) in the components of the quadrate protractor system, as in *G. abingoni*, *Dendropicos fuscescens* (protractor pterygoidei Fig. 2), all *Meiglyptes* and *Chrysophlegma* species, and *H. concretus*. *Celeus flavescens*, *Colaptes melanochloros*, *Melanerpes cruentatus*, *Dinopium javanense*, *D. rafflesii*, and *Dryocopus pulverulentus* are exceptions to this rule. Notably, in the case of the latter species, secondary foraging activity could explain the increased development of the components of the quadrate protractor system, which was associated with the complexity of the whole cranial bone structure of this species in comparison with the other species (zygomatic, suprameatic, quadrate bone, and pes pterygoidei processes). In the case of *Celeus flavescens*, *Colaptes melanochloros*, *M. cruentatus*, *Dinopium javanense*, and *D. rafflesii*, other primary ways to obtain food besides gleaning can be explained by the greater development and complexity of the *M. protractor quadrati* (*Celeus flavescens* (Fig. 3), *Colaptes melanochloros*, and *M. cruentatus*) or pterygoidei (*D. javanense* and *D. rafflesii*).

Interestingly, in species that employ pecking and hammering as a method for obtaining food, even as a secondary behavior, the protractor quadrati and pterygoideus systems are relatively more developed than in species that do not engage in this behavior. *Dryocopus pulverulentus* and *Dendropicos griseocephalus*, which have less developed quadrate protractor systems, are exceptions). In those species, the M. adductor mandibulae externus compensate for the less developed protractor quadrati and pterygoideus – which act as rapid jaws adductors during. In the case of *H. concretus*, the only species that primary feeds on fruit, all cranial muscles and osteologi-

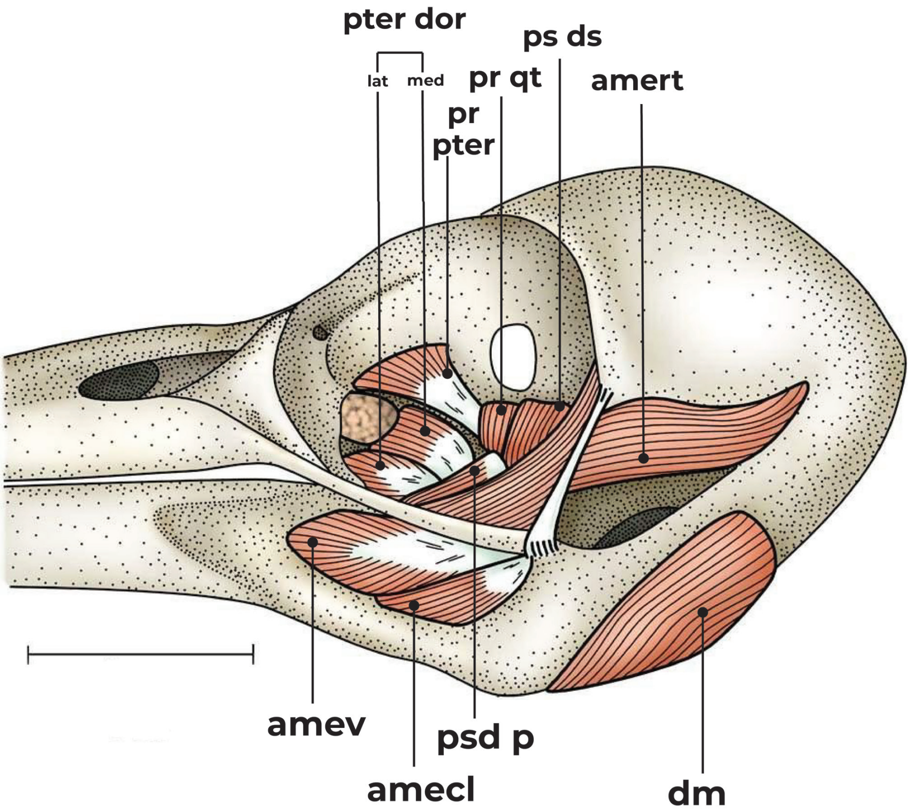

Figure 2. The jaw apparatus of *Dendropicos fuscescens* as a representative of species that utilize the probing method to obtain food. Of note is the poor development of the protractor quadrati complex. (amecl) Adductor mandibulae externus caudalis lateralis; (amerm) adductor mandibulae externus rostralis medialis; (amert) adductor mandibulae externus rostralis temporalis; (amev) adductor mandibulae externus ventralis; (dm) depressor mandibulae; (pr pter) protractor pterygoideus; (pr qt) protractor quadrati; (ps ds) pseudotemporalis superficialis; (psd p) pseudotemporalis profundus; (pter dor lat) pterygoideus dorsalis lateralis; (pter dor med) pterygoideus dorsalis medialis. Scale bar: 1 cm.

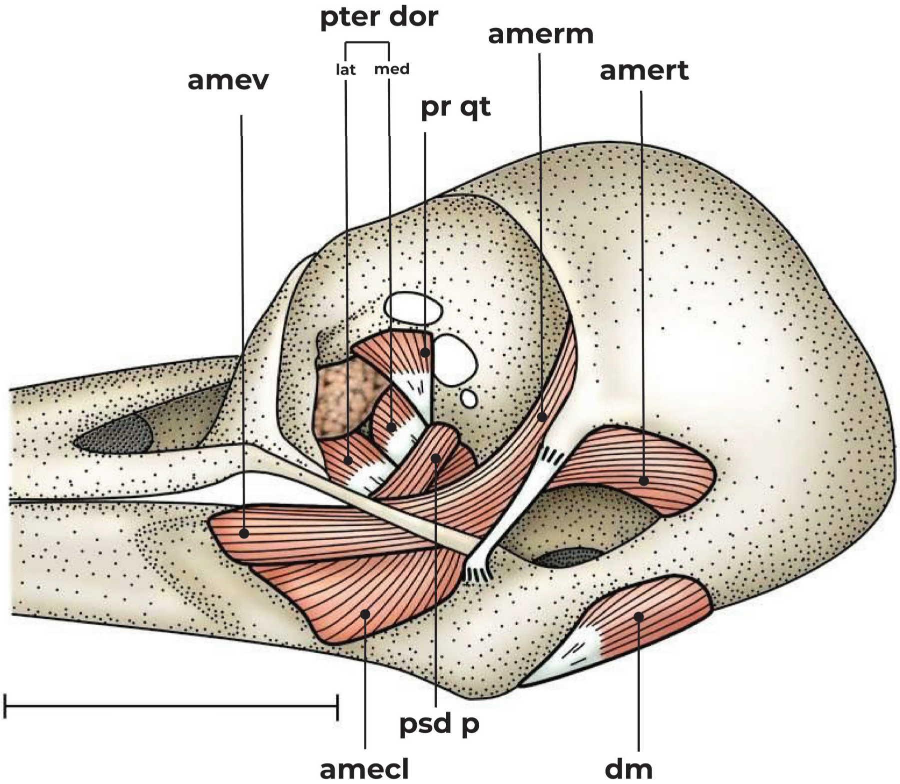

Figure 3. The jaw apparatus of *Celeus flavescens* as a representative species that utilizes the gleaning method to obtain food. Of note is the poor development of the protractor quadrati and pterygoideus complex, despite the relative development of M. protractor pterygoideus. (amecm-adductor) Mandibulae externus caudalis medialis; (amerm-adductor) mandibulae externus rostralis medialis; (pr pt) protractor pterygoidei; (psd p) pseudotemporalis profundus; (pter dor lat) pterygoideus dorsalis lateralis; (pter dor med) pterygoideus dorsalis medialis. Scale bar: 1 cm.

cal systems are relatively less developed (structure and shape, development, and complexity) compared with other Picinae species. Furthermore, in *G. olivaceus* (Fig. 4), the only species that adopts the tongue-feeding habit, there the M. protractor quadrati has two independent points of origin. This feature is shared with *D. griseocephalus* (no primary foraging action), *Celeus flavescens* (gleaning and probing as primary foraging actions), and *Campephilus rubricollis* (unknown foraging actions). There is no information in the literature about the foraging habits of *C. rubricollis*. The behavior of this species can be inferred from the jaw apparatus: the complex structure of the adductor muscles, the development of the components of the quadrate protractor system, the development of the zygomatic process, the postorbital process, and the depth of the ventral fossa suggest that this species primarily engages in pecking and hammering and that gleaning is secondary.

Following this analysis of the structural variations in the mandibular musculature in woodpeckers, it would be informative to combine what we know about form and function with the mechanisms of movement in these structures in relation to the biology of Picinae. Woodpeckers mainly specialize in feeding on insects, but not exclusively, and they occasionally consume other foods such as fruit, acorn, seed, sap, and even honey. Since insects are the main component of the diet of woodpeckers, one must consider the methods they use to obtain this food source, which are highly variable among species. Considering the structural variation in woodpeckers and their methods for obtaining food, species with a relatively more developed mandibular apparatus (structure and shape, development, and complexity) obtain food via pecking, hammering, and excavating. These species engage in fewer secondary feeding strategies than the other species (Table 1). Included in this group are *Piculus flavigula*, *C. rubricollis* (Fig. 5), *D. namaquus*, *B. rubiginosus*, and *R. validus*. In other species, the mandibular apparatus is relatively less developed (quadrates, protractors, and pterygoids less

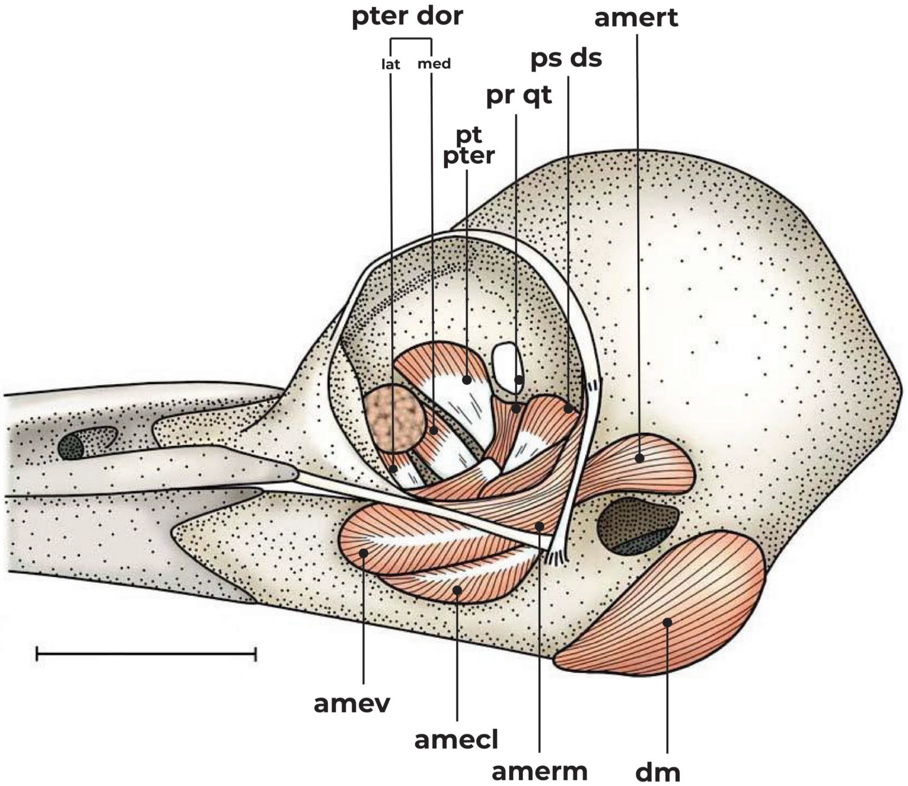

Figure 4. The jaw apparatus of *Geocolaptes olivaceus* as a representive species that utilizes the tonguing method to obtain food. Of note is the poor development of the protractor quadrati and pterygoideus complexes despite the relative development of M. protractor pterygoideus. (amecl) Adductor mandibulae externus caudalis lateralis; (amerm) adductor mandibulae externus rostralis medialis; (amert) adductor mandibulae externus rostralis temporalis; (amev) adductor mandibulae externus ventralis; (dm) depressor mandibulae; (pr pter) protractor pterygoidei; (pr pter) protractor pterygoideus; (pr qt) protractor quadrati; (psd p) pseudotemporalis profundus; (pter dor lat) pterygoideus dorsalis lateralis; (pter dor med) pterygoideus dorsalis medialis. Scale bar: 1 cm.

developed at various levels). They primarily obtain their food via gleaning or probing and secondarily via tapping. Most species in this group obtain food by gleaning (Table 1). Of all the species studied, the uniquely frugivorous *H. concretus* was noticeably distinct from the others, owing to the poor development of most components of the mandibular apparatus, accompanied by a well-developed external mandibular adductor system (Pars rostralis medialis).

Evolutionary hypotheses of food sources and foraging habits in relation to the jaw apparatus

The parsimony analysis recovered the evolution of 1) gleaning/probing; 2) pecking/hammering (Fig. 6), with ci = 1 and 1 step: frugivory to insectivory in the ancient lineage of Picinae sensu lato; and foraging mode (Fig. 6), with ci = 0.66 and 6 steps: 1) the gleaning/probing increased in the basal clade of Picinae strictu sensu; 2–4) pecking/hammering as an independent secondary behavior in *Dryocopus*, *Celeus*, and *Dendropicus*; 5°–6°) pecking/hammering as a primary behavior independently increased in the *Blythipicus*/*Reinwardtipicus*/*Camphephilus* clades and in *Piculus*.

The parsimony analysis recovered the evolution of the jaw apparatus (Fig. 6), with ci = 0.75 and three steps: 1) the transformation from the poorly developed jaw apparatus observed in *Hemicircus* to that of the intermediate complexity observed in the last common ancestor of true woodpeckers; 2) the complexity of jaw apparatus increased in the *Blythipicus*/*Reinwardtipicus*/*Camphephilus* clades and 3°) in *Piculus*.

The comparison of the evolution of the food source/foraging mode (Fig. 6) with jaw apparatus complexity (Fig. 6) identified the following topological correspondence: a) frugivory, with the lowest complexity of the jaw apparatus

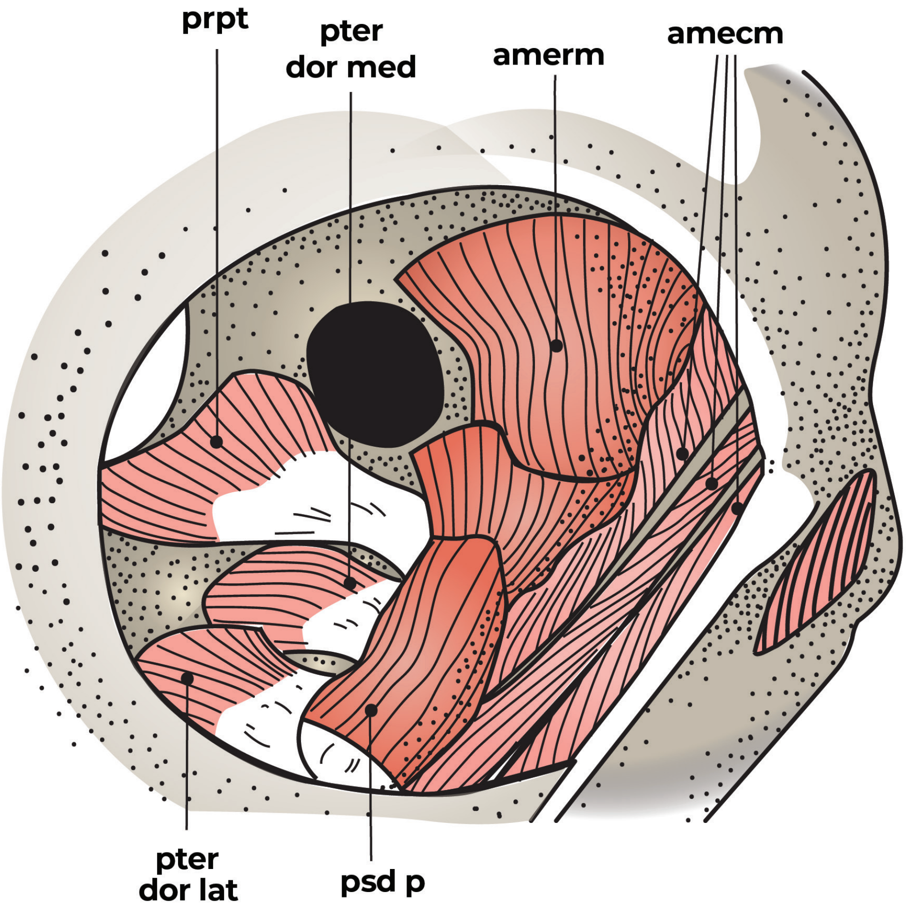

Figure 5. The jaw apparatus of *Campephilus rubricollis* as representative species that utilizes the pecking method to obtain food. Of note is the outstanding development of the quadrate-pterygoid complex. (amecl) Adductor mandibulae externus caudalis lateralis; (amert) adductor mandibulae externus rostralis temporalis; (amev) adductor mandibulae externus ventralis; (dm) depressor mandibulae; (pr pter) protractor pterygoidei; (pr pter) protractor pterygoideus; (pr qt) protractor quadrati; (psd p) pseudotemporalis profundus; (ps ds) pseudotemporalis superficialis; (pter dor lat) pterygoideus dorsalis lateralis; (pter dor med) pterygoideus dorsalis medialis.

(both present in *Hemicircus*); b) the intermediate complexity of the jaw apparatus associated with insectivory and gleaning, and probing and/or pecking and hammering as a secondary behavior (*Dryocopus*, *Celeus*, and *Dendropicus*); and c) the highest complexity of the jaw apparatus, with pecking and hammering as a primary behavior in the *Blythipicus*/*Reinwardtipicus*/*Camphephilus* clades and in *Piculus*.

DISCUSSION

Aspects of the morphology of the jaw apparatus

All woodpeckers share four jaw musculature components, which function as a muscular package with a primary function in the adduction of the mandible. These components are important as they compensate for the less developed muscle groups of several woodpecker species, such as the internal mandibular adductor, the protractor of the quadrate, and the pterygoideus systems, as described by Donatelli (1996, 2012b, 2013) and Donatelli et al. (2014). According to Richards and Bock (1973) and Bühler (1981), the protractor system of the quadrate primarily functions in the protrusion of the upper jaw, whereas the pterygoideus system primarily retracts the upper jaw and secondarily acts on the adduction of the jaw bill shape. The development of the M. pterygoideus protractor thus correlates with the forces that act on the bill during drilling (Bock 1999).

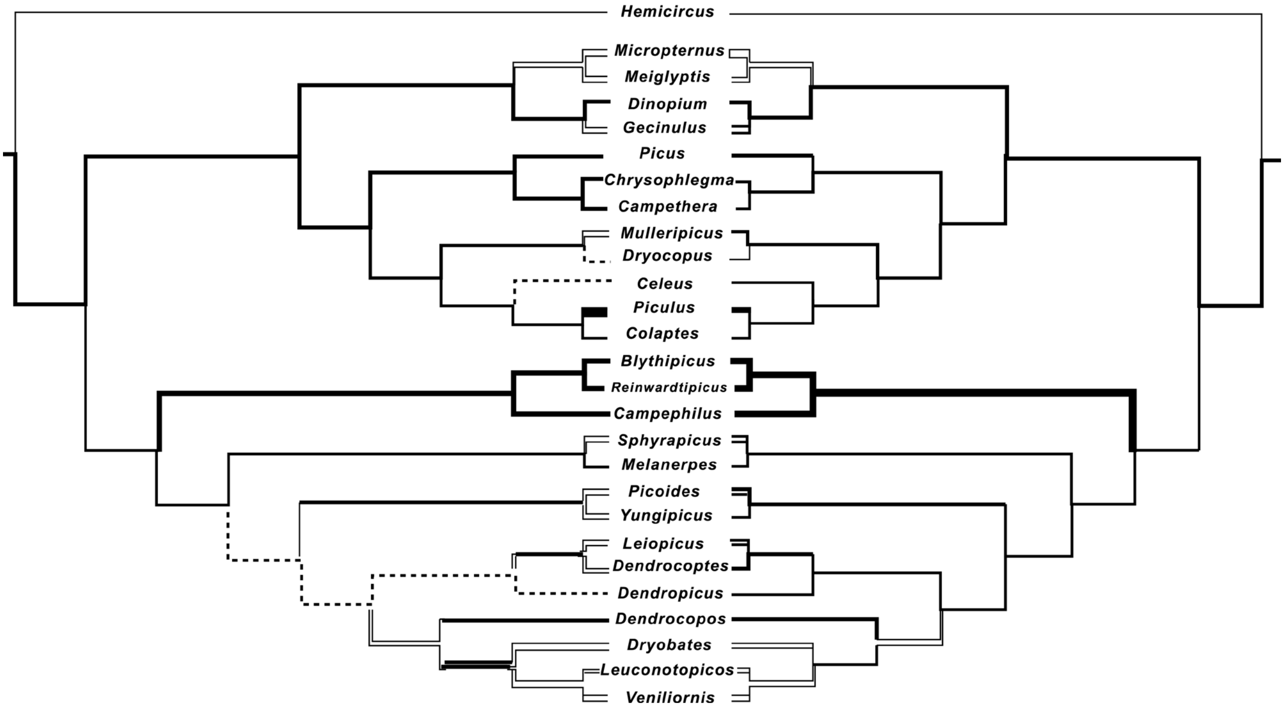

Figure 6. Most parsimonious hypotheses for the evolution of the: (Left) foraging mode (ic = 1, 1 step) and feeding habits (ic = 0.66, 4 steps) and (Right) jaw apparatus (ic = 0.75, 3 steps) mapped in the consensus strictu cladogram from Shakya et al. (2017). Thin line (frugivorous on the top of the tress); intermediate line (gleaning/probing); thick line (pecking/hammering as a primary behavior); spotted line (gleaning/probing with pecking/hammering as a secondary behavior) and grey line (absent in the analysis). Thin line (low complexity of the jaw apparatus); intermediate line (high complexity of the jaw apparatus); thick line (higher complexity of the jaw apparatus) and grey line (absent in the analysis).

As described in Donatelli (2013), the jaw musculature of all Meiglyptini woodpeckers is less developed (in size and structure) when compared with the other true woodpeckers (Donatelli 1996, 2012b). This is particularly true in the case of *H. concretus*, the only frugivorous woodpecker in this group. In contrast, the M. protractor quadrati and M. protractor pterygoidei are underdeveloped in all *Meiglyptes* spp. The only exception is found in *Mulleripicus* spp. Poor development of the muscles in the quadrate protractor system was observed in *Chrysophlegma* spp. when compared to other Picini. The muscles of the pterygoideus system are more highly developed in *B. rubiginosus*, which is combined with the greater relative depth of the ventral palatine fossa. Moreover, the protractor pterygoidei muscle in *D. rafflesii* and *D. javanense* is more developed than in other species. In *R. validus*, the quadratic protractor muscle is relatively more complex, whereas in *Dinopium* spp., this muscle is rudimentary.

In general, there is a clear distinction in the jaw musculature of *Chrysophlegma* and *Picus* compared to other Picini (Donatelli 2012b). In these genera, the structures of most components are underdeveloped in many aspects (size, morphology, and development of fibers and associated aponeurosis). Thus, probing and gleaning are the primary foraging methods for the species of *Chrysophlegma* and *Picus*. Conversely, in other Picini (e.g., *Crysocolapte*s and *Blythipicus*) there are obvious strong primary jaw protractors (M. protractor quadrati and M. protractor pterygoidei), as well as secondary jaw protractor muscles of the pterygoideus system, a condition that is found in all other true woodpeckers.

Evolutionary interpretations of the relationship between feeding habits and foraging behaviors with jaw apparatus complexity

Donatelli et al. (2014) subdivided the jaw apparatus into three classes according to their development: (i) robust, developed, and complex; (ii) poorly developed; and (iii) intermediate in complexity and development, which is in-between the first two classifications. According to these authors, *Chrysophlegma miniaceum* and *H. concretus* have a poorly developed jaw apparatus when the structure, shape, size, and complexity are considered. Both the anatomical descriptions and reconstruction of the ancestral state (parsimony method) indicate that the jaw apparatus was poorly developed during the early stages of woodpecker evolution, such as in *Hemicircus*, which feeds on fruits on treetops. Manegold and Topfer (2013) observed that the condylus lateralis of the quadrate was not enlarged and the cotylae medialis and lateralis of the mandible were fused, contrasting with true woodpeckers. In the case of woodpeckers that preferentially feed on fruit but do not engage in specific capture methods, the technique of opening these fruits should be the same as that used by Corvidae, which do not exhibit characteristic bone support in their jaws (Zusi 1967). In these birds, the jaws remain closed, and the movement of the body helps break the fruit open. Their jaws are tensioned by the muscles of the external mandibular adductor system, the pterygoideus system, and M. pseudotemporalis profundus. In Corvidae, with this support, the jaw slowly peels the fruit with the help of the feet while fixed on a support, such as a tree branch, and only after the fruit is peeled the action of both jaws employed (Zusi 1967). As a result, the bill remains closed and acts as a drill to pierce the fruit. In this way, an enlarged condyle lateralis and fused cotylae medialis and lateralis of the mandible, which would avoid disarticulation, is not necessary, as it can be observed in the frugivorous *Hemicircus*.

The jaw apparatus became more complex than that in the frugivorous species in the basal clade of true woodpeckers (Campephilini and Melanerpini) that were omnivorous/insectivorous and clearly displayed gleaning and/or probing behaviors. This included *Chrysophlegma* (*C. mentale* and *C. miniaceum*), *Dinopium*, *Meiglyptes*, *Geocolaptes abingoni*, *Dryocopus pulverulentus*, *Colaptes melanochloros*, *Melanerpes cruentatus*, and *Celeus flavescens*. However, an intermediate food preference was observed in the same woodpeckers. According to Bock (1970), among nut-eating woodpeckers, *Melanerpes lewis* (Gray, 1849) is the only species that peels the nut before storing it. Individuals of this species catch insects in flight during the summer. During the winter, however, they feed almost exclusively on fruit. According to Bent (1939) and Bock (1970), the term probing can used to describe when woodpeckers such as *M. lewis* catch insects during flight, but the most common term used in cases like these is sallying (Remsen and Robinson 1990). Woodpeckers that forage for insects or glean and probe may easily raise the upper jaw without lowering the lower jaw. To do this, they contract the muscles that act directly on the quadrate, causing their tongue to be projected between the jaws. This is sufficient to capture prey items by grasping them using the spines on the entoglossus. This mechanism does not require a more complex structure of the quadrate and pterygoideus protractor systems, as is found in species that glean and probe (Bock 1964). Manegold and Topfer (2013) also observed other adaptations in the ancestral lineage of Picinae related to the articulation between the upper jaw and the quadrate bone, as well as the tail and toes. According to these authors, both the support tail and ectodactyly toe might have been prerequisites to compensate for the increased body mass seen in various lineages within Picinae.

Although woodpeckers are primarily arboreal, terrestrial habits have developed through secondary adaptations (Short 1971). Exclusively terrestrial (e.g., *Geocolaptes olivaceus*, *Colaptes rupicola* d'Orbigny, 1840, *C. campestris* (Vieillot, 1818)) and preferentially terrestrial woodpeckers (*C. auratus* (Linnaeus,1788), *C. ferdinandae* Vigors, 1827, *P. viridis* Linnaeus, 1758, *P. canus* Gmelin, 1788, and *P. squamatus* Vigors, 1831) primarily peck and probe (actions involving joint movement of the two jaws), and secondarily glean and tongue when foraging (Short 1982). However, this does not prevent the tongue from being used for tonguing or gleaning. Apparently, terrestrial habits have arisen without modifications to the jaw apparatus.

According to Short (1982), Winkler et al. (1995), and Winkler and Christie (2002), gleaning and probing, with pecking and hammering as a secondary behavior, can be observed in *Dryocopus*, *Celeus*, and *Dendropicus*. However, such intermediate behavior does not require a more complex structure of the quadrate and pterygoideus protractor systems, as it can be observed in species that utilize pecking and hammering as their primary behavior. In general, the quadrate-pterygoideus complex of species whose main foraging actions are gleaning, probing, and tonguing is not as developed as the quadrate-pterygoideus complex of birds whose method of food capture involves more complex behaviors, such as pecking, hammering, and excavating (Donatelli et al. 2014).

According to our evolutionary analysis, the jaw apparatus is even more complex in species that adopt pecking and hammering as their primary behavior. This behavior has evolved twice independently, once in *Piculus* and once in the *Blythipicus*/*Reinwardtipicus*/*Camphephilus* clade. A complex and robust jaw apparatus in terms of structure and shape, combined with strong neck muscles (May et al. 1976), are the primary adaptations that enable woodpeckers to repeatedly apply a strong force when hammering their bills against a tree to catch wood-boring insect larvae, and for tunneling holes for nesting and defense of their territory (Schuppe and Fuxjager 2018). In addition, this prevents both mandibular disarticulation and injuries to the brain, which can be caused by strong forces and vibrations during pecking and hammering (Peng et al. 2021). Furthermore, similarly to the subdural space between the brain and skull, the beam-like bar structure of the jugal bone is a highly developed hyoid bone with a special spongy bone microstructure that has a high degree of mineralization (Burt 1930, Bock 1999, Wang et al. 2011, 2013, Zhu et al. 2014, Liu et al. 2017, Jung et al. 2018, 2019).

Further investigations into the form, function, and evolutionary history of woodpeckers are required to improve our comprehension of the diverse anatomy and behavior within this intriguing group of birds. For instance, analysis of the content and biomass of the items consumed might reveal that the effort required by a species to feed through pecking, hammering, or excavating is justified, as it yields a greater biomass when compared with gleaning or probing.

Proposing a new classification based on phylogeny must be based on congruent results from several independent studies (Fuchs and Pons 2015). However, there is no consensus uniting results among the various authors. Studies usually agree in the relationships among genera forming a clade or accepting in refuting the monophyly of certain groups. An example of this is Temminck's (1822) proposal to transfer *D. galeatus* (Temminck, 1822) to *Celeus* (Benz et al. 2015), while Benz and Robbins (2011) confirmed the monophyly of *Celeus* and revealed several new relationships between *C. spectabilis* Sclater and Salvin, 1880 and *C. obrieni* Short, 1973, both forming a clade with *C. flavus* (Müller, 1776). Another example is the relationship between *Campephilus* and the Asian genera *Blythipicus*, *Reinwardtipicus*, and *Reinwardtipicus* (Fuchs et al. 2013). These authors concluded that the species limits and evolutionary mechanisms that shaped the diversification of woodpeckers and allies (Picidae) remain obscure since the relationships between the tribes also remain uncertain. According to the latter author, a series of studies based on DNA sequence data have clarified the main groups within Picidae and the relationships among species (Moore and DeFilippis 1997, Prychitko and Moore 1997, Webb and Moore 2005, Benz et al. 2006, Fuchs et al. 2013, Benz and Robbins 2011, Winkler et al. 2014, Fuchs and Pons (2015). The consensus from these studies, generally, is that the five major clades are monophyletic: Jynginae, Picumninae (excluding *Nesoctites*), Picini, Melanerpini, and *Reinwardtipicus* + *Blythipicus*, and the placement is not well resolved for *Nesoctites*, *Hemicircus*, and *Campephilus*. However, the relationship between these groups and among the many subclades within them are also unresolved. According to Winkler et al. (2014), no molecular studies focused on Picidae have included enough samples at the species level of all genera; the most comprehensive study to date analyzed only 65 of the 235 species present.

According to Manegold and Töpfer (2013), in the last common ancestor of the Picidae, the ability to excavate nest cavities using the beak and climb tree trunks had not been developed. The first adaptations for perforation were the rhamphotheca, the dorsal bulge in the frontal bone, and the dorsalis pterygoidei process. Such characteristics would have evolved in the ancestral lineage of Picumninae and in true woodpeckers (Picinae). Other adaptations for drilling and hammering are the lateral condyle of the quadrate and the fused medial and lateral cotyles of the mandible, but such features are absent in *Hemicircus concretus*. In addition, this species is also distinct in the way it obtains food, the type of food consumed, and the low complexity of the mandibular apparatus compared to other true woodpeckers. Thus, there appears to agreement among researchers that *Hemicircus* should be placed in its own tribe (Winkler 2015) or even in a distinct subfamily, Hemicircinae (Manegold and Töpfer 2013).

Dufort (2016) used DNA sequence data from public repositories for a phylogenetic inference on a taxonomic scale using supermatrix approaches. Such accumulations of DNA sequence data for Picidae were also used in mitochondrial-based molecular analyses. The results obtained by the author agree with those obtained for the clades in this work: [*Blythipicus* – *Reinwardtipicus* + *Campephilus*] [*Melanerpes* – *Sphyrapicus*] ([*Micropternus* – *Meiglyptes*] [*Dinopium* – *Gecinulus*]) [*Chrysophlegma* – *Campethera* + *Picus*], [*Piculus* – *Colaptes*], considering the cladogram topology of the mandibular apparatus and the methods used to obtain food. The clades [*Piculus* – *Colaptes*] and [*Melanerpes* – *Sphyrapicus*] coincided with the work of Fuchs and Pons (2015). Fuchs et al. (2013) presented a ram typology consisting of [*Blythipicus* – *Reinwardtipicus* + *Campephilus*] and ([*Piculus* – *Colaptes*] + [*Celeus*]) that was also corroborated by this investigation.

The methods for obtaining food were associated with the complexity of the mandibular apparatus and the type of food consumed by true woodpeckers and may be used to study the relationship among Picidae taxa. Examples of this are the simplicity of the mandibular apparatus associated with tree-top fruit-feeding species when compared with a basal taxon such as *H. concretus*, or the complexity and development of a cranial musculoskeletal system in the mandibular apparatus that can be used to obtain specific types of food by digging, tapping, or hammering, or an intermediate system capable of gleaning or searching for food. The associations between genera are interconnected with the developmental complexity of the jaw apparatus and the differentiation of the food consumed (Donatelli et al. 2014). The results of the topology presented in recent works by Fuchs et al. (2013), Fuchs and Pons (2015), and Dufort (2016), are largely consistent with the evolution of the complexity of the mandibular apparatus of the true woodpeckers recovered in this study.

Bird anatomy was widely studied in the transition of the 19th and 20th centuries, as seen in Beddard (1898), Pycraft (1903) and Shufeldt (1909). In the middle of the 20th century morphological studies on birds were focused on how morphology correlates with biomechanics in birds (Bock 1960, 1964, Zusi 1984, 1993). Although these anatomical studies contributed to the understanding of the major orders of birds, they were not focused on solving questions in evolution. Furthermore, their samples were often small and comparisons were made between taxa that were phylogenetically distant from each other. After the advent of phylogenetic systematics, there has been an increase in the number of anatomical studies on birds. These studies have aimed to test the hypotheses of traditional classifications (Mckitric 1991).

After the DNA hybridization study of Sibley and Ahlquist (1990), studies on bird evolution have focused mainly on molecular data. As a result, morphological data has been largely neglected. One exception is the study of Livezey and Zusi (2001).

Bird morphology deserves attention because it can reveal important evolutionary traits, and the interactions among form, function and environment, in addition to providing robust data for systematics. In this way, we hope that this study encourages other researchers to carry out evolutionary studies based on morphological data in birds.

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