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Relationship Between Jaw Apparatus, Feeding Habit, and Food Source in Oriental Woodpeckers

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Associations among feeding habit, beak type, and food source in birds have been widely studied and are well known to exist. The relationship between feeding habit and jaw apparatus in birds has not attracted attention from ornithologists, perhaps because of the complexity of the skeletal morphology of the feeding system of birds. The goal of this study was to compare the jaw apparatus and foraging strategies of various Oriental species of the Picidae (Meiglyptini and Picini tribes) using a morphofunctional analysis of the skeletal structure of the jaw apparatus. This study showed that there are at least three types of jaw apparatus in these woodpeckers, as follows: 1) robust, developed, and complex; 2) complexity and development intermediate, as observed in *Meiglyptes tristis* and *Dinopium* spp., whose main foraging method involves gleaning, probing, and tapping; and 3) poorly developed, as observed in *Picus miniaceus* and *Hemicircus concretus*. The success of woodpeckers as a natural group is due not only to their feeding diversity, but also their ability to explore a wide range of different resources, as appropriate to their jaw apparatus.

Key words: birds, Oriental Picidae, jaw apparatus, feeding habits, form and function

INTRODUCTION

In living organisms, the combination of form and function creates relative stability and survival over time. Although the two ideas of form and function are closely linked, they can be conceptually distinguished from one another (Dullemeijer, 2001).

Associations among feeding habit, beak type, and food source in birds have been universally studied and are well known to exist. Studies about the role of skeletal structural elements, cranial ligaments, and the functions of the maxillary musculature were conducted by Bock on various occasions (1960; 1964; 1966). However, the relationship between feeding habit and jaw apparatus in birds has not drawn the attention of ornithologists, perhaps because the skeletal elements of the feeding systems of birds are highly complex, making morphological analyses challenging. Richards and Bock (1973, p.78), who were aware of the lack of information about the relationship between form and function, formed hypotheses about the relationship between feeding strategy and jaw apparatus in the genus *Loxops* (Aves: Drepanididae) that can be used as a reference for future studies of other groups of birds.

Regarding the Picidae tribe, Bock (2001) states that woodpeckers "have an interesting feeding apparatus consisting of two different parts – the bill for drilling into trees to explore their prey and the tongue for capturing their prey." The question to be answered in this study is related to jaw apparatus function. The behaviors and feeding specializations described for woodpeckers (Short, 1982), which are associated with certain foraging strategies (Winkler et al., 1995) and food sources (Winkler and Christie, 2002), may or may not be related to variation in the form of the jaw apparatus.

The aim of the present study was to examine the jaw apparatus of various species of the Oriental woodpeckers (Picidae: Meiglyptini and Picini tribes, *sensu* Winkler and Christie, 2002) and, based on a morphofunctional analysis of jaw structure, relate it to the foraging strategy. We intended to answer the following questions: is there a relationship between foraging strategy and structure of the jaw apparatus in the Oriental woodpeckers? Can a form-and-function relationship be identified between structural characteristics of the jaw apparatus and foraging strategy?

MATERIALS AND METHODS

Material

The present study examined the cranial osteological and musculature characteristics that move the jaws of 15 Meiglyptini specimens, pertaining to six species and three genera, and 31 Picini specimens, pertaining to 14 species and six genera. The materials used in the study were from the collections of the National Museum of Natural History (USNM), Smithsonian Institution, Washington D.C., United States of America, and the Zoologicum Bogoriense Museum, Indonesian Institute of Sciences (LIPI), Natural History

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Museum of the Indonesian Institute of Sciences (MZB), Indonesia. The nomenclature of scientific names follows Winkler and Christie (2002). Specimens with their museum abbreviations and numbers of collections included in this study are as follows: (1) Meiglyptini – *Hemicircus concretus* (Temminck, 1821) LIPI MZB.Skt 125 Hc1 and LIPI MZB.Skt 126 Hc2; *Meiglyptes tristis* (Horsfield, 1821) LIPI MZB.Skt 123 Mtr1, MZB.Skt 124 Mtr2 and USNM 292228 ♂ ; *Meiglyptes tukki* (Lesson, 1839) LIPI MZB.Skt 121 Mtu1, MZB.Skt 122 Mtk1 and USNM 489269 ♀ ; *Mulleripicus pulverulentus* (Temminck, 1826) LIPI MZB.Skt 127 Mp1, MZB.Skt 128 Mp2, USNM 19201 ♀ and USNM 562042 ♀ ; *Mulleripicus fulvus* (Quoy and Gaimard, 1830) USNM 491227 ♀ and USNM 226191 ♀ ; *Mulleripicus funebris* (Valenciennes, 1826) USNM 489265 ♂ . (2) Picini - *Reinwardtipicus validus* (Temminck, 1825) LIPI MZB.Skt 119 Rv1; MZB.Skt 120 Rv2; *Gecinulus viridis* Blyth, 1862 USNM 620306 ♀ ; *Blythipicus rubiginosus* (Swainson, 1837) LIPI MZB.Skt 117 Br1; MZB.Skt 118 Br2; USNM 489267 ♀ , USNM 559840 ♀ ; *Chrysocolaptes lucidus* (Scopoli, 1796) USNM 613082 ♂ , USNM 431475 ♂ , USNM 613081 ♂ ; *Dinopium benghalense* (Linnaeus, 1758) USNM 346830 ♀ , USNM 289692 ♀ , USNM 490202 ♂ ; *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; *Picus viridis* Linnaeus, 1758 USNM 557540♂; *Picus vittatus* Vieillot, 1818 USNM 290962 ♀ , USNM 321099 ♂ ; *Picus flavinucha* Gould, 1834 USNM 620313 ♀ ; *Picus canus* Gmelin, 1788 USNM 289905 ♂ , USNM 292049 ♂ , USNM 321598?; *Picus mentalis* Temminck, 1825 LIPI MZB.Skt 110 Pm1; MZB.Skt 110 Pm2; *Picus miniaceus* Pennant, 1789 LIPI MZB.Skt. 112 Pmi3; *Picus puniceus* Horsfield, 1821 LIPI MZB.Skt 113 Pp2.

Methods

A complete anatomical description and details of the parts that compose the jaw apparatus of the woodpecker species in this study can be found in Donatelli (2012a, b, c, d).

Only the anatomical features most relevant to foraging are discussed in the present study. Furthermore, information about the foraging strategies (methods of obtaining food) of the Picidae species was collected from a specialized literature (e.g., Short, 1982; Winkler et al., 1995; Winkler and Christie, 2002). Definitions of woodpecker foraging behaviors are presented in Winkler et al. (1995), with additional suggestions in 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 between the cracks in 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 perforation, 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 found.

Anatomical data, presented in Donatelli (2012a, b, c, d), were compared with methods for obtaining food by various species. Based on this comparison, the relationship between form and function, i.e., between the specific structure of the jaw apparatus of a species and its characteristic way of obtaining food, was analyzed. The results of this analysis were used to address the questions proposed in the description of the study objectives, above.

RESULTS

Anatomical aspects of the jaw apparatus of the Meiglyptini woodpeckers

In addition to the structural differences observed in the cranial osteology of the Meiglyptini birds (Donatelli, 2012a), there are a number of other differences that are worth mentioning because of their exclusivity, relative to the degree of development or other particularity to a group of species. The following characteristics were noted: 1) there is a thin bone elevation in the middle portion of the frontal region, named the frontal overhang by Bock (1999), which is only observed in *H. concretus*; 2) the parietal region has nearly 2 ×, 1.5 ×, and 2.5 × the lateral expansion of the frontal region in *H. concretus*, *M. pulverulentus* and *M. tristis* and *M. tukki*, respectively; 3) the zygomatic process is thick and long in species from *Mulleripicus* and short in all other species; 4) the suprameatic process is only conspicuous in species from *Mulleripicus*; 5) the *pes pterygoidei* is relatively large in species from *Mulleripicus*; relatively small, thin and narrow in species from *Meiglyptes* and inconspicuous in *H. concretus*; 6) the fossa *choanalis* is relatively wide in *H. concretus*, followed by *Meiglyptes* spp. and then *Mulleripicus* spp.; 7) the ventral palatine fossa is deep in *M. tristis*, less deep in *Mulleripicus* spp. and shallow in *M. tukki* and *H. concretus*; 8) the ectetmoid projection is relatively short and thin in *Mulleripicus* spp., and more developed in *H. concretus*; 9) the medial condyle is generally the most developed element in all of the species, but it is prominent and pointed in *M. tristis*; 10) the caudal condyle is an extension of the lateral condyle in all species; 11) the *pars symphisialis mandibulae* is short and slightly more than 1/3 of the total length of the mandible in *Meiglyptes* spp., while it is approximately 40% of the total length of the mandible in *M. pulverulentus* and nearly 45% of the total mandible length in *H. concretus*.

In addition to the structural differences in the components of the mandible musculature in Meiglyptini species (Donatelli, 2012b), there are a few other notable characteristics: 1) the components of the external mandibular adductor system of *H. concretus,* particularly the *M.a.m.e. caudalis medialis,* are relatively poorly developed compared to other species; 2) *Meiglyptes* spp. have a structure that differs from the other species in terms of certain components of the external mandibular adductor system (*rostralis temporalis*, *externus ventralis*, *caudalis lateralis*); 3) the muscles of the internal mandibular system are relatively poorly developed in size and structure in *H. concretus* and are structurally differentiated in *Meiglyptes* spp.; 4) the *M. protractor quadrati* is vestigial in *Meiglyptes* spp.; 5) the muscles of the protractor system of the quadrate are relatively poorly developed in *H. concretus*; 6) most of the muscles of the *pterygoideus* system are structurally different in *Meiglyptes* spp.

The external and internal mandibular adductor system, the protractor system of the quadrate and the *pterygoideus* system in *H. concretus* are relatively less developed than in other Meiglyptini species. In *Meiglyptes*, these components are differentiated from the other species by certain muscles of the external adductor system, namely *M. pseudotemporalis profundus* and *M. pterygoideus dorsalis medialis*.

Anatomical aspects of the jaw apparatus of Picini woodpeckers

In addition to the structural differences in the components of the cranial osteology of Picini woodpeckers (Donatelli, 2012c), there are a number of characteristics noteworthy for their exclusivity, relative development, or other particularity in a species, genus or group of species: 1) the parietal/frontal diameter ratio is typical and relatively large in smaller woodpeckers; 2) the post-orbital process is relatively standard in Picini woodpeckers (1/3–1/5), except for *C. lucidus* (4/5); 3) the *pes pterygoidei* is a well-developed structure that stands out in all Picini woodpeckers; 4) the presence of a frontal overhang differs between the genus *Picus* and other Picini members; 5) the orbital process of the quadrate is relatively larger in *B. rubiginosus*; 6) the ventral palatine fossa is relatively deep in *B. rubiginosus*; 7) there is a clear distinction between species of the genus *Picus* and other Picini species in relation to the general cranial bone structure; 8) *B. rubiginosus*, *C. lucidus*, *R. validus*, *G. viridis* and the other species of *Dinopium* have particularities that, based on the current level of understanding, are too complex to identify the relationships between them.

In addition to the structural differences in the components of the mandibular musculature of the Picini woodpeckers (Donatelli, 2012d), some characteristics are worth to mention: 1) in general, the components of the external mandibular adductor system in Picini woodpeckers are relatively more developed in larger species (e.g., *R. validus* and *D. rafflesii*); 2) there is a clear association between the *ventralis lateralis* and *dorsalis lateralis* adductor muscles by means of fleshy connecting fibers in all of the species; 3) the jaw musculature of *Picus* spp. differs from the rest of the Picini members with regards to the poor development of the muscles of the quadrate protractor system (*M. protractor quadrati* and *M. protractor pterygoidei*); 4) the orbital process of the quadrate is relatively larger in *B. rubiginosus*, while the *M. pseudotemporalis profundus* is relatively less developed; 5) the muscles of the *pterygoideus ventralis* system are more developed in *B. rubiginosus* in combination with the greater relative depth of the ventral palatine fossa in this species; 6) generally, the *M. pseudotemporalis superficialis* begins in the ventrocaudal region of the laterosphenoid (lower part of the pleurosphenoid region), with the only notable exception being that it begins in the upper part of the pleurosphenoid region in *D. javanense*; 7) the *M. pterygoideus ventralis medialis* has a third component in *D. rafflesii*; 8) in addition to *B. rubiginosus*, the *protractor pterygoidei* muscle in *D. rafflesii* and *D. javanense* is more developed than in other species; 9) in *R. validus* the *protractor quadrati* muscle is relatively more complex, while in the other *Dinopium* species this muscle is rudimentary; 10) there is a clear difference in the structure of the mandibular musculature between *Picus* species and other Picini. *B. rubiginosus*, *C. lucidus*, *R. validus*, *G. viridis,* and *Dinopium* species all have additional particularities, but given the current level of understanding, it is difficult to identify relationships among them.

Food strategies of woodpeckers

According to Short (1982), Winkler *et al.* (1995) and Winkler and Christie (2002), Meiglyptini species occupy arboreal habits and their foraging strategies can be divided into four categories: 1) gleaning, 2) probing, 3) tapping, and 4) excavating. Most Picini species also occupy arboreal habits, and their principal foraging habits can be divided into five categories: 1) gleaning, 2) probing, 3) tapping, 4) excavating and 5) tonguing. Table 1 shows the foraging strategies of these woodpeckers, the importance of each of these methods for each species, the location where the food items are found and the type of food consumed by each species.

Jaw apparatus and food strategies

What is the relationship between these feeding parameters and the jaw apparatus? According to the above results, at least three types of jaw apparatus may be

Table 1. Methods of obtaining food and types of food of woodpeckers from the Oriental region.

Species	G	T	P	E	To	Local	Food
M. pulverulentus	■	□	□	○		trees	ants and beetle larvae
M. tristis	■	□○	○			trees	ants and other insects
M. tukki	■	□	□○			trees	ants and other insects
H. concretus	■	□	□			trees	fruits
P. miniaceus	■	□	□			trees	ants, eggs and larvae
P. puniceus		■	■	■		trees	ants, eggs and termites
P. mentalis	■	□	■	□		trees	ants, termites, beetles
P. vittatus	■	■	■			ground	beetles, flies
P. squamatus			■			both	ants, termites, berries (W)
P. viridis		□	■		□	ground	ants, earthworms, snails, fruits & berries, nectar
P. canus	□	□	□	○	□	ground	ants, earthworms, snails, fruits & nuts, acorn, nectar
D. rafflesii	■	■	■			trees	ants, termites, pupae
D. javanense	■		■			trees	ants, larvae, scorpions
D. benghalense	■					trees	ants, larvae, fruits, nectar
C. lucidus	□	■		■		trees	lizards, beetle larvae, ants, pupae, nectar
G. viridis	■		■			trees	ants, larvae, beetles
S. noguchii		■		■		trees	large arthropods, fruits, berries, seeds
B. rubiginosus				■		trees	beetles, insect larvae
R. validus		■		■		trees	beetle larvae, ants, termites, berries

■ – primary or main action; □ – secondary action; ○ – eventual action.
W – Winter. G – gleaning; T – tapping; P – pecking; E – excavating; To – tonguing.
Categories based on Short (1982), Winkler et al. (1995) and Winkler and Christie (2002).

inferred. 1) Robust, developed and complex: greatest development of the zygomatic, suprameatic, and quadratic processes and of the *pes pterygoidei*; all of the components associated with the muscles that act in cranial kinesis; protractor muscles of the quadrate and external mandibular adductors relatively more developed, which is observed in *M. pulverulentus*, whose principal food source is ants, larvae, and beetles; especially the protractor muscles of the quadrate and external mandibular adductors, as observed in *B. rubiginosus and R. validus*, which are primarily excavators that feed on ants, ant larvae and beetles. 2) Poor developed: particularly the protractor muscles of the quadrate and the external mandibular adductors, as observed in *Picus* spp., whose principal foraging strategy is gleaning and who feed on ants and termites (and beetles, in the case of *P. mentalis*). Moreover, the components of the external and internal mandibular adductor system and of the protractor of the quadrate system are relatively poorly developed. This is observed in *H. concretus*, which feeds on fruits in the tree canopy. 3) Intermediate type between the previous types, as observed in *Dinopium* spp., who glean, probe and tap and who feed on ants, termites and (secondarily) beetles and their larvae (*D. javanense*); particularly with regard to the protractor muscles of the quadrate, external mandibular adductors and muscles of the *pterygoideus* system; for example, the *M. protractor quadrati* is vestigial, and some components of the external mandibular adductor system are differentiated (*rostralis temporalis*, *externus ventralis*, *caudalis lateralis*). This is observed in *Meiglyptes*, spp., whose principal food is ants and other insects.

DISCUSSION

In a classic work of interpretation of the development of the jaw apparatus in relation to feeding habit, Richards and Bock (1973) associated the cranial bone development and the musculature that moves the *maxillae* with the feeding strategies and food type of Hawaiian honeycreepers from the genus *Loxops* (Drepanididae). The authors found that in species with more robust skulls, the development of the musculature of the *maxillae* is greater. Furthermore, the species that have used this musculature in a less vigorous way are the same species that have less robust skulls, less developed maxillary musculature and methods for obtaining food that require less effort, such as feeding on nectar and catching insects (gleaning) from leaf surfaces (Richards and Bock, 1973, p. 79–81). In the same field of research Zusi (1993) carried out a revision work of the relationship between the morphology of the skull and functional anatomy; his analysis was based on the different types of bird cranial kinesis and their roles in the movement of the jaw relative to the braincase. Both classical works are used here but in a distinct direction: the morphology of the jaw apparatus area related to feeding habits and food source, that is associated with feeding ecology.

Of the Meiglyptini woodpeckers studied, all are characterized as having arboreal habits. However, they can be divided into three main foraging categories, according to Short (1982), Winkler et al. (1995) and Winkler and Christie (2002): 1) gleaning, 2) probing and 3) tapping. According to these authors, excavating occurs occasionally in *M. pulverulentus* and tonguing has not been observed in any Meiglyptini woodpecker. Furthermore, nothing is known about the feeding behavior of *M. fulvus* and *M. funebris*, and this analysis will be restricted to *M. pulverulentus* and the other species of Meiglyptini woodpeckers. *Mulleripicus pulverulentus*, *Meiglyptes tristis* and *M. tukki*, in addition to *H. concretus*, primarily glean to obtain food items, which are mainly ants, larvae, and other insects (except in the case of *H. concretus,* which feeds on fruits). *Mulleripicus pulverulentus* and *H. concretus* use probing and tapping as secondary techniques, but no species of *Meiglyptes* appears to use probing or tapping, even as a secondary strategy. Therefore, the primary foraging action of these woodpeckers is gleaning, irrespective of the type of food item consumed. No Meiglyptini species has a generalist feeding behavior, but some are generalists with regard to type of food. While *M. pulverulentus* and the *Meiglyptes* species search for insects on tree trunks, *H. concretus* searches for fruits in the tree canopy. Smaller woodpeckers, such as *M. tristis* and *M. tukki*, have a more complex jaw apparatus (type 2) and are more generalist in terms of feeding habit (insects). *Mulleripicus pulverulentus* is a specialist and has a relatively complex mandible (type 1), and it feeds on both ants and beetle larvae. However, this does not justify the distinction in complexity in relation to *Meiglyptes* spp. The smallest species (type 3), *H. concretus*, has a feeding strategy that differs from the other species, and it only consumes fruits. Based on this comparison, it is possible that natural selection has resulted in a more complex structure for birds that capture insects, and a less complex structure for species that do not need to capture insects, driven either by ecological (competition) or behavioral (foraging in the canopy of trees) factors. Either way, it appears that anatomical characteristics of the jaw apparatus are associated with feeding behavior, feeding location and competition for food.

With regards to the Picini woodpeckers studied, all of the species can be characterized as having arboreal habits. Furthermore, they can be divided into five main foraging categories, according to Short (1982), Winkler et al. (1995) and Winkler and Christie (2002): 1) gleaning, 2) probing, 3) tapping, 4) excavating, and 5) tonguing. Only *P. puniceus* has five primary foraging behaviors. Of these feeding strategies, some are primary behaviors: a) gleaning and probing (*P. mentalis*); b) gleaning, probing and tapping (*D. rafflesii* and *D. javanense*); c) excavating (*B. rubiginosus* and *R. validus*); d) tapping (*R. validus*); and e) gleaning (*P. miniaceus*). Some are secondary behaviors: a) probing and tapping (*P. miniaceus*) and b) tapping (*P. mentalis*). A relationship between foraging category and type of food taken can also be observed: 1) *P. puniceus* feeds on ants and termites and uses all types of foraging; 2) *P. mentalis* feeds on a wide range of food items (ants, termites, crickets, beetles, grasshoppers and even green berries) and uses gleaning and probing as primary foraging strategies; 3) *B. rubiginosus* and *R. validus* feed on beetles, beetle larvae and ants, and primarily use excavating; 4) *P. miniaceus* feeds on ants, and its principal foraging strategy is gleaning; and 5) *D. rafflesii* and *D. javanense* feed on ants, termites and larvae (except beetles), and their principal foraging strategies are gleaning, probing and tapping.

Thus, the primary foraging strategies used by these woodpeckers are gleaning and probing, followed by tapping, excavating, and tonguing. The principal food items, independent of foraging mode, are ants (and their larvae), termites, and beetles.

Picus puniceus is the most generalist species in terms of foraging strategies and is an ant and termite specialist (as is *P. mentalis*). In contrast, *P. miniaceus* is an ant specialist, but it primarily gleans. Woodpeckers that primarily glean and probe have a wide range of food items available to them. Excavating specialists also consume harder food items such as beetles (*B. rubiginosus* and *R. validus*). Smaller woodpeckers (except for *B. rubiginosus*) have a less complex jaw apparatus (type 2), are more generalist in terms of food items (insects), and use gleaning and probing as their main foraging strategies. Relatively large woodpeckers (with the exception of *B. rubiginosus*) are specialists in terms of food items and foraging strategies and have relatively complex mandibles (type 1). Type 3 can be found regardless of size.

The success of woodpeckers as a natural group is due not only to their feeding diversity but also their wide ability to explore different resources. Additionally, foraging strategies are related to the diameter, type, conditions and height of tree trunks for arboreal species and soil type for terrestrial species (Winkler and Christie, 2002). Furthermore, the jaw apparatus of oriental woodpeckers is closely related to the feeding habits and food sources of these species.

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