Evolutionary morphology of the woodpeckers (Picidae)

Walter J. BOCK

Abstract: 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“. Over the ensuing decades, the adaptiveness and evolution of these diverse woodpecker features has been examined by many workers but with limited success. A major problem was that these evolutionary explanations were not supported by logically prior functional explanations. Structures of the toes, hind limb and tail are associated with climbing. All forces acting on the climbing bird can be determined with the Method of Free-Body Analysis, which together with measurements of hind limb and tail features and of the tree surfaces used by different species, will permit understanding of the evolution of climbing adaptations. Bill shape and M. protractor pterygoidei development correlate with forces on the bill during drilling. Again Free-Body Analysis shows that compressive shocks acting on the bill do not travel directly into the brain case and hence the brain, but result in a compressive stress in the base of the skull. The frontal overhang in specialized drilling woodpeckers provides a bony stop that prevents excessive abduction of the upper jaw during non-impact periods while drilling into trees. Specializations of the tongue are connected with greater protraction of the tongue to obtain food. These features not only include longer protractor and retractor muscles, but a universal joint between the basihyal and the fused paraglossalia and the enlargement of two pairs of intrinsic muscles inserting on the paraglossalia enabling movement of the tip of the corneous tongue in all directions. With a better understanding of the adaptiveness and evolution of these diverse features of woodpeckers, it is possible to obtain an improved comprehension of their ecological associations, adaptations and evolutionary history. Earlier analyses which omit the mechanics of the avian cranial kinesis and the vertebrate muscle-bone systems have failed to solve how woodpeckers deal with the large impact force when drilling into trees. Extrapolation of analyses this impact force on woodpecker skulls to impact forces on human skulls is not possible because the akinetic mammalian skull cannot be compared to the kinetic avian skull.

Key words: Woodpeckers, Picidae, anatomy, adaptations, bill, tongue, climbing, drilling, evolution

Introduction

In the Introduction to his *On the Origin of Species*, DARWIN cited woodpeckers as the very first example to illustrate the evolutionary origin of adaptations, saying „... the woodpecker, with its feet, tail, beak and tongue, so admirably adapted to catch insects under the bark of trees“ and then asks the question of how these excellent, but not perfect, adaptations came into being. Indeed woodpeckers not only possess a most outstanding suite of adaptive features, but the diverse species within this avian family display a broad spectrum of modifications of these adaptive features. In this paper, I would like to examine some of the adaptive features in the true woodpeckers (Picinae) for climbing, drilling into trees, and capturing food with their tongue (see BOCK 1999a, 2001). Unfortunately the wrynecks (*Jynx*; Jynginae) and the piculets (Picumninae) are excluded from this discussion as I have not had the opportunity to study these members of the Picidae and there is still too little known about their morphology. I will stress that functional analyses required for the assessment of the adaptiveness of these several features for climbing, pecking and food-catching, and will indicate how these functional-adaptational analyses serve as essential foundations for further ecomorphological and evolutionary studies. Further, I will emphasize that functional explanations in biology are logically prior to and essential for evolutionary explanations, that is, in the absence of proper functional explanations, evolutionary explanations (including classifications and phylogenetic analyses) lack the necessary foundation and are vacuous. Most importantly, there are still many new developments and many interesting things to learn in the old, but not tired, field of avian morphology which include a deeper understanding of avian cranial kinesis (BOCK 1964, 2002) and new articulations, such as the secondary articulation of the lower jaw (BOCK 1960, 2002), the ectethmoid-mandibular articulation in the Meliphagidae (BOCK & MORIOKA 1971), and the accessory occipital condyle in the hornbills (BOCK & ANDORS 1992).

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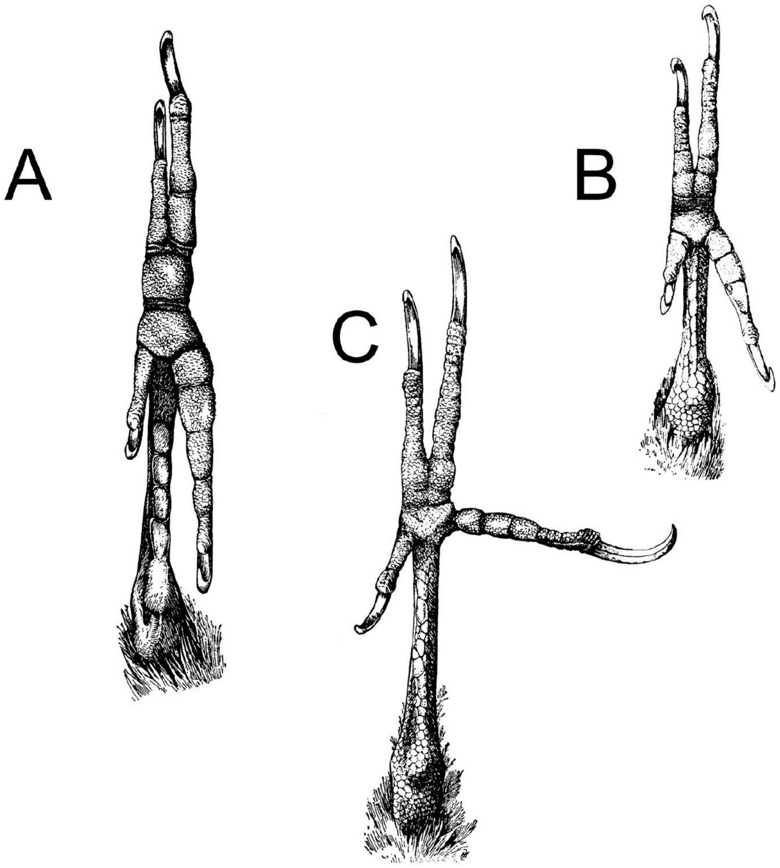


Fig. 1: Plantar Surface of the foot to show the arrangement of the toes. (**A**) *Pteroglossus* (Ramphastidae; perching foot). (**B**) *Celeus elegans* (Picidae; perching and climbing foot). (**C**) *Dryocopus pileatus* (Picidae; climbing foot). (From Bock & Miller 1959: Fig. 1).

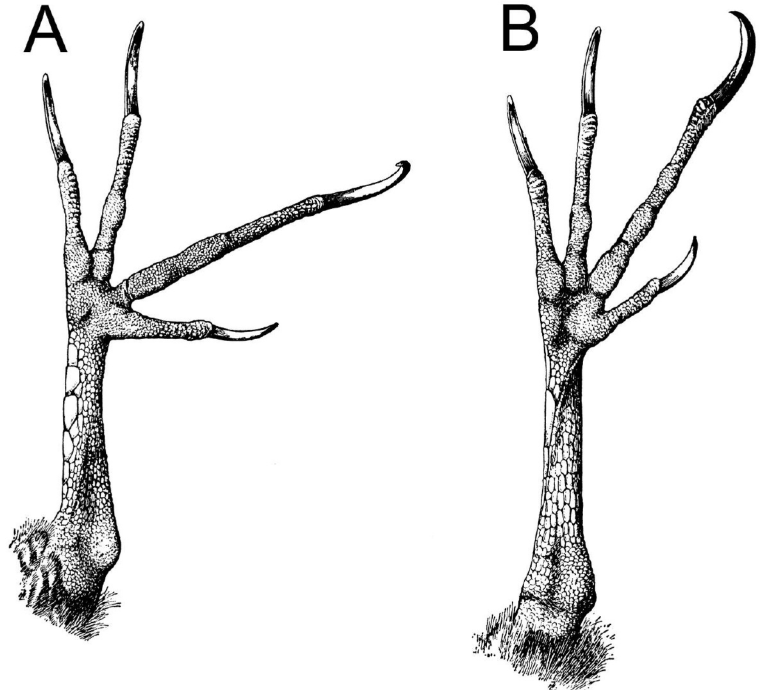


Fig. 2: Plantar surface of the foot to show moderate and extreme forward rotation of the fourth toe and hallux in the ivory-billed woodpeckers. (**A**) *Campephilus melanoleucos*. (**B**) *Campephilus rubicollis*. (From Bock & Miller 1959: Fig. 6).

Climbing

Analysis of climbing in woodpeckers will include the arrangement of the toes, investigation of the mechanical forces on the climbing bird, and structure of the hind limb muscles. I will not cover in detail the stiffened tail feathers in members of the Picinae which provide support when the bird is climbing (see Short 1982 for details). In most picines the two central tail feathers are stiffened, although some as *Dendrocopos noguchii*, *Meiglyptes* and *Hemicircus*, have only somewhat stiffened central tail feathers. Specialized forms, such as *Campephilus*, *Chrysocolaptes*, *Reinwardtipicus* and *Blythipicus* have the two central pairs of rectrices stiffened with a very concave (below) and strengthened vane. *Jynx* possesses a soft and non-supportive tail and the piculets have a very short tail that does not contact the tree similar to nuthatches.

The legs of the larger, more powerful species of woodpeckers are longer as these species generally hold their feet widely apart with the tarsometatarsus pressed against the tree and the body relatively far away from the tree. In these larger forms (*Campephilus*, *Chrysocolaptes*, *Reinwardtipicus* and *Blythipicus*), a callus is present at the proximal end ("heel") of the tarsometatarsus and covered with small scales (Winkler et al., 1995: 16; 2002: 305, illustration caption) as shown in Photo 1; the callus is covered with small scales. In addition the posterior surface of the tarsometatarsus is covered with small scales as are the palmar surfaces of all toes; the last feature seems to be common to most or all species of the Picinae and perhaps of the Picidae. The small scales provide a better gripping surface and greater resistence to abrasion of the feet and of the tarsometatarsus against the surface of the tree. The callus at the "heel" of the tarsometatarsus provides greater protection to the abrasive action at this part of the legs. These large species of woodpeckers press the entire tarsometatarsus against the tree when they are hammering on it during feeding and evacuating nesting and sleeping holes in the tree. The "heels" of the tarsometatarsus are subjected to larger compressive forces from the tree surface which are directed directly to the tibiotarsus – the central bone of the three bones of the avian leg, A good survey of these aspects of woodpecker legs is not available at this time because they are not readily observed in study skins due to the construction of these specimens.

Woodpeckers, as all members of the Piciformes, possess a zygodactyl foot or ”yoke arrangement“ of the toes in which the fourth toe is reversed to the rear of the foot (Scharnke 1930, 1931; Stolpe 1932; Steinbacher 1935). Modifications evolved in the condyle of the fourth toe to permit an efficient reversal of the tendons to this toe (Steinbacher 1935). Because woodpeckers possess a zygodactyl foot and because they are mainly climbing birds, most ornithologists have simply concluded that the zygodactyl foot is an adaptation for climbing. Not so, as argued in the early part of this century by Waldron de Witt Miller (see Bock & Miller 1959) who showed that the zygodactyl foot is an adaptation for perching and that the arrangement of the toes in climbing woodpeckers is not zygodactyl. Most members of the Piciformes, Psittaciformes and Cuculidae, all of which possess a zygodactyl foot, are perching birds; the basic requirement of a perching foot is having opposing toes to provide a grip on the branch. In climbing birds, including those that cling to vertical surfaces, as many toes as possible should oppose the downward pull of gravity. When woodpeckers perch, such as commonly done by the wryneck (*Jynx*), the toes are held in the zygodactyl arrangement. But when climbing, the fourth toe of woodpeckers is not reversed to the rear of the foot, but is extended laterally (Figs 1, 2). The position of the toes in many species of climbing woodpeckers can be clearly seen in numerous photographs in Winkler & Christie (2002). The lateral extension of the fourth toe (Fig. 1 C) provides support against any sideward directed forces when the bird is climbing or drilling into the tree. Generally the short hallux (first toe) does provide little or no support, and is reduced or lost in several genera of woodpeckers. In some genera, such as in the New World Ivory-billed Woodpeckers (Fig. 2), the hallux is long and is held to the lateral side or even positioned in the front of the foot when the bird is climbing (see Tanner 1942, Jackson 2015: Photograph p. 23).

The claws of the toes in woodpeckers must be strongly curved and sharply pointed so that they can penetrate into the bark when the bird is climbing trees and when the ventral surface of the toes is pressed against the bark surface. Strongly curved claws are also found in both the foot and the hand of *Archaeopteryx* and have been used as important evidence supporting the argument that this bird was arboreal and used both its forelimbs and hind limbs to climb up trees (Feduccia 1996). With woodpeckers climbing on the trunks and branches of trees, the next questions would be: What are the mechanical forces acting on a climbing woodpecker? And how does the placement of the feet and tail affect these forces? Forces on a climbing woodpecker were analyzed by earlier workers (Stolpe 1932, Bock & Miller 1959), but erroneous assumptions were made on the direction and placement of various forces and incorrect physical model were used (Fig. 3). A proper model was presented by Winkler & Bock (1976; see also Bock & Winkler 1978) employing the method of free body diagrams. This model includes both the rotational and linear displacement effects of all forces acting on a climbing bird, as well as the frictional forces at the contacts between the bird and the tree (Fig. 4). From this analysis, it is possible to show what measurements are needed to undertake a full bio-mechanical analysis and to calculate all forces acting on a climbing woodpecker. Moreover, one can inquire into the consequences of modifying various factors, such as holding the body closer or further from the tree, varying the length of the tail, or climbing without a supporting tail as in piculets. Free body analysis shows the incorrectness of any model in which the position of the forces acting on the legs and the tail of climbing birds are assigned in an arbitrary manner (e.g. along the axis of the leg or tail or through the articulation of the leg with the limb girdle). Any method ignoring frictional forces at the contact points (i.e. contact forces placed at right angles to the contact surface) is also wrong.

The free-body model for the forces on a climbing woodpecker indicates that the flexor muscles of several

Photo 1: Right foot and tarsus of a juvenile Black Woodpecker. Photo: H. Winkler

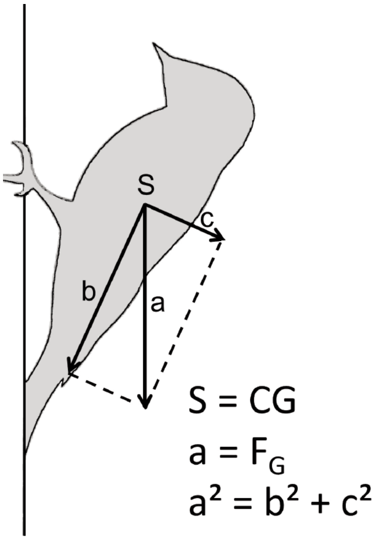
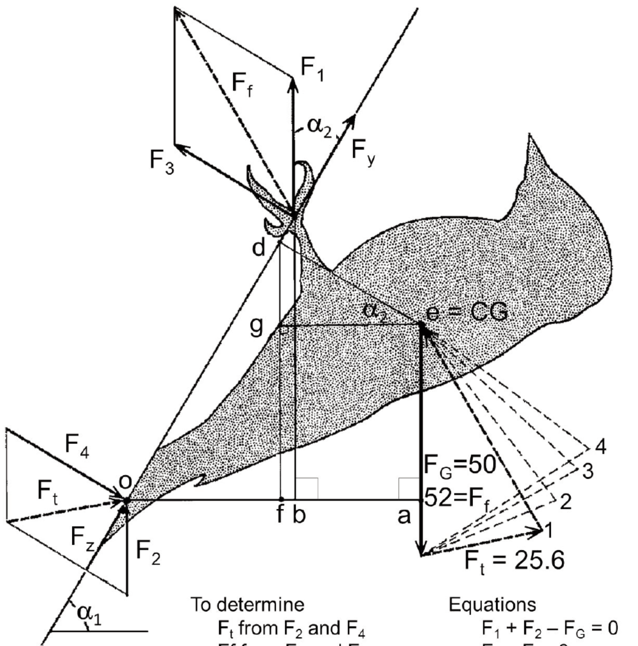


Fig. 3: Earlier model of forces acting on a climbing woodpecker redrawn from Stolpe (1932: Fig 37, p. 212) using his symbols but with conversions to the model of Winkler and Bock. The slight deviation of force vector 'b' from the longitudinal axis of the tail is copied carefully from Stolpe. (After Winkler & Bock 1976: Fig. 1.)



To determine
F_t from F_2 and F_4
Ff from F_1 and F_3

Measure (minimum)
F_G; F_z or F_y
α_1 or α_2; $\alpha_1 + \alpha_2 = 90°$

Equations
$F_1 + F_2 - F_G = 0$
$F_4 - F_3 = 0$
$F_G(oa) - F_1(ob) - F_3(oc) = 0$
$F_1 = F_y / \cos\alpha_2$; $F_2 = F_z / \cos\alpha_2$
oc = distance: tail – feet
$ob = oc \cdot cosa_1$
$oa = of + fa = od \cdot \cos\alpha 1 + ed \cdot \cos\alpha_2$
fa = eg

Fig. 4: The woodpecker (tailed) model: general case with the bird at rest clinging to an oblique (overhanging) surface. The tail contacts the tree at point 'o' and both feet at point 'c'. The force of gravity (F_G) acts at point „e"', the center of mass (CG). To be determined are the two unknown forces (heavy dashed arrows) between the tree surface and the tail (F_i) and the feet (F_1) with the minimum number of measurements. The force of gravity is set at 50 gm-wts, and F_1 is arbitrarily assumed to be 30 gm-wts, hence F_2 is 20 gm-wts. The results of the analysis are shown on the figure and summarized in the closed polygon of forces (# 1) of heavy arrows. Results of three additional analyses are summarized in the closed polygons of lighter dashed lines; for analysis 2, F_i = 20 gm-wts, for 3, F_i = 10 gm-wts, and for 4, F_i = 5 gm-wts. (After Winkler & Bock, 1976: Fig. 2).

segments of the hind limb should be larger in cross-sectional area (i.e., develop more force) to hold (flex) the limb segments together against the effects of the gravitational force on the bird. One indication of this development is the absence of the M. accessorius semitendinosus in specialized drillers (*Dendrocopos*, *Picoides*, *Sphyrapicus*, etc.) although this muscle is present in less specialized taxa (Burt 1930: 502). Unfortunately nothing is known about the relative size and hence force development of the hind limb muscles, especially the flexors, in the different species of woodpeckers with respect to their climbing specialization.

Some years ago, Selander & Giller (1963) and Selander (1966) showed that different species of woodpeckers and even the two sexes of the same species used different parts of the tree for foraging, and that these diverse foraging patterns resulted in modifications in foot and tail structure. Climbing on trunks, branches and twigs of differing diameters represents a significant part of the niche requirements of the two sexes and of the individual species; one that can be readily analyzed with the methods of ecomorphology (Leisler & Winkler 1985, 1991). Understanding the functional significance of toe arrangement during climbing and analysis of the forces on climbing woodpeckers permit a better appreciation of the measurements, including lengths of the tail, hind limb, position of the bird on the tree, the hind limb muscles, to be taken in such an ecomorphological study as well a better foundation for analyzing the results.

Drilling

If you bang your head against the wall, it feels good only when you stop — which leads to the commonly asked question of why don't woodpeckers get headaches when they are drilling into trees? Or to put it in a more serious way, how do woodpeckers protect their brain from damage resulting from the impact of their bill tip when drilling into trees? The impact force with which the woodpecker's bill hits the tree depends, among other things, on the terminal speed of the head during drilling. This terminal speed may well depend on a whip-lash effect as discussed by Liu et. al. (2015) although their conclusion is not supported by their analysis. They claim (Liu et. al. 2015: 183) that: „When the woodpecker's body moves backward, the muscles on one side stretch the tendons, and the tendons store elastic deformation energy." And further (Liu et. al. 2015: 184) that: „Muscle torque is determined by the muscle mass of the joint (By joint, I assume the segment of a limb or the vertebral volume)." If a muscle contracts, its force does not stretch the tendon of the antagonistic muscle (e.g., contraction of the M. biceps does not stretch the tendon of the M. triceps if the latter muscle is not contracting. Rather contraction of the M. biceps will stretch the relaxed M. triceps). Further, since torque is force X length of the moment arm, their statement that muscle torque is determined by muscle mass is completely meaningless because the force of a muscle has no relationship to its mass (Gans & Bock 1965, Bock 1974). Further down in that column, they say „muscles contract backwards" which is a meaningless statement as muscles cannot contract backwards. Muscles can be stretched while they are contracting which is a completely different thing, but this occurs only when the load on the muscle is greater than the force being produced by the muscle which does not appear to be the case when a woodpecker is drilling into trees.

A number of suggestions have been made on the possible existence of shock-absorbing mechanisms based on cranial kinesis and stretching of contracting muscles

(Bock 1964: 29–30, Spring 1965). It should be stressed that many of the proposed explanations are based on the erroneous idea that birds possess an akinetic skull similar to that found in mammals (including humans) and hence are wrong from the onset. Most of these explanations were offered to provide an understanding how to provide humans with a suitable crash helmet that will lessen impact forces on the skull in the case of an accident. These shock-absorbing mechanisms work by increasing the duration of the impact and thereby reduce the maximum impact force. Such mechanisms, however, would reduce the impact force by the woodpecker on the tree and, hence, result in reduction in the efficiency of drilling. Many of the proposed crash helmets would not be suitable for humans. Furthermore the suggestions offered on the structure and functioning of shock-absorbing mechanisms to reduce forces acting on the brain case and brain of woodpeckers during drilling can be rejected simply because the knowledge of the structure of the woodpecker skull is wrong. Woodpeckers, as all birds, possess a kinetic skull in which some or all of the upper jaw can rotate up or down relative to the braincase (Bock 1964, 2002). The consequences of the reaction forces by the tree on the bill during drilling can only be understood in terms of avian cranial kinesis (Bock 1964, 1974). In the following analysis, for the sake of brevity, only the forces acting on the upper jaw will be treated as these relate most directly to possible damage to the brain, although the forces on the lower jaw can be readily added to the analysis.

The structure of the woodpecker skull, and especially the kinetic hinge between the rostral end of the brain case and the caudo-dorsal base of the upper jaw must be carefully examined (Figs 5, 6, 7). Earlier workers analyzing the forces on the woodpecker bill during drilling have overlooked this hinge and have shown a compressive shock passing directly from the upper jaw into the brain case, assuming that the result of an impact force on the tip of an avian bill is similar to what happens in a mammalian (e.g., human) skull. However, given that the upper jaw can rotate relative to the brain case around the nasal-frontal hinge, the actual consequence of the impact force are quite different. Consideration will be given to the instance of impact of the woodpecker bill on the tree in which all forces acting on the upper jaw are included using a free-body analysis (Fig. 7). For the purposes of this analysis, the upper jaw will be assumed to be static with respect to the brain case at the moment of impact. The forces on the upper jaw will tend to rotate it and also to move it in some linear direction, hence equations are needed for both the rotational and the linear effects of the forces acting on the upper jaw. Forces on the upper jaw (Fig. 7) are: (a) the reaction(= impact) force (F_i) of the tree on the tip

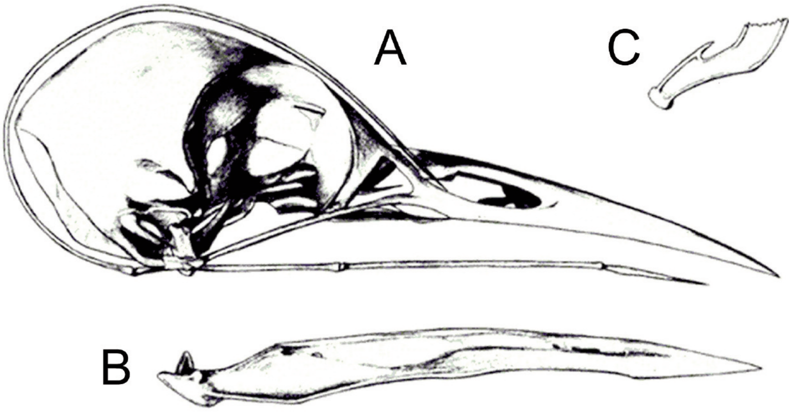


Fig. 5: Skull and hyoid apparatus of the Red-bellied Woodpecker *Melanerpes carolinus* in lateral view. (**A**) Braincase and upper jaw with the hyoid apparatus in place. (**B**) Mandible. (**C**) Pterygoid bone showing the large spine for the insertion of the M protractor pterygoidei. (Adapted from Bock 1999a).

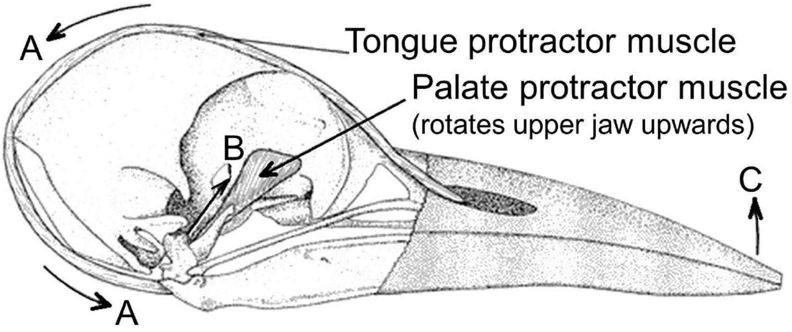
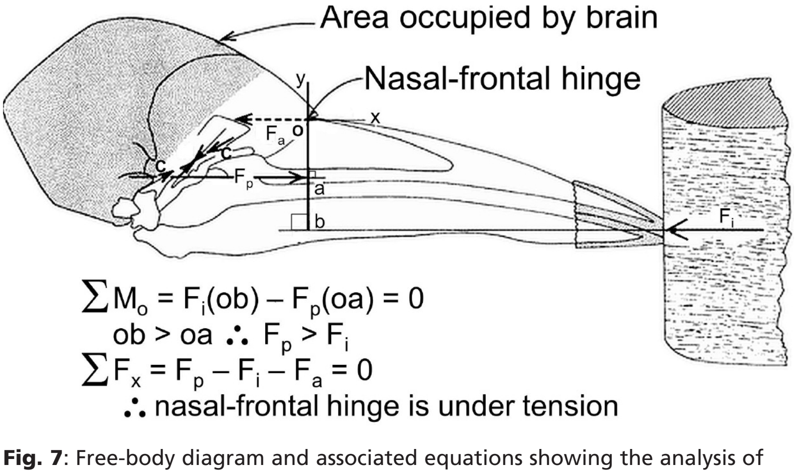


Fig. 6: Lateral view of the skull and hyoid apparatus of the Red-bellied Woodpecker, *Melanerpes carolinus*, showing the protractor muscles of the tongue and of the palate (pterygoid). Contraction of the tongue protractor (arrow A) results in protrusion of the tongue out of the mouth. Contraction of the palate protractor (arrow B) results in protraction (= elevation) of the upper jaw (arrow C). (Adapted from Bock 1999a).



$$\sum M_o = F_i(ob) - F_p(oa) = 0$$

$$ob > oa \therefore F_p > F_i$$

$$\sum F_x = F_p - F_i - F_a = 0$$

$$\therefore \text{nasal-frontal hinge is under tension}$$

Fig. 7: Free-body diagram and associated equations showing the analysis of the forces on the upper jaw at the moment of impact of the jaw tip against a tree. The upper jaw is assumed to be static at the impact. Note that force Fa of the brain case on the upper jaw at the nasal-frontal hinge and its equal and opposite force of the upper jaw on the brain case (not shown) results in the bone of the nasal-frontal hinge being under tension. The consequence of the large impact force of the tree on the tip of the upper jaw (Fi) is a large compression force C in the base of the brain case below the rain between origin and insertion of the M. protractor pterygoidei. (Adapted rom Bock 1999a).

of the jaw, which will rotate the upper jaw (1) in a clockwise direction around the nasal-frontal hinge; (b) the force (F_p) resulting from the contraction of the M. protractor pterygoidei and acting at the caudo-ventral base of the upper jaw which will tend to rotate the upper jaw in a counterclockwise direction; and, (c) the force (F_a) of the brain case acting on the upper jaw at the nasal-frontal hinge which does not rotate the upper jaw because this force passes through the center of rotation of the upper jaw. Assuming that the upper jaw is static, the sum of the torques (moments) of F_i and of F_p must be equal to zero as shown in the equation for the sum of the moments ($\sum M_0$). Inspection of the free-body diagram and the moment equation shows that moment arm „oa" of force F is less than moment arm „ob" of force F_i; hence, force F_p must be greater than force F_i. Again because the upper jaw is static, the sum of the linear affects of the forces, F_i, F_p, and F_a, must equal zero as shown in the equation for the sum of the linear effects of these three forces ($\sum F_x$). Hence the vector direction of the force of the brain case on the upper jaw at the nasal-frontal hinge is directed caudad as shown; this is a tensile force of the brain case on the upper jaw (see Bock 1974). That is, the bone comprising the nasal-frontal hinge is under a tensile stress, not under compression as had been concluded by almost all earlier workers. The woodpecker brain case is being pulled away from the upper jaw at the moment of impact of the bill tip with the tree, under the assumption that the upper jaw is in static equilibrium with respect to the brain case at the time of impact. Pulling apart of the brain case and the upper jaw results from the contraction of the M. protractor pterygoidei which pulls the brain case backward and pulls the pterygoid (and hence the rest of the bony palate and the upper jaw) forward because of the positions of origin and insertion of this muscle. The existence of a tensile stress at the nasal-frontal hinge means that a compression shock cannot exist in this position at the moment of impact of the bill tip with the tree. Simultaneous tension and compression forces cannot exist at the same location and along the same force vector in a bone at the same time. And therefore no compression shock passes from the upper jaw into the brain case and to the brain. The consequence of the large impact force by the tree on the tip of the upper jaw is a large compressive stress between the origin and insertion of the M. protractor pterygoidei in the bone below the brain (Fig. 7). As will be shown below, the compression in the skull base is a continuous stress during the period that the woodpecker is drilling into a tree, not a suddenly appearing shock.

The large size of the M. protractor pterygoidei in woodpeckers is indicated by the sizeable process on the lateral end of the pterygoid bone onto which the muscle inserts (Fig. 5 C), quite different from the morphology of most birds.

A comparison of woodpecker species reveals that with increasing specialization for drilling, several changes occur in the structure of the bill. In less specialized forms, the bill is slightly decurved and is deep in the ventre-dorsal direction. With specialization, the bill becomes straighter and ventrodorsally compressed. These changes bring the vector lines of the impact force (Fi) and the protractor force (Fp) more in line which reduces the force at the nasal-frontal hinge (Fa) to a minimum. The bill also becomes wider at its base which provides a better support for laterally directed components of the impact force, but this is another aspect of the analysis which will not be covered here.

This functional significance of avian cranial kinesis, in which the resulting force in the upper jaw-brain case system is shifted from one part of the brain case to another, does not require any movement of the upper jaw, just the existence of the kinetic hinge and associated muscles. This should be always kept in mind because it is not generally realized that the functional properties and adaptive significance of avian cranial kinesis depend on movement of the upper jaw (either entire or partial) relative to the brain case.

As shown above, the brain of woodpeckers is not affected by large compression shocks resulting from the impact force of the bill hitting the tree and entering the anterior end of the brain case when the bird is drilling into a tree. This is what would happen in mammals, such as humans who, as all mammals, possess an akinetic skull. What happens to the brain of woodpeckers when they are drilling into trees is still unknown. It can be assumed the brain case, as well as both eyes, decelerates rapidly when the bill hits the tree. If the brain is not firmly anchored to the inside of the brain case, it will move forward and hit the inner wall of the rostral part of the brain case at the moment of impact just as people are thrown forward when a car or train stops suddenly. Hitting of the brain against the front wall of the brain case could well result in damage to the brain, but it is simply not know what is the exact morphological relationships of the brain to the brain case, how tightly the brain fits into the brain case and whether the brain is held by a harness comprised of the dura mater, and hence understanding is not possible of how the woodpecker brain escapes injury when the bird is drilling into the tree.

Still another problem exists in this story, namely that of the contraction of the M. protractor pterygoidei, the force of which is essential for countering the impact force acting on the bill tip when the woodpecker is drilling into a tree. If this muscle contracts only after detection of the impact with the tree by sense organs and this information is transmitted to the brain followed by processing of this information in the brain and finally sending out motor nerve impulses to stimulate contraction of the M. protractor pterygoidei, then the impact force of the tree on the bill would be long over before the necessary muscle force would develop. Hence, the M. protractor pterygoidei has to contract continuously when the bird is drilling into a tree, which leads immediately to the question of what happens to the upper jaw during the nonimpact intervals when there is no impact force on the tip of the bill? What prevents excessive upwards rotation (protraction) of the upper jaw during the non-impact intervals, thereby averting possible damage to the bone and other tissues of the nasal-frontal hinge? Another structure found only in some woodpeckers, namely the frontal overhang of the brain case which lies directly over the thin flexible bone comprising the nasal-frontal hinge, must be examined.

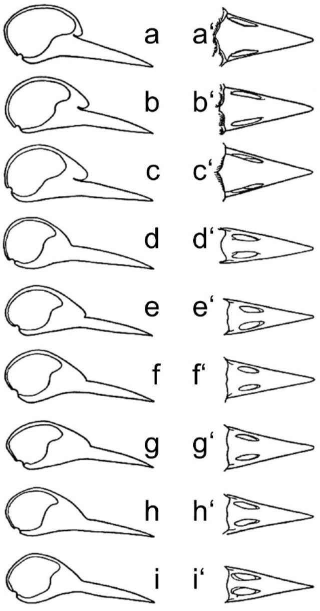
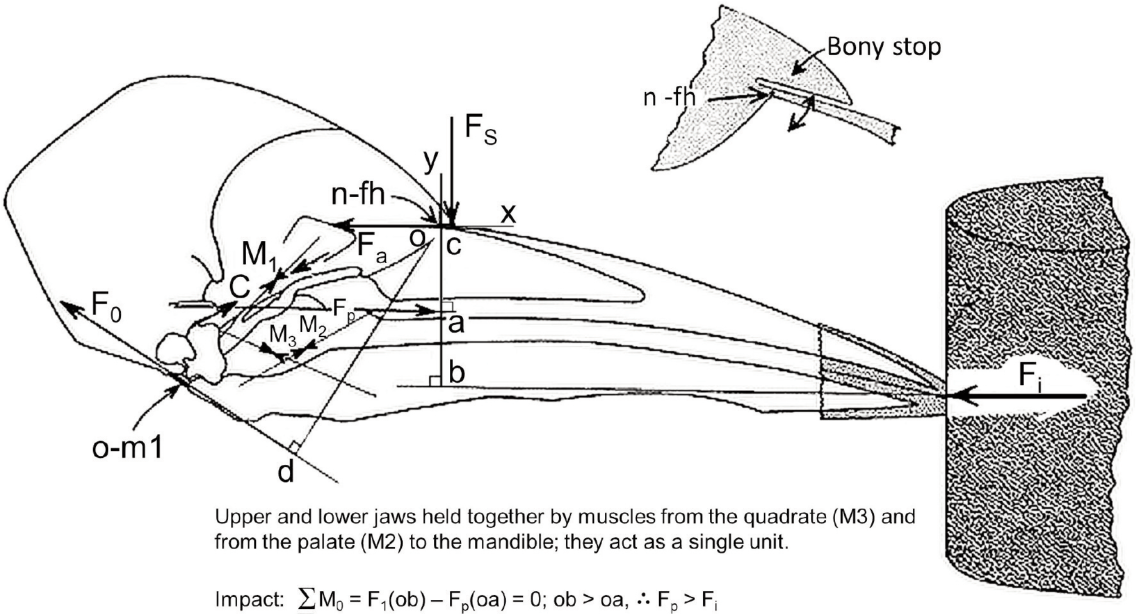


Fig. 8: Series of skulls of woodpeckers in lateral view (a- I) and upper jaw in dorsal view showing the change in the frontal overhang. The taxa shown are: (**a**) *Picoides tridactylus* or *arcticus*; (**b**) *Picoides villosus* = *Leuconotopicus villosus, Leuconotopicus villosus*; (**c**) *Sphyrapicus varius*; (**d**) *Dryocopus pileatus;* (**e**) *Melanerpes carolinus*; (**f**) *Melanerpes formicivorus*; (**g**) *Melanerpes erythrocephalus*; (**h**) *Melanerpes lewis*; (**i**) *Colaptes auratus*. These are arranged in order of the most specialized (**a**) to the least specialised forms in obtaining their food by pecking into trees. (Modified from Burt 1930: Fig. 2).



Upper and lower jaws held together by muscles from the quadrate (M3) and from the palate (M2) to the mandible; they act as a single unit.

Impact: $\sum M_0 = F_1(ob) - F_p(oa) = 0$; $ob > oa$, $\therefore F_p > F_i$
$\sum F_x = F_p - F_i - F_a = 0$; F_a is the force at the braincase on the upper jaw, $\therefore$ n–f h is under tension.

A compression force (C) exists in the base of the braincase between the origin of the Mppq and the quadrate articulation.

Non-impact: $\sum M_0 = -F_p(oa) + F_S(oc) + F_0(od) = 0$

$\vec{F} = \vec{F}_p + \vec{F}_S + \overleftarrow{F}_i + \overleftarrow{F}_a = 0$; F_a is the force at the n-f hinge.
F_S = force of frontal overhang on upper jaw.
F_0 = force of occipitomandibular ligament on lower jaw.

Fig. 9: Free-body diagram and associated equations showing the analysis of forces on the upper jaw at the moment of impact and during the non-impact periods. The frontal overhang as a bony stop and its relationship to the nasal-frontal hinge are shown in the insert; this bony stop prevents excessive elevation of the upper jaw. The equations for the impact time are as discussed in Fig. 10. A stout L. occipitomandibular connects the base of the brain case to the posterior end of the mandibular ramus. Two muscles, the M. pterygoideus and the M. pseudotemporalis profundus hold the upper and lower jaws together so that they act as a single unit. During the non-impact intervals, the moments of the resisting forces of the L. occipitomandibular (F_0) and/or the bony stop (F_s) prevent balance the moment of the palatal protractor force (F_p), and thereby prevent excessive dorsal rotation of the upper jaw. M. protractor pterygoidei during non-impact intervals (Fig. 7). (Adapted from Bock 1999a).

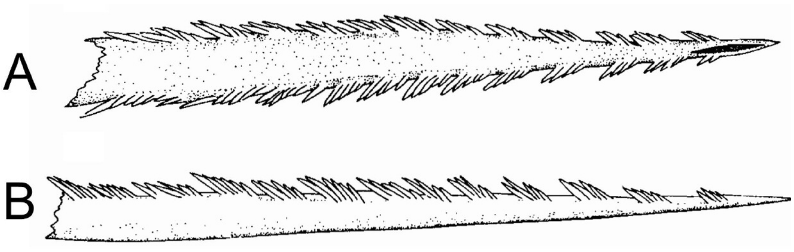


Fig. 10: Tongue tip of *Melanerpes carolinus* in dorsal view (**A**) and in lateral view (**B**) to show the barbs along the dorso-lateral edges of the tongue. (From Bock 2001)

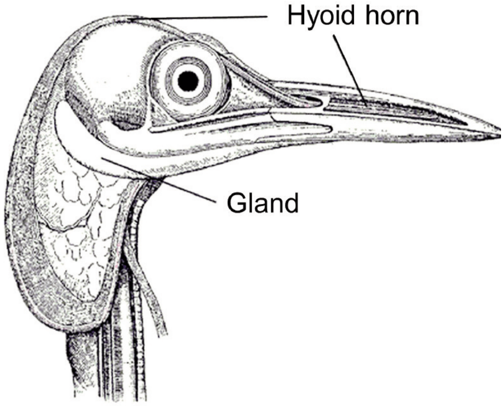


Fig. 11: Head of *Picus viridis* in lateral view to show the elongated hyoid horns and M. branchiomandibularis. Note the passage of both hyoid horns into the right nostril and cavity of the upper jaw. Also note the large mucus secreting salivary gland below and behind the mandible and brain case. (Adapted from Bock 1999a; after Leiber 1907: Fig. 10).

The frontal overhang was mentioned briefly by Shufeldt (1900: Fig. 2, p. 587), but he did not consider it further. This feature was discussed in detail by Burt (1930: 470-477, Fig. 2) who showed that this feature varied considerably among woodpeckers from non-existence to well developed, and that the development of the frontal overhang varies with the degree of specialization of each species for obtaining food by drilling (Fig. 8). Burt did not provide a reasonable functional explanation, or a proper morphological description as he never showed the relationship between the frontal overhang and the nasal-frontal hinge. His discussion of the possible adaptational significance of the overhang is vague at best, comparing the woodpecker condition with ‘telescoping’ of the skull in whales (Burt 1930: 475). He did, however, demonstrate a correlation between the variation in the overhang and the environmental interactions of the several species of woodpeckers included in his study which permitted a proper adaptive explanation once the descriptive and functional morphology was clarified.

The frontal overhang is a bony stop that prevents the upper jaw from rotating too far upwards by the force of the M. protractor pterygoidi during non-impact intervals. But this overhang is not the only feature that prevents excessive upward rotation of the woodpecker upper jaw. Combined action of the occipitomandibular ligament between the ventral edge of the occipital plate and the posterior surface of the medial process of the mandible and the M. pterygoideus would also prevent excessive upward rotation of the upper jaw during non-impact intervals; this is an indirect system and requires expenditure of muscular energy, and hence would be an inferior adaptation in those woodpeckers lacking the frontal overhang. This ligament-muscle system is found in most or all birds, and may have worked originally in less specialized species of woodpeckers lacking the frontal overhang. The frontal overhang originated (almost certainly evolving several independent times) and becoming increasingly developed in those species that have specialized for obtaining food by drilling. During a bout of drilling, the M. protractor pterygoidei contracts continuously and provides a constant protractor force on the upper jaw. During the non-impact intervals, the forces on the upper jaw are described by the lower set of equations (Fig. 9). They change to the upper set of equations with the occurrence of the impact and the rise of the impact force, and then back again to the lower equations with the fading away of the impact force. Depending on the magnitude of all forces, one result of the different consequences of the forces during the impact and the non-impact intervals can be a slight depression (impact period) and elevation (non-impact interval) of the upper jaw which I have been able to observe in high-speed motion pictures.

An entire series of comparative ecomorphological analyses of different species, as well as sexual dimorphism (see Wallace 1974), are possible from this functional explanation, including the shape of the upper jaw from being somewhat decurved, dorso-ventrally deep, and laterally narrow with no frontal overhang in less specialized drilling woodpeckers to straight, dorso-ventrally shallow and laterally wide with a well-developed overhang in more specialize species. It is more difficult to say at this time what evolutionary changes may occur in a unspecialized drilling woodpecker that evolved from a specialized ancestor. That is whether there will be a reversal of the modifications in the structure of the upper jaw back to the conditions present in the primitive and unspecialized forms.

Capturing food

Most or all woodpeckers obtain their food with their tongue which can be protruded out of the mouth a short to a very long distance. The tip of the tongue may possess a series of barbs to spear food items and/or it may be coated with a sticky mucus from large salivary glands which serve to glue these food items. I will not consider further the large and well-known mucus secreting salivary glands of woodpeckers (Leiber 1907). Not only can woodpeckers protrude and retract their tongues over a long distance, but they have considerable control over the movement of its tip and hence the direction that the tongue will take in following the twists and turns of an insect tunnel. Each aspect of tongue function will be treated separately. The muscles that protrude the tongue out of the mouth to capture food and retract it back into the mouth must be sufficiently long to move the tongue the required distance (Bock 1974, 1991). These muscles have been first described in full detail by Leiber (1907). A most interesting description was published 300 years ago by Waller (1716) including the protracting and retracting muscles of the tongue in the Green Woodpecker (*Picus viridis*). For woodpeckers that protract their tongue a great distance, these muscles must be very long, at least three times as long as the distance that the tongue is protruded. The muscles involved are the protracting M. branchiomandibularis (M b m; Figs 11, 12) and the retracting M. cricohyoideus (M cr h = M. ceratotrachealis of Burt 1930: 511; Fig. 12).

Simultaneous elongation of the M. branchiomandibularis and the bones of the hyoid horn was essential for increased protraction of the tongue. The hyoid horns must lengthen to increase the length of the paired M. branchiomandibularis between their origin on the tip of the hyoid horns and their insertion on the lower jaw. The elongated hyoid horns and associated branchiomandibularis muscles curve around the skull and, in extreme cases, as in *Picus* (Fig. 11), enter the right nostril and extend to the rostral end of the space inside the upper jaw. In woodpeckers with an extremely long tongue, again as in *Picus* as well described by Leiber (1907), the hyoid horns and muscles may loop ventrally around the enlarged mucus glands below the head before passing around the brain case (Fig. 11).

The modifications in the tongue retractors in woodpeckers are considerably greater. The usual retractor muscle of the tongue in birds (M. stylohyoideus; m st h; Figs 12, 16) is vestigial to absent in woodpeckers. Evolutionary reduction in the M. stylohyoideus of woodpeckers appears to have resulted because this muscle did not (or could not) increase its needed length to retract the tongue over a great length by a change in its site of origin on the base of the skull to a position on the lateral side or top of the brain case; thereby it lost its role as the major tongue retractor in the woodpeckers. The paired cricohyoideus muscles have elongated and serve as retractors of the tongue. These muscles no originate from the larynx as in most other birds, but from a more

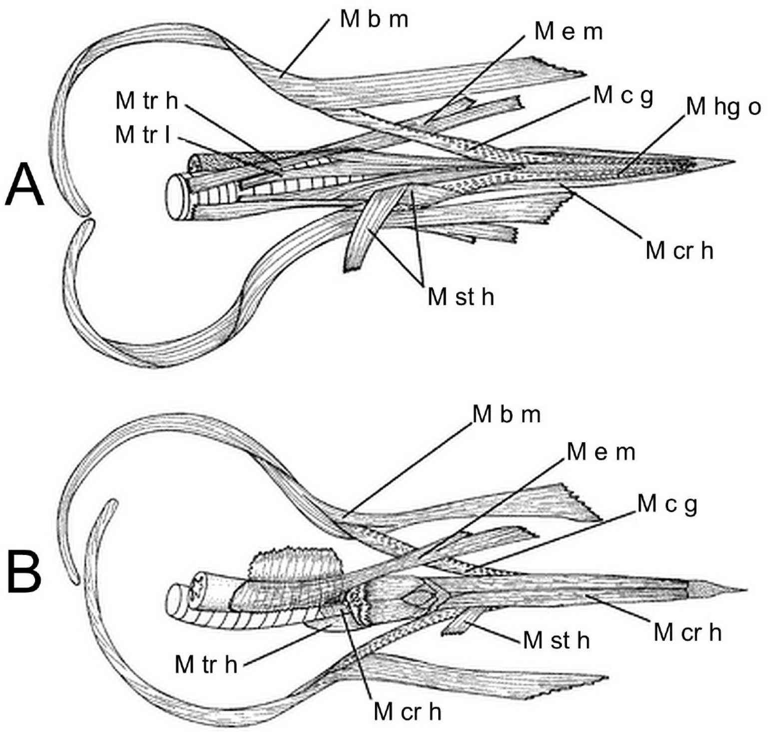


Fig. 12: Tongue muscles of *Melanerpes carolinus* in ventral view (**A**) and in dorsal view (**B**). Note the M. branchiomandibularis (M b m; tongue protractor), the M. cricohyoideus (M c r; tongue retractor), the vestigial M. stylohyoideus (M st h), and the M. esophagomandibularis (M e m). (Adapted from Bock 1999a).

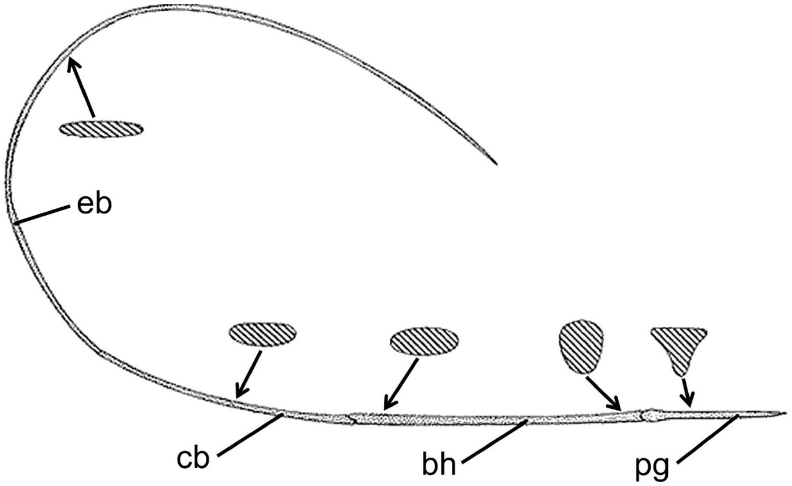


Fig. 13: Hyoid horns of *Melanerpes carolinus* to show the change in cross section from a thick and rigid anterior end to an increasingly thinner and flexible posterior end. (Adapted from Bock 1999a).

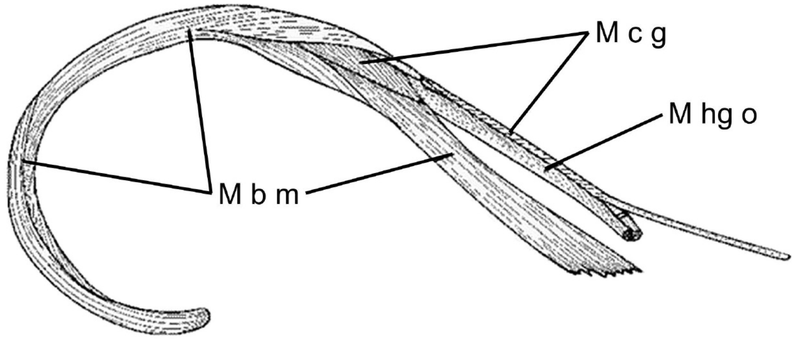


Fig: 14. Hyoid horn of *Melanerpes carolinus* to show the muscles completely encasing the thin bones of the hyoid. Note the M. branchiomandibularis (M b m; tongue protractor), the M. hypoglossus obliquus (M hg o), and the M. ceratoglossus (M c g) which are the two paired muscles that can rotate the tongue tip in all directions. (Adapted from Bock 1999a)

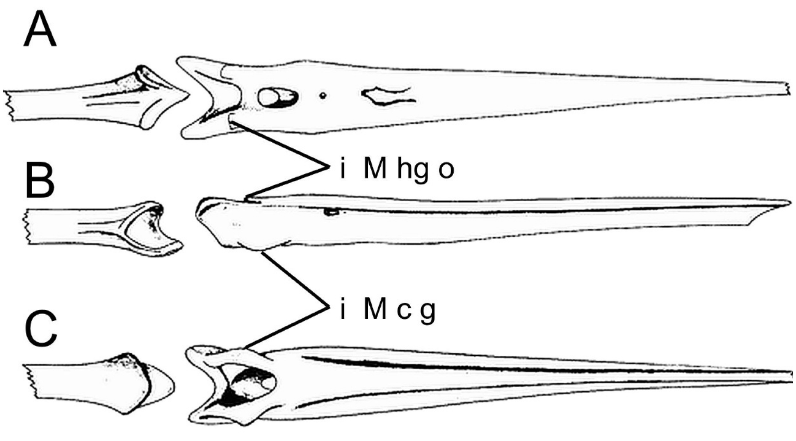


Fig. 15: Fused paraglossalia bones and the basihyal of *Melanerpes carolinus* in dorsal (**A**), lateral (**B**), and ventral (**C**) views to show the saddle-shaped articulation between these bones which permits movement of the fused paraglossalia in all directions relative to the basihyal. Note the insertion of the paired hypoglossus obliquus muscles (M hg o) at the two dorso-lateral comers and of the paired ceratoglossus muscles (M c g) at the two ventro-lateral corners of the fused paraglossalia. (Adapted from Bock 1999a).

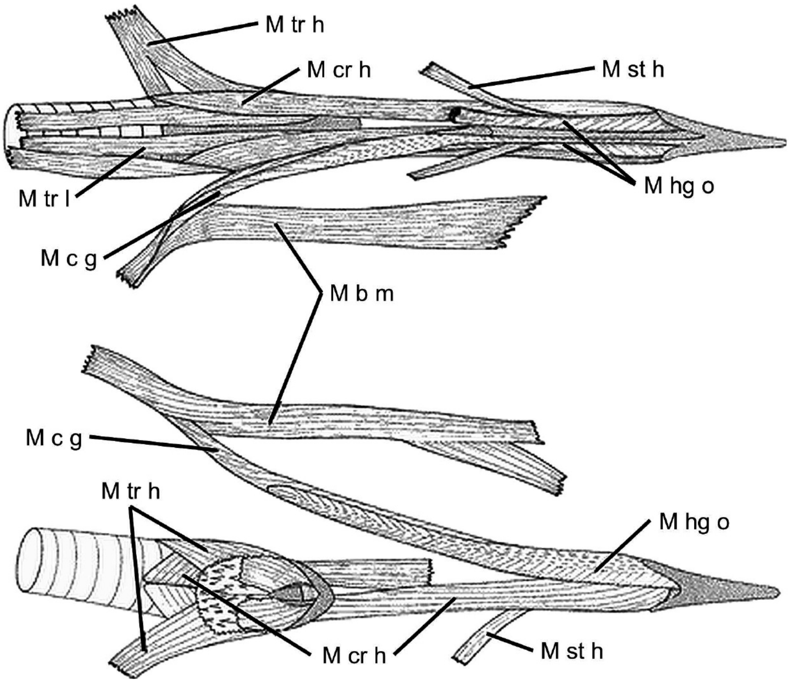


Fig. 16: Tongue muscles of *Melanerpes carolinus* in ventral view (**A**) and in dorsal view (**B**). Note the M. cricohyoideus (M cr h; tongue retractor), the M. hypoglossus obliquus (M hg o) and the M. ceratoglossus (M c g) which are the two paired muscles rotating the tongue tip in all directions. Also note the vestigial M. stylohyoideus (M st h; the usual tongue retractor in birds, but not in woodpeckers). (Adapted from Bock 1999a).

caudad point on the trachea. Increased length of these muscles is achieved by their winding around the trachea several times from their origin to where they pass forward of the larynx to insert on the rostral end of the basihyal. The paired muscles may interweave with each other as they wrap around the trachea.

Most interesting is a 'new' skeletal muscle described by Leiber (1907), the M. esophagomandibularis (M e m; Fig. 12; = M. geniothyroideus of Leiber 1907: 39) which is an anterior slip of the muscular sheath of the oesophagus that extends to and inserts on the medial surface of the mandibular ramus. In unspecialized woodpeckers, this muscle still originates from the oesophagus but in more specialized woodpeckers, its origin is from the larynx and/or the trachea; thereby the M. esophagomandibularis has become a true skeletal muscle. The M. esophagomandibularis pulls the larynx and the cranial end of the trachea forward when the tongue is protruded from the mouth and thereby increases the distance that the tongue can be protruded outside of the mouth.

The bony elements of the hyoid horns of the tongue apparatus change gradually from being thick and rigid at their rostral end to flattened dorso-ventrally and flexible along the hyoid horns (Fig. 13). When the muscles surrounding the hyoid horn, especially the M. branchiomandibularis contract, they apply force around the entire bone of the hyoid horn and change this bone from a flexible structure to a rigid one (Figs 14, 17). This is an example of a „hydrostatic structure", but one in which filling is a thin flexible bone rather than a fluid filling; with the contraction of the M. branchiomandibularis, the flexible bone of the hyoid horns become rigid and can transmit the force of the M. branchiomandibularis from its insertion on the distal tip of the hyoid horn along the entire length of this horn to the basihyal, and thereby protrude the corneous tongue further out of the mouth.

Control of movement of the rostral tip of the corneous tongue depends on the structure of the articulation between the basihyal and the fused paraglossalia, and the insertions of the paired ceratoglossus (M c g) and the paired hypoglossus obliquus (M hg o) muscles on the posterior end of the fused paraglossalia. The articulation between the two bones is saddle-shaped (Fig. 15) so that this joint is a universal one, permitting the fused paraglossalia to move in any direction relative to the basihyal. The paired ceratoglossus muscles (M c g) insert at the two ventro-lateral corners of the fused paraglossalia while the paired hypoglossus obliquus muscles (M hg o) insert at the two dorso-lateral corners of this bone (Figs 15, 16). Both pairs of muscles are pinnate, possessing a large number of short fibers indicative of short excursion and large force applied to the bone at their insertions (Fig. 16). The M. hypoglossus obliquus usually originates only from the basihyal in birds, but in woodpeckers, it originates not only from the basihyal, but also from much of the ceratobranchiale (Fig. 14). With differential force application from each of these four muscles onto the four caudo-lateral corners of the

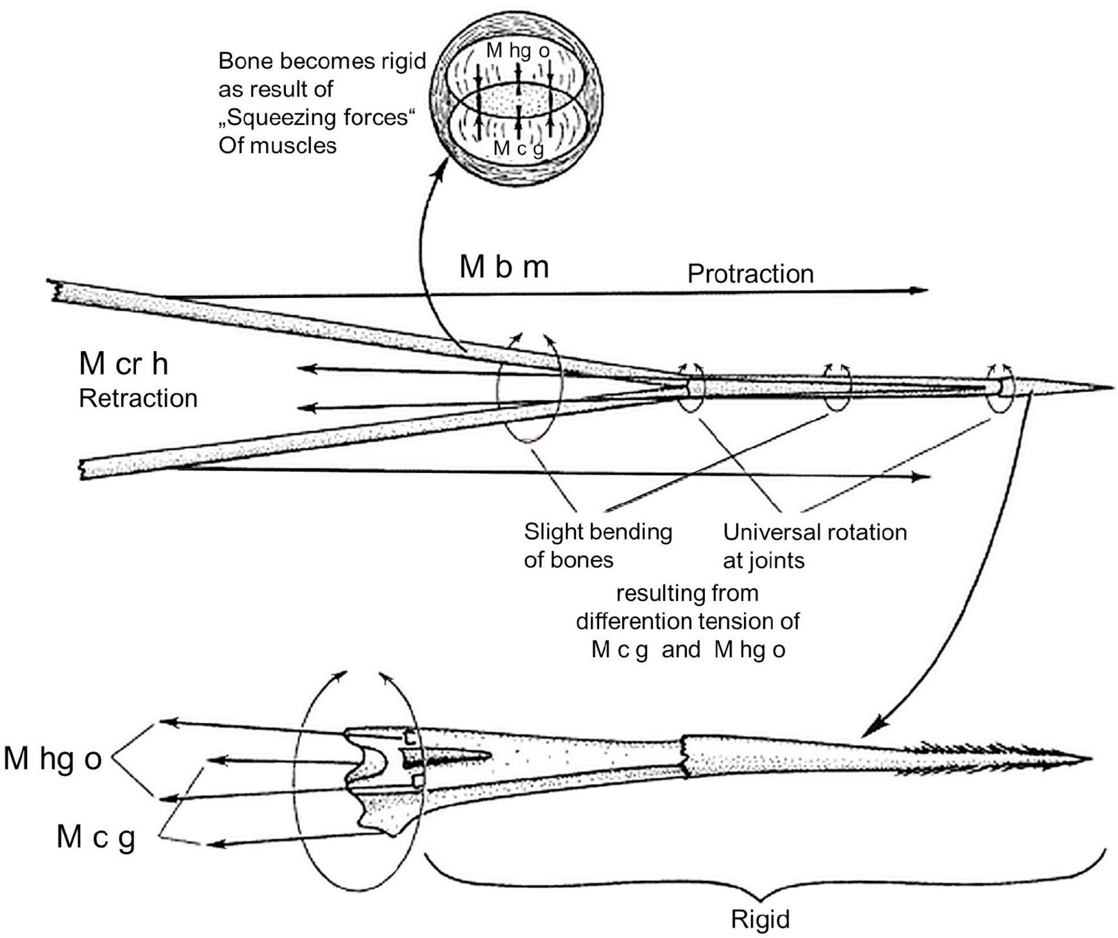


Fig. 17: Schematic model showing the rotation of the anterior tip of the woodpecker tongue by differential contraction and hence force development of the paired hypoglossus obliquus (M hg o) and paired ceratoglossus muscles (M c g). Protraction and retraction of the tongue by the branchiomandibularis (M b m) and cricohyoideus (M cr h) muscles is also shown as well as stiffening of the flexible bones of the hyoid horns by the squeezing forces of the surrounding muscles (M hg o and M c g; and more distally, the M b m, not shown). (Adapted from Bock 1999a).

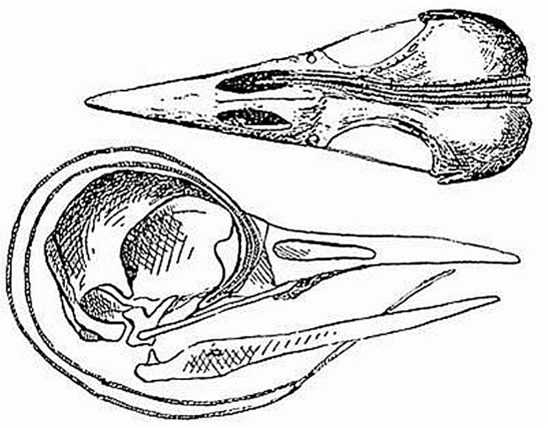


Fig. 18: Skulls and hyoid horns of *Colaptes auratus* (upper) and of *Picoides villosus* = *Leuconotopicus villosus* (lower; not *Picus* as claimed by Coues and followed by Shufeldt) to show the different ways in which the elongated hyoid horns are accommodated in the head of woodpeckers. In *Colaptes*, these horns enter the right nostril and extend into the cavity of the upper jaw. In *Picoides villosus*, they curve around the right orbit. (From Bock 1999a; after Shufeldt 1900: Figs 6 and 7; originally from Coues 1884: Figs. 73 and 74).

fused paraglossalia, the tip of the corneous tongue can move in all possible directions relative to the basihyal and the rest of the tongue (Fig. 17). Hence the tip of the tongue can change its direction as the insect tunnel turns and, thereby can direct movement of the tongue through the insect tunnel in the tree. Presumably touch organs exist in the tongue tip, which can detect the walls of the tunnel and transmit this information to the brain, and hence to differential stimulation signals in the motor nerves to these two pairs of muscles.

Diverse species of woodpeckers differ in the distance they probe with their tongue for their food, from very short in the North American sapsuckers (*Sphyrapicus*) to very long in the Old world green woodpeckers (*Picus*) and the New World flickers (*Colaptes*). The lengths of the hyoid horns and of the branchiomandibularis and the cricohyoideus muscles increase as the woodpeckers evolve longer probing abilities and presumably shorten secondarily if they evolve shorter probing foraging methods. Hence, it would be difficult to impossible to ascertain the primitive state of these muscles in the Picidae and especially in the Picinae. Modifications also exist in the degree of specialization of the M. esophagomandibularis with this muscle originating more directly onto the trachea in woodpeckers having increased specialization for longer probing. Moreover, the vestigial M. stylohyoideus has become smaller in the evolution of woodpeckers and finally disappeared in those species with increased specialization for longer probing. In the case of these last two mentioned muscles, one should not necessarily expect a reverse in their structure in woodpeckers that have become secondarily short probers.

Specialization for drilling and for longer probing in woodpeckers are not tied to one another so that it is possible to have species that are specialized drillers, but short probers, or unspecialized drillers and long probers, etc. The consequences of these two types of specialization is that the associated morphological modifications may interact with one another in interesting ways, requiring the need to analyze the morphology of the woodpecker head from an integrated, constructional viewpoint in addition to a functional consideration of each separate unit.

In most woodpeckers with long probing tongues, the elongated hyoid horns and muscles extend around the entire brain case and enter the right nostril to extend to the rostral end of the cavity within the upper jaw. In a few forms, such as the North American Hairy Woodpecker (*Leuconotopicus villosus*), the hyoid horns do not enter the right nostril, but instead encircle the right eye (Fig. 18; see also COUES 1884; SHUFELDT 1900; LEIBER 1907). Any attempt to explain the arrangement of the hyoid horns in the Hairy Woodpecker or the difference between that seen in most long-probing species with the hyoid horns entering the right nostril and that seen in the Hairy Woodpecker with the hyoid horns encircling the right eye only using functional explanations for the tongue apparatus would be doomed to failure. The answer is an integrated, constructional explanation based on functional explanations of the upper jaw for drilling combined with those explanations of the tongue for probing. The Hairy Woodpecker is a specialized driller and, hence, has a dorso-ventrally flattened upper jaw which reduces the articular force at the nasal-frontal hinge as discussed earlier. Consequently there is simply no space within the cavity of the upper jaw to accommodate the hyoid horns and muscles. With a lengthening of the hyoid horns in the Hairy Woodpecker for longer probing, the only way that these elongated hyoid horns can be accommodated within the head of the bird is to encircle the eye. Interesting is that, to my experience, the elongated hyoid horns ibn the Picidae always extend to the right side of the head, passing into the right nostril or around the right eye. In hummingbirds (Trochilidae), the elongated hyoid horns extend to the right or the left sides (or possibly both) of the head, although I do not know whether there is variation in their position within the same species.

Woodpeckers and headache

True woodpeckers (Picinae; and to a much lesser extent the whynecks (Junginae) and the piculets (Picumninae) are characterized by having a bill specialized for drilling into trees and use their drilling behavior for getting food, evacuating nesting and sleeping holes and drumming. Drilling into trees requires strong impacts of the bill on wood which results in an equally strong impact force by the tree on the tip of the bill. This strong reaction force (= a compression) of the tree on the bill and hence on the rest of the head has led to the question of how does the bird protect its entire skull and contained organs, especially the brain and the eyes from damage (WINKLER et al. 1995). Several ornithologists have investigated how this impact force is resisted by the skull (BEECHER 1953, 1962; BOCK 1964: 29-30, 1966; SPRING 1965: 481-486). These analyses are based on the mechanical properties of the avian kinetic skull but were not quite successful. The solution of how the impact compression shock by the tree on the tip of the woodpecker bill is resisted by the bones of the bird's skull was provided by BOCK (1974, 1999a; herein); this analysis was based on the mechanics of the avian kinetic skull (= avian cranial kinesis, BOCK 1964, 1966, 1974, 1999b, c, 2002). The most interesting finding of this analysis is that the force between the upper jaw and the brain case at the nasal-frontal hinge is a tension, not a compression as assumed by almost all workers. The impact compression of the tree onto the tip of the upper jaw results in a compressive stress on the bone in the skull base between the origin and insertion of the paired M. protractor pterygoidei. The explanation provided by BOCK accounts for all of the specializations of the woodpecker skull and jaw musculature, including the property of cranial kinesis (all birds), the large M. protractor pterygoidei, prominent protractor process of the pterygoid (Fig. 5C), thin roof of the brain case (most likely all birds), and the frontal overhang (Fig. 8) of the braincase over the thin plate of bone comprising the nasal-frontal hinge.

It must be emphasized that the nasal-frontal hinge between the brain case and the upper jaw is generally a thin plate of bone that can withstand only small compressive and/or tensile forces. Hence the shape of the bill and the forces on it must be arranged so that whatever resulting force exists at the nasal-frontal hinge is small compared to the other forces acting on the upper jaw (BOCK 1966). This is seen in both those birds which apply a large biting force (such as parrots and finches) nad those which apply a strong pecking force (such as woodpeckers).

However, beginning in the mid-1970's with a paper by MAY et al. (1976a, b, 1979) a series of workers approached the analysis and consequence of the impact force acting on the tip of the woodpecker bill, largely under the question of: Why don't woodpeckers get headaches? A large literature on this subject developed quickly and includes the following papers by (in no chronical order): BECHER (1953), CHAPIN (1949), CHO

(2002), Gibson (2006), Gordon (1976), Lee et al. (2014a, b), Mei (2004), Nadis (2006), Oda et al. (2006), Ollerenshaw (1976), Ommaya & Hisch (1971), Potter (1976), Schwab (2002), Self (2012), Sielmann (1959), Stark et al. (1990), Villard & Cuision (2004), Vincent et al. (2007), Wang et al. (2011a, b, 2013), Wygnanski-Jaffe et al. (2007; eye), Yoon & Park (2011; Fig. 1 is *Sphyrapicus varius*, not *Melanerpes carolinus*), Zhou et al. (2009), Zhu et al. (2012, 2014a, b). Most of these papers followed the ideas advanced by May and his coworkers of the central role played by the hyoid horns. In their papers, May et al. (1976 a, b, 1979) introduced the concept that the long hyoid horns with their surrounding hyoid muscles wrapping about the brain case serves as the mechanism absorbing the impact force of the bill against the tree and hence that the wall of the brain case could be thin because it was not subjected to large stresses. I will discuss the major assumptions and claims made by these workers under several difference features of the woodpecker head.

A) Most important is the proposed role of the hyoid horns and surrounding muscles (see, Figs 6, 7, 13, 14, 15) which was introduced by May et al. (1976a, b, 1979) which has been seized by most other workers in their analysis of the woodpecker anti-shock mechanism in spite of its erroneous foundation. It must be noted emphatically that the hyoid apparatus, especially that portion claimed to be involved in resisting the impact blow of the woodpecker bill, does not start at the tip of the lower jaw. The M. branchiomandibularis (= M. geniohyoideus of some authors) is central to the hyoid theory; it originates on the medial surface of the lower jaw about half way between the tip of the bill and the quadrate articulation. The other end of the hyoid horns, including the insertion of the M. brachiomandibularis, are not attached to the brain case in any way; this muscle inserts from the free tip of the hyoid horns (= distal end of the ceratobranchial). Further each hyoid horns is encased in a sheath, similar to a tendon sheath, allowing them to slip along the brain case as the M. branchiomandibularis contracts and shortens to push the tongue out of the mouth; hence there is no direct attachment of this muscle to the surface of the brain case. It should be pointed out that there is a similar sheath surrounding the bones of the hyoid horns allowing these bones to slip past the surrounding M. branchiomandibularis which is shortening to push the corneous tongue out of the mouth; the length of the bones of the hyoid horns remains the same. If the hyoid horns are to resist the impact blow of the bill on the tree, the muscles (including the paired M. branchiomandibularis which surround the hyoid horns to their free tip) must be contracting. Gordon (1976: 802) does state clearly that the M. geniohyoid (= M. branchiomandibularis) is at rest, not contracting, when the woodpecker is drilling and hence could not be involved in the resistence of the large compressive shocks acting on the bill tip; I concur completely. Muscles can serve to reduce the stress on the bones to which they are attached (Pauwels 1965, Bock 1974: 222-3), but only when they are contracting; muscles at rest are readily deformed (generally stretched) when any force is placed on them and cannot serve to reduce stress in the skeleton.

There are several problems to the hyoid solution advanced by May and his coworkers and basically accepted by other workers cited above. These are:

1) The M. branchiomandibularis has a small cross-sectional area and hence produces a rather small force compared to the size of the impact force of the bill;

2) Second, contraction of the M. branchiomandibularis would provide little, if any, force perpendicular to the long axis of the hyoid horns and hence on the surface of the brain case which would be essential to this muscle reducing the stress on the woodpecker skull;

3) Third, its contraction would cause the tongue to move forward, causing problems because the bill is closed when it strikes the tree. Hence at the minimum, the M. cricohyoideus (the tongue retractor) must also contract to hold the tongue in place which would place serious stresses on most of the bones of the hyoid apparatus.

It is simply not true that the hyoid apparatus of woodpeckers and other birds is of great strength. Rather this apparatus consists of thin bones and relatively weak muscles, especially the hyoid horns and the M. branchiomandibularis, even in those species, such as parrots, ducks and flamingos which use their tongues actively while feeding. Hence, there is no evidence that the bones and muscles of the woodpecker hyoid horns have any role in resisting the impact compression on the bill tip during drilling into trees.

B) All of the analyses cited above (second paragraph), with the exception of Becher (1953), fail to take into account the fact that in all birds possess the property of cranial kinesis, i.e., the upper jaw (all or part) moves with respect to the brain case (Bock 1964, 1999c). Cranial kinesis originated with the origin of jaws in vertebrates and continued throughout vertebrate evolution to present day birds, snakes and lizards and several groups of fish. This property of cranial kinesis has been lost in the evolution of mammals, turtles, crocodiles and living amphibians, all of which have an akinetic skull. Most workers, including morphologists, center on the skull structure of these groups and believe that the akinetic skull is typical for most vertebrates. Cranial kinesis is the original state of the vertebrate skull and akinesis derived; once lost in the evolution of vertebrates, cranial kinesis never re-evolves. Moreover, most workers believe that it is possible to extrapolate findings and conclusions between forms possessing a kinetic and an akinetic skull, but this is not so because these two types of skull construction are too different from one another. Hence the results of an analysis on the woodpecker skull cannot be simply applied to a human skull.

Hence in birds, including woodpeckers, impact forces to the tip of the upper jaw are not transmitted directly to the brain case; rather the resulting force between the upper jaw and the brain case has to be determined by an analysis of all the forces acting on the upper jaw as shown above (Figs 7, 9; see also BOCK 1966). This is completely different from the effect of a blow to the tip of the akinetic upper jaw in mammals in which the compression is transmitted directly to the brain case and the brain. With the exception of BECHER (1953) and the papers by BEECHER, BOCK and SPRING cited above, all of the analyses of the impact forces acting on the tip of the woodpecker bill fail because they have ignored that all birds possess cranial kinesis. It must be emphasized that the necessary papers on avian kinesis and its significance to the analysis of drilling forces in the woodpecker skull were published prior to all of the analyses cited above; these workers either did not know or did not understand the literature.

The impact force of the woodpecker bill on the tree would serve to rotate the upper jaw downwards with respect to the brain case (see BOCK 1966, 1974, 1999a, this paper). This rotation would be counted by the force of the M. protractor pterygoidei (Fig. 10) which is strongly developed in woodpeckers with a sizeable insertion process on the pterygoid (Fig. 5); hence this muscle can develop a significant force. A free-body analysis of the forces acting on the upper jaw (Figs 7, 9) shows that a tensile force exists at the attachment of the upper jaw to the brain case at the nasal-frontal hinge at the time the impact force. Therefore, quite to the contrary assumption of almost everyone who have considered the question of woodpecker drilling, no compressive shock passes directly from the upper jaw to the brain case at the nasal-frontal hinge when the woodpecker hits the tree with its bill. That a tensile force exists at the woodpecker nasal-frontal hinge where its upper jaw attaches to the anterior end of the brain case is counter-intuitive but that is the conclusion of free-body analysis of the woodpecker upper jaw during drilling (BOCK 1966, 1974, 1999a, this paper, Figs 7, 9). Rather, a large compressive stress exists in the base of the brain case between the origin from the ventral edge of the orbital septum and the insertion on the pterygoid of the M. protractor pterygoidei, the muscle countering the impact shock of the tree on the upper jaw. The insertion of this muscle is on the substantial process on the dorsal edge of the pterygoid (see Fig. 5C), not seen in most or all other birds. The bony material of the orbital septum, base of the brain case and quadrate is substantial and able to withstand the large compressive stresses in it when the M. protractor pterygoidei contracts. Further, it should be noted that this muscle most likely contracts continuously during a bout of drilling resulting in differences in the free-body analyses during the impact and the non-impact periods (Fig. 9); there are no sudden compressive shocks acting on any part of the brain case during woodpecker drilling.

No comparative observations have been made, but I would suspect that the size of the M. protractor pterygoidei and its process of insertion on the pterygoid bone would increase in more specialized drilling species of woodpeckers

During the non-impact periods in a drilling bout, the force of the M. protractor pterygoidei will rotate the upper jaw upwards (Fig. 9) and presumably could cause damage to the very thin plate of bone comprising the nasal-frontal hinge. Upward rotation of the upper jaw during the non-impact periods is limited by the resistence of the occipitomandibular ligament in non-specialized woodpeckers and the frontal overhang in specialized woodpeckers (Figs 8, 9). The occipitomandibular ligament acts as like a spring and the frontal overhang as a structural stop both of which restrict excessive upward rotation of the upper jaw, similar to the working of springs and of stops restricting excessive opening of a door. Apparently the frontal overhang is the subsequent adaptation compared to the original adaptation of the occipitomandibular ligament which is found in all woodpeckers and probably in all birds. The frontal overhang is found only in the most specialized drilling woodpeckers, and has most likely originated independently several times in the evolution of woodpeckers.

In addition to the frontal overhang other specializations for increased drilling in woodpeckers are the straightening and the dorsoventral narrowing of the upper jaw; again this specialization probably appeared several independent times in woodpeckers. These modifications would result in the force vectors of the tree on the upper jaw (F_i) and of the palatal protractor force (F_p) being far closer in line with one another, thereby reducing the magnitude of the tensile force on the thin plate of bone comprising the kinetic nasal-frontal hinge (BOCK 1966). With the vectors of the forces F_i and F_p

lining up closer to each other so that their moment arms are almost identical, the magnitude of F_p can decrease resulting in a relatively smaller M. protractor pertygoidei and a lower stress in the bones of the base of the brain case (Figs 7, 9; Bock 1966: 27-29, 1974: 148-9).

C) the bone comprising the roof of the avian brain case is relatively weak and cannot resist large forces. Chapin (1949) states that the skull roof of woodpeckers is a single layer of bone, thicker than that found in immature passerine birds and that it does not form two-layers of thin laminar bone with spongy bone between them – a condition called, erroneously, by most ornithologists as pneumatization. He states, without any analysis that he considered this single layer of bone of the brain case in woodpeckers as an adaptation for their drilling into tree with their chisel-like bill. His observations may not be valid as I have observed woodpecker skull roofs with the typical double layered laminar bone with intermediate spongy bone which may well be the typical structure of the brain case roof in woodpeckers.

The weakness of the brain case roof in small birds, such as the passerines was made clear to me when I was an undergraduate student and helped prepare as skeletons birds which were donated to the Department of Conservation, Cornell University. I prepared a number of Evening Grosbeaks (*Hesperiphona vespertina* – a larger species of finches with a heavy, seed cracking bill), all of which showed a bloody area on the top of the skull. I was puzzled by this observation until I realized that these grosbeaks were probably at a bird feeding station just outside a window and when startled flew quickly in all directions. Some of these birds must have hit the glass of the window pane with the top of their skull sufficiently hard to be fatally injured; the bone comprising the roof of the brain case is thin and could not resist a strong blow.

D) Muscles can be arranged in the muscle-bone system so that their contractile force decreases the stress within the bones (Pauwels 1965, Bock 1974: 222-3) including the system present in woodpeckers as described above. How muscles reduce stresses in the skeleton varies considerably depending on the arrangement of the bones and of the muscles; there is no single mechanism.

E) Last is the question of why the brain and the eyes of woodpeckers are not damaged when the head of the bird stops very quickly during the drilling cycle; this problem lies outside of the solution of how its skull deals with this impact force.

The solution may be a simple one as suggested by Gibson (2006). She pointed out that all woodpeckers, even the largest species, are small compared to humans and a number of other species of mammals. It is well known that as animals increase in size, they become relatively weaker, both in providing force and withstanding impact forces acting on their body (Bonner 2011). Horses are relatively stronger than elephants, humans relatively stronger than horses, dogs relatively stronger than humans and down the size scale to small rodents and bats. Hence a mouse can survive a fall from a five story building which would possibly seriously injure a dog and kill a human, horse and elephant. This would also apply to organs such as the brain and eyes. The impact force on the upper jaw of a human would cause the brain within the cranium to stop quickly and hit the inner wall of the brain case with a larger force than the brain of a woodpecker simply because of the much larger size of the human brain. Impact force is mass x acceleration so that with the same change in acceleration, the considerably smaller woodpecker brain would be subjected to a much smaller impact force. If the structure of the brain and of the surrounding dura in woodpeckers and humans are about the same, than these structures in woodpeckers would be subjected to less damage in the same way that a mouse would be damaged less than a human falling a five story building.

Several conclusions can be drawn from this analysis:

First, it is not possible to reach a correct understanding of how an apparatus works, be it a organism or a machine, unless the structure of the apparatus is known correctly. In the many attempts by engineers and psychologists to understand the consequences of the strong impact forces on the woodpecker's bill during drilling, only Becher (1953) had a correct knowledge of the structure of the avian head. All others omitted the critical aspect of the cranial kinetsis structure of avian skulls and hence their analyses are doomed to failure.

Second, it is not possible to extrapolate the findings on one organism to another, the difficulty of comparisons in biology, unless the two organisms are sufficiently similar in their organization. The understanding of a number of critical working of the avian head is difficult to impossible to apply to mammals, such as humans, because birds have a very different construction of the head – kinetic in birds and akinetic in mammals. Hence, even with a correct analysis of the consequences of the impact forces on the tip of the woodpecker's bill, it is not possible to extrapolate these results in any valid way to humans.

And finally, if I were to ride on a bicycle or a motorcycle, I would wear a conventional crash helmet, not one proposed by May et al. (1976a).

Conclusions

With an understanding of both the functions and adaptations of the diverse features associated with climbing (hind limb and tail) or with feeding (jaws and tongue, both the skeleton and muscles) in woodpeckers, it is possible to inquire into the evolution of these systems within this avian family. Reasonable arguments can be presented which of the several conditions of the toe arrangement, soft versus stiffened rectrices, one versus two pairs of modified central rectrices, absence versus presence of the frontal overhang, shorter versus longer hyoid bones and muscles are all evolutionary specializations within woodpeckers. However, it is also almost certain that most or all of these specialized features evolved several times within the Picinae (Bock 1963) and that these features have undergone „reverse“ evolution to a secondarily „primitive“ state with changes in climbing and feeding habits of these birds. For example, the frontal overhang has almost certainly originated several times in the history of this family. And the elongated branchiomandibularis and cricohyoideus muscles could have shortened during the evolution of some woodpeckers such as in the sapsuckers.

For these reasons and because these features of the hind limb, tail, jaw, and tongue systems can undergo independent evolution or can undergo, many or all of the features discussed herein may not serve as useful clues in classificatory and phylogenetic analyses of this group. These conclusions reduce considerably confidence in earlier papers on the classification of woodpeckers and related groups (Goodge 1972, Simpson & Cracraft 1981, Swiercrzewski & Raikow 1981; see also Olson 1983) which exclude all functional analyses of the features used in their systematic studies. The analyses of Short (1982) and Winkler et al. (1995) are based on sets of features for which the functional significance and the adaptations are reasonably well understood and provide a classification in which one can have greater confidence.

The functional-adaptational conclusions presented herein can provide the foundation needed for further ecomorphological analyses of this avian family, allowing a better basis on which to choose the features to be measured and on which to interpret the statistical results.

What is still lacking is comparative information on the morphology of the many genera of woodpeckers (Picinae), especially of tropical genera, the wrynecks (Jynginae), and the piculets (Picumninae); almost nothing is known about the last two groups. Although most ornithologists assume that the wrynecks and the piculets are primitive groups within the Picidae, there is little to no evidence supporting this conclusion. The piculets could be an advanced group within the Picidae which has evolved a climbing habit excluding the use of the tail as a brace. And the wrynecks could be another advanced group specialized on feeding on non-tree burrowing insects for which climbing on vertical surfaces was no longer required; therefore, the use of the tail as a stiff prop during climbing decreased during the evolution of this subfamily. At this time sufficient reliable evidence simply does not exist on which to reach a decision on whether these two subfamilies are primitive or advanced in the evolution of the Picidae.

My major conclusion is that there are still many new and interesting studies to do within avian anatomy. This does not mean only numerous fascinating and hitherto unknown features to describe, of which there are still many. Good examples are the two different types of secondary articulations of the lower jaw in many birds (Bock 1960, Bock & Morioka 1971, see Bock 1999b: 30–31, for comments on the functional role of these articulations as braces of the lower jaw) and the secondary occipital condyle characteristic of the hornbills (Bucerotidae; Bock & Andors 1992). Of greater importance are the development and application of new methods of functional and adaptational analyses, such as the method of free-body diagrams which can be applied to almost every type of static biomechanical analysis of the skeletomuscular system and a fuller understanding of muscle physiology (Bock 1974). All of these studies depend on carefully done morphological descriptions, but they also depend on looking outside of traditional morphological studies for useful methods of functional analyses, on being a biological engineer to think about how these structures can work, on being a naturalist to think about how these functioning morphological systems are used in the life of birds, and on being a comparative biologist and evolutionist to think about the medley of evolutionary explanations that can be formulated on prior descriptive and functional analyses. Simply depending on a listing of features that have been described only morphologically is not sufficient. With all that has been learned about the physiology, behavior and ecology of birds over the past century, it is possible to return to the study of avian structure and develop a real biological and evolutionary avian morphology. There is shall a great deal of interesting work to be done in the old, classical field of avian morphology.

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