AN ADAPTIVE MODIFICATION IN THE RIBS OF WOODPECKERS AND PICULETS (PICIDAE)

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ABSTRACT.—Woodpeckers and piculets (Picidae) exhibit a pronounced broadening of the first thoracic rib at the articulation between the vertebral and sternal portions of the rib. In addition, the last cervical rib is enlarged, as are the vertebral attachments of both these modified ribs. The mean ratio of the first sternal rib width to femur length (×100) for 89 species ranges from 2.9 (*Jynx torquilla*) to 14.8 (*Picoides tridactylus*). The Jynginae have noticeably lower rib to femur ratios than the rest of the Picidae. Complexity in the musculature of the anterior ribs also increases from *Jynx torquilla* through *Colaptes auratus* to *Picoides villosus*. These increasing ratios parallel an increase in the specialization of skull structure for pounding behavior. A survey of the foraging modes employed by 61 species shows that genera containing species that excavate frequently have higher rib ratios than genera whose species primarily glean and probe. Woodpeckers that pound frequently and hard require a more highly developed musculature at the base of the neck to provide the strength needed to pull the neck forward and down in blow delivery and to stabilize the neck against the resulting impact. *Received 7 March 1978, accepted 7 February 1980.*

THE pecking and climbing habits peculiar to the woodpecker family (Picidae) correlate with particular structural modifications. Earlier workers have studied adaptations of the skull (Burt 1930, Richardson 1942, Spring 1965), pygostyle (Burt 1930, Richardson 1942), and foot (Richardson 1942, Bock and Miller 1959) to pecking and climbing behavior. Modifications of the anterior trunk have received no attention beyond Shufeldt's (1900) observation that a conspicuous widening occurs in the anterior ribs of Picidae. The latter author also mentioned that this broadening in the anterior ribs is less apparent in *Colaptes*. Since Shufeldt's comment no further investigation has been made into this feature, and its presence in woodpeckers is unexplained. This paper describes the anatomical and functional aspects of the modified ribs in Picidae, surveys the variation in this character within the family, and attempts to explain its adaptive significance.

METHODS

To survey variation in the rib modification, I measured specimens of 31 of the 36 genera and 89 of the 211 species of Picidae, including species of the wryneck, piculet, and true woodpecker subfamilies (Jynginae, Picumninae, and Picinae, respectively). I follow the nomenclature of the AOU Checklist (1957), its supplements (1973, 1976) and that of Peters (1948) for species not included in the Checklist and its supplements.

I measured the width of the first sternal rib and the length of the femur for each specimen using dial calipers accurate to the nearest 0.1 mm. The width of the sternal rib was measured at the widest point where it articulates with the vertebral rib. I measured the greatest length of the femur. Only specimens with fully ossified skulls were measured. In measuring small specimens, I used a dissecting microscope.

To separate differences in proportion from differences reflecting body size, I divided the width of the rib by the length of the femur of the same individual. Spring (1965) showed that the relative length of the femur is less variable among the Picidae than other limb measurements, and I found a significant correlation ($r = 0.940$) between mean femur length and mean cube root of body weight for 53 species of Picidae. I then multiplied all ratios by 100 to facilitate comparisons.

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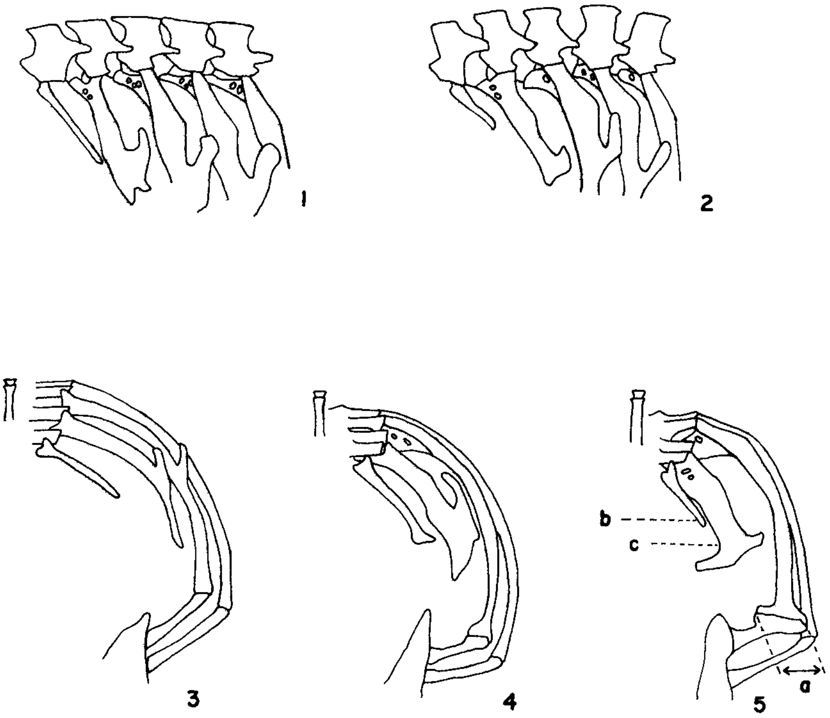

Fig. 1. Lateral view of the first and second floating ribs and first three vertebral ribs in *Colaptes auratus* (1) and *Picoides arcticus* (2). Note the difference between (1) and (2) in the degree of enlargement in the vertebral attachments of the second floating rib and first vertebral rib. Anterior view of ribs in *Jynx torquilla* (3), *Colaptes auratus* (4), and *Picoides villosus* (5). Note in (5) the degree to which the first sternal rib is broadened at its attachment to the vertebral rib (a), the lack of modification in the first floating rib (b), and the degree of enlargement in the second floating rib (c).

Ratios from both sexes were pooled when I calculated the mean ratio of each species. Inspection of my data suggested no sexual differences in rib width or femur length. This impression was confirmed for the Hairy Woodpecker (*Picoides villosus villosus*) where Student-t tests showed no significant difference between males and females (rib width, $t = 1.20$, df = 27, $P = <0.10$; femur length, $t = 1.20$, df = 26, $P < 0.20$). I chose this species because enough data were available for a statistical test of one subspecies and because differences in foraging behavior between the sexes have been observed (Kilham 1965).

I dissected the trunk musculature of three preserved specimens each of the Wryneck (*Jynx torquilla*), the Common Flicker (*Colaptes auratus*), and the Hairy Woodpecker (*Picoides villosus*). All dissections were bilateral. Also, two fresh specimens each of these species and *Dryocopus pileatus* were dissected and manipulated.

Information on the foraging behavior of the Picidae was compiled from the literature. I relied heavily on Short's (1969–1978) observations because he supplied information on most of the species included in this paper and thus provided a uniform approach to the description of foraging modes.

RESULTS

OSTEOLOGY OF THE TRUNK

Two cervical (floating) ribs and six thoracic (attached) ribs form the rib cage in the Picidae. The two floating ribs articulate with the 13th and 14th vertebrae, and are located immediately anterior to the thoracic ribs (Fig. 1). Each thoracic rib consists of a dorsal or vertebral portion and a ventral or sternal portion. The vertebral portion articulates with the transverse process and centrum of a vertebra and extends caudoventrally to a hinge-like articulation with the sternal portion. It is at the articulation of the vertebral and sternal portions of the first attached rib that an exaggeration in width is most evident in woodpeckers. Correlated with the expansion of the first attached rib is a broadening of the second floating rib and the vertebral attachments of both ribs (Fig. 1). No widening of the first floating rib was noted.

Initially I measured the width of the articulation within each of the attached ribs in 20 species of Picidae. I decided to consider only the first attached rib in the final study, because the widening that is apparent in this rib is not noticeable in the second, third, and fourth ribs. Dissection of the anterior trunk musculature further supported my decision to eliminate these ribs from consideration; except for Mm. intercostales externi, the muscles associated with the enlarged first thoracic rib do not attach on the more posterior ribs.

Among the Picidae, there is marked variation in the amount of widening in the first attached rib and associated characters (Fig. 1). The anterior ribs of *Jynx* show no widening when compared with the other thoracic ribs, while those of Picumninae and Picinae are strikingly modified. Considerable differences in the width of the first attached rib and its associated muscles are found among the species of woodpeckers and piculets.

RATIOS OF THE FIRST STERNAL RIB WIDTH TO FEMUR LENGTH

The ratios of the width of the first sternal rib to femur length (×100) for 89 species of Picidae range from 2.9 ($n = 1$) and 3.0 ($n = 2$) in *Jynx torquilla* and *J. ruficollis*, respectively, to 14.8 ($n = 9$) in *Picoides tridactylus*. *Colaptes pitius* ($\bar{x} = 5.8$, $n = 1$) and *Micropternus brachyurus* ($\bar{x}$ 6.1, $n = 2$) of the Picinae have the next to the lowest ratios, noticeably higher than the Jynginae. The genera of Picinae can be characterized by the positions of their component species along the spectrum, although there is broad intergeneric overlap (Fig. 2). Species of *Colaptes* have the lowest ratios ($\bar{x} = 5.8$–6.7), followed by *Melanerpes* ($\bar{x} = 6.9$–9.4) and *Picoides* ($\bar{x} = 9.6$–14.8). *Verreauxia africana, Sasia abnormis,* and species of *Picumnus* of the Picumninae have relatively high ratios ($\bar{x} = 9.4$, 9.9, and 9.6–11.6, respectively), comparable to some species of *Picoides*. *Nesoctites micromegas* ($\bar{x} = 7.8$, $n = 3$) has a noticeably lower ratio than the rest of Picumninae, comparable to that of *Melanerpes erythrocephalus* ($\bar{x} = 7.8$, $n = 13$).

MUSCULATURE OF THE THREE ANTERIOR RIBS

In the Picidae, the cranial trunk muscles that attach to the first three ribs include M. scalenus, Mm. levatores costarum, and Mm. intercostales externi (Fig. 3). Also attaching is an additional slip of the Mm. intercostales externi, described here, which I call the ventral slip of the first intercostal externus. Other than this cranial-most slip, the function of Mm. intercostales is not discussed, because they show no modification in relation to the broadened ribs. In the following discussion, muscles of the anterior trunk are described for the Common Flicker. The musculature of the Wryneck and the Hairy Woodpecker is then contrasted to *C. auratus*. The great difference in muscle complexity between *Jynx* and *Picoides* is illustrated in Fig. 3.

M. scalenus, description.—M. scalenus extends from the tip of the transverse process of the 12th cervical vertebra to insert on the entire length of the cranial edge of the first floating rib. The muscle is

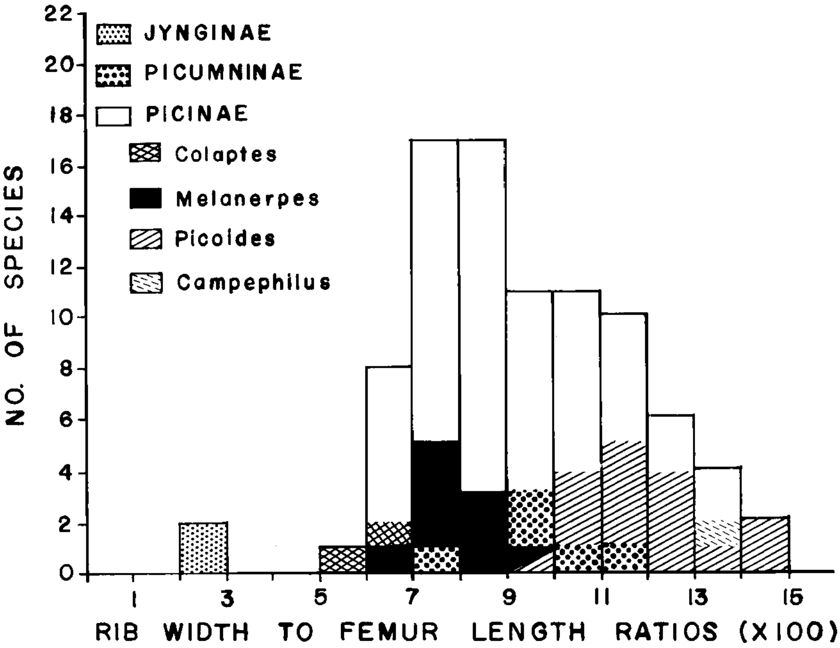

Fig. 2. Ratios of the width of the first sternal rib to the length of the femur (×100) in 89 species of Picidae. Each bar represents the number of species having a ratio within a given ratio interval. The ratios of four genera are shown to illustrate adaptive radiation within the Picinae. The overlapping columns are independent and not additive. The ratio averages for the 89 species of Picidae are available from the author upon request.

triangular and fans out caudoventrally. A superficial aponeurotic sheet runs from its vertebral attachment along the cranial edge of the belly.

Comparisons.—In *Jynx torquilla* the origin of M. scalenus is less tendinous in that the superficial aponeurotic sheet running along the length of this muscle in *Jynx* is neither as extensive nor as tough. Also, the muscle is thinner than in *Colaptes.*

M. scalenus is more extensive in *P. villosus* than in *C. auratus*; it extends in the former caudoventrally to attach on the aponeurotic surface of the first external intercostal. The vertebral attachment is more tendinous and the superficial aponeurosis more extensive in *Picoides;* the muscle is also thicker than in *Colaptes.*

Mm. levatores costarum, description.—The first levator of Mm. levatores costarum originates from the tip of the transverse process of the 13th vertebra and extends caudoventrally to insert on the entire craniolateral surface of the last cervical rib, including the uncinate process. Ventrally, its fibers blend with Mm. intercostales. From its vertebral attachment, a superficial aponeurotic sheet extends caudoventrally half of its length.

The second levator extends from the tip of the transverse process of the 14th vertebra and a superficial aponeurosis caudoventrally to a tendinous sheet between the second floating rib and the first attached rib and to the cranial edge of the first attached rib. It is unipinnate in structure.

The third levator from the 15th vertebra is indistinguishable from Mm. intercostales.

Comparisons.—Compared with *Colaptes,* the origin of the first levator in *Jynx* is less tendinous, and the superficial aponeurotic sheet less extensive. In *P. villosus,* the aponeurosis is most extensive. The caudoventral attachment of the muscle is less extensive in *Jynx* than in *Colaptes,* covering the cranial and lateral surface of only the upper third of the last cervical rib, and the muscle is not as thick in *Jynx* as in *Colaptes.* In the second levator, the overlapping aponeuroses and the muscle become progressively larger from *Jynx* through *Colaptes* to *Picoides.*

Mm. intercostales externi, description.—The dorsal Mm. intercostales running between the two float-

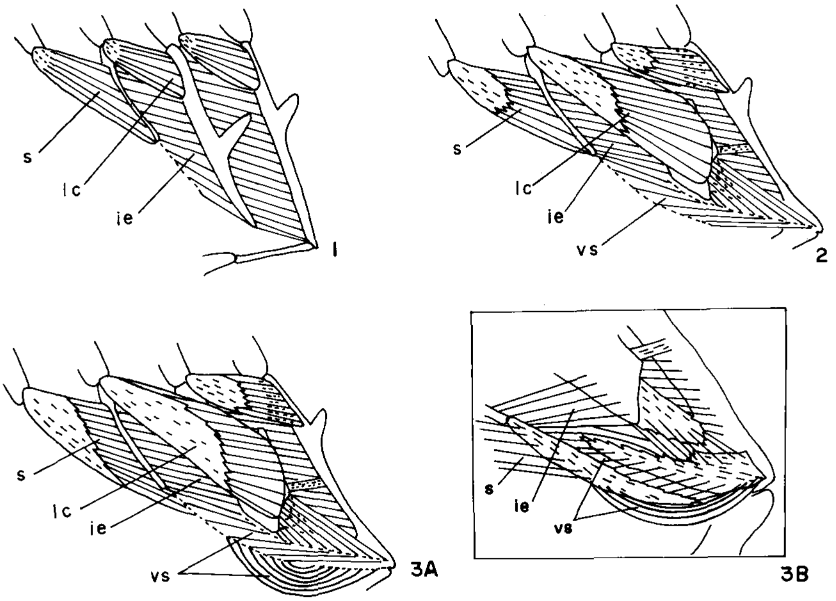

Fig. 3. Diagram of the superficial musculature of the first three ribs in *Jynx torquilla* (1), *Colaptes auratus* (2), and *Picoides villosus* (3A). (3B) is a deeper view of the muscles and aponeuroses at the articulation of the first thoracic rib in *Picoides villosus*. The first of the levatores costarum and the superficial lateral fibers of the ventral slip have been removed. Abbreviations: s = M. scalenus; lc = M. levator costarum; ie = M. intercostalis externus; and vs = ventral slip of the first M. intercostalis externus.

ing ribs and between the second floating rib and first attached rib are thin sheets of muscle extending from the caudal edge of each rib caudolaterally to the cranial edge of the next rib. Some fibers also attach on an aponeurosis from the ventromedial surface of the second floating rib. These fibers extend caudoventrally to insert on the ventromedial surface of the first vertebral rib. A short ligament runs from the tip of the second floating rib to the cranial edge of the first vertebral rib.

Colaptes and *Picoides* have an additional slip on the first of the Mm. intercostales externi, termed here the ventral slip. It extends caudoventrally from the tip of the first floating rib and an aponeurotic extension of that rib to the cranioventral surface of the first vertebral rib and one or more aponeuroses extending forward from the broadened end of the first vertebral rib. This slip is probably present in all woodpeckers.

Comparisons.—The intercostal muscles show increasing development from *Jynx* through *Colaptes* to *Picoides*. The aponeurosis from the ventromedial surface of the second floating rib and its associated fibers are lacking in *Jynx*, as is the ventral slip. In *Jynx*, fibers of Mm. intercostales externi arising from the tip of the first floating rib attach only on the cranial edge of the second floating rib. In *Colaptes*, the ventral slip is bipinnate, whereas in *Picoides* it is multipinnate and enlarged. In *Picoides*, a wing of the aponeurosis from the broadened end of the first vertebral rib attaches along the ventrolateral edge of the first vertebral rib. This wing receives fibers from the aponeurosis on the tip of the second floating rib. The short ligament is better developed in *Picoides* and is absent in *Jynx*.

FUNCTION OF THE ANTERIOR TRUNK MUSCLES

The anterior trunk muscles connect the first three ribs with the three caudal-most cervical vertebrae. By describing the limits of motion of the ribs and vertebrae and the direction of pull of the muscles connecting these elements, I determined the probable function of the anterior trunk muscles.

Each vertebral rib is restricted in its movement by its double articulation with

TABLE 1. Foraging modes of 61 species in Picidae with species arranged in order of increasing rib width to femur length ratios, and foraging modes in order of increasing stress placed on the base of the neck (frequency of foraging modes: U = uncommon, C = common).

	Foraging modes					
Species	Glean/ probe	Dig	Drill	Bark-scale	Excavate	References[a]
1. *Jynx torquilla*	C	C				1, 8, 61, 65, 68
2. *Jynx ruficollis*	C	C				8, 61, 65
3. *Colaptes pitius*	C	C				53
4. *Micropternus brachyurus*	C	C			U	1, 54, 57
5. *Colaptes campestris*	C					48, 61
6. *Chrysoptilus punctigula*	C				U	53
7. *Colaptes auratus*	C	C			U	9, 10, 13, 48
8. *Dinopium javanense*	C				U	54
9. *Meiglyptes tukki*	C				U	54, 57
10. *Meiglyptes tristis*	C				U	54, 57
11. *Picus flavinucha*	C				U	54
12. *Picus mentalis*	C				U	54, 57
13. *Picus canus*	C	C			U	1, 54
14. *Melanerpes rubricapillus*	C				U	61
15. *Chrysoptilus melanochloros*	C				U	48, 53
16. *Nesoctites micromegas*	C				U	56
17. *Melanerpes erythrocephalus*	C				U	9, 10, 11, 13, 28, 30, 31, 42, 70
18. *Melanerpes uropygialis*	C				U	9
19. *Melanerpes lewis*	C				U	9, 10, 11, 13, 23
20. *Piculus rivolii*	C				U	49
21. *Picus vittatus*	C			C	C	54
22. *Piculus chrysochloros*	C				U	49
23. *Trichopicus cactorum*	C					49
24. *Melanerpes aurifrons*	C				U	10, 47, 61
25. *Melanerpes carolinus*	C				U	9, 10, 11, 13, 28, 31, 42, 69, 70
26. *Melanerpes formicivorus*	C				C	9, 10, 11, 13, 22, 40, 61, 63
27. *Sphyrapicus varius*	C		C	U	U	9, 13, 18, 19, 22, 37, 46, 61, 62, 66, 70
28. *Picus viridis*	C	C	U		U	8, 15, 67
29. *Campethera bennettii*	C				C	39, 50
30. *Campethera abingoni*	C				C	39, 51
31. *Dendropicos fuscescens*	C				C	45, 51
32. *Melanerpes striatus*	C				C	47, 56, 69
33. *Sphyrapicus thyroideus*	C		C			9, 22
34. *Picus chlorolophus*	C				C	54
35. *Sasia abnormis*	C				C	54, 57
36. *Hemicircus concretus*	C				C	54, 57
37. *Blythipicus rubiginosus*	U			C	C	54
38. *Veniliornis passerinus*	C				C	49
39. *Picoides canicapillus*	C				C	1, 54
40. *Picoides macei*	C				C	54
41. *Dryocopus javensis*	U			C	C	54, 57
42. *Dryocopus lineatus*	U			C	C	34, 49, 61
43. *Chrysocolaptes lucidus*	U			C	C	54, 57
44. *Thripias namaquus*	U				C	39, 51
45. *Picoides syriacus*	C				C	71
46. *Picumnus cirrhatus*	C				C	49
47. *Picoides pubescens*	C		U	U	C	7, 9, 18, 19, 22, 27, 33, 36, 52, 61, 62, 70
48. *Phloeoceastes melanoleucos*	U			C	C	34, 49
49. *Picoides major*	U		U	C	C	15, 24, 26, 61, 67, 71
50. *Picoides borealis*	U			C	C	29, 38
51. *Picoides nuttallii*	C			C	C	9, 41, 52
52. *Picoides arizonae*	C			C	C	14, 38
53. *Picoides scalaris*	C				C	6, 9, 52
54. *Dryocopus pileatus*	U			C	C	9, 10, 13, 22, 34, 35, 61, 64
55. *Picoides lignarius*	C				C	49
56. *Picoides villosus*	U		U	C	C	7, 9, 13, 18, 22, 32, 33, 36, 52, 61, 62
57. *Mulleripicus pulverulentus*	C				C	1, 54, 57
58. *Picoides leucotos*	U			C	C	15, 26, 68

TABLE 1. Continued.

Species	Foraging modes Glean/ probe	Dig	Drill	Bark-scale	Excavate	References[a]
59. *Campephilus principalis*	U			C	C	2, 9, 16, 61, 64
60. *Picoides arcticus*	U			C	C	9, 13, 32, 55, 62
61. *Picoides tridactylus*	U		U	C	C	7, 9, 13, 15, 24, 25, 26, 55, 62, 67

[a] Numbers refer to numbered references in Literature Cited used to obtain information on the species' foraging modes.

the vertebra that forms a hinge joint (Fig. 1). It can rotate about this joint in a craniodorsolateral direction or in a caudoventromedial direction. Contraction of M. scalenus and of the first levator costarum could draw the first and second floating ribs craniodorsolaterally; contraction of the ventral slip and of the second levator could move the first thoracic rib in the same direction. The direction of pull of these muscles, however, is inefficient for moving the ribs. Much of the force of the muscle is wasted in the compression of the rib because the axis of the direction of pull passes close to the center of rotation of the rib. The more dorsal the attachment of the levator muscle on the rib, the greater the lifting action and the less the compression. For this reason, in woodpeckers the second levator probably exerts more of a dorsal pull on the first vertebral rib than would either M. scalenus or the first levator on the floating ribs.

The articulations of the 12th, 13th, and 14th cervical vertebrae allow for lateromedial and dorsoventral rotation around their articulations with the centrum of the adjacent vertebra. The potential for movement is greatest at the 12th vertebra and least at the 14th, where only restricted movement is possible.

The pull of the scalenus and levators on the tip of the transverse process provides effective leverage by which to move the vertebra laterally. Because the axes of pull of these muscles also lie well below the center of rotation of the vertebra, these muscles are efficiently positioned to produce downward rotation of the vertebrae. The muscles could also act to counteract opposing forces on the vertebrae and thus to stabilize the base of the neck. The ventral slip of M. intercostalis externus found in woodpeckers probably serves mainly to anchor the first floating rib against the force of the scalenus and thereby to enhance the action of that muscle on the 12th vertebra. In addition the ventral slip may act on the 13th vertebra directly through the first floating rib. The ventral slip is enlarged in those woodpeckers that pound harder and more frequently, and its enlargement is directly associated with the increase in rib width in woodpeckers.

In summary, the modified anterior trunk musculature appears to have its main action on the vertebrae rather than on the ribs. The enlarged muscles could stabilize the base of the neck when a woodpecker uses its whole body or only its upper neck to deliver a blow, or they could contribute to the motion of the neck in delivering a blow. Increase in the width of the anterior ribs is a functional correlate of the increase in size and complexity of these muscles.

FORAGING MODES AND THE RIB MODIFICATION

The foraging modes employed by a woodpecker are an indicator of how frequently and forcefully it pounds. In Table 1 the frequency of foraging modes is indicated for 61 species arranged in order of increasing ratios of rib width to femur length. Definitions of feeding actions are listed as follows roughly in order of increasing stress placed on the base of the neck. *Gleaning* is the taking of prey from the bark or ground surface; *Probing* is the poking of the bill into a crevice or into an ant or termite nest to obtain hidden prey; *Digging* is the "shovel-like pushing . . . with the bill" into the ground or into a terrestrial ant or termite nest (Short 1973: 313); *Drilling* is the perforating of the tree trunk or branch bark "with small roundish holes reaching the cambium, less than an inch apart, disposed in parallel horizontal rings" (Forbush 1907: 251); *Bark-scaling* is the knocking loose of bark "with sidewise blows and quick flicks of the bill" (Tanner 1942: 41); and *Excavating* ranges from "a burst of three to four pecks, usually not repeated, serving to penetrate barely beneath the bark surface," to "a long burst of taps or series of tappings immediately repeated, serving to penetrate the surface layers of bark" (Short 1971b: 89). Excavations can be small and shallow or large and deep.

When species of the Picidae are listed in order of increasing ratios, the extremes in foraging behavior can be clearly differentiated from each other despite the wide range of foraging modes employed by the Picidae (Table 1). Whereas most species engage in gleaning and probing, those with higher ratios do so less frequently, but they excavate more frequently and also employ drilling and bark-scaling techniques. Those species with higher ratios employ foraging modes where the blows are more frequent and forceful. The Wrynecks (Jynginae), *Jynx torquilla* ($\bar{x}$ = 2.9) and *J. ruficollis* ($\bar{x}$ = 3.0), forage by gleaning and probing on the ground and trunk surface and also by digging into ant and termite nests on the ground (Bannerman 1933, Voous 1960, Ali and Ripley 1970, Tarboton 1976). Species of *Colaptes* excavate infrequently and spend much time digging, gleaning, and probing for ants (Table 1). At the other extreme, the Arctic Three-toed Woodpecker, *Picoides arcticus* ($\bar{x}$ = 14.6), and the Black-backed Three-toed Woodpecker, *P. tridactylus* ($\bar{x}$ = 14.8), have the highest rib ratios in the Picidae and pound more frequently in foraging than most members of the family. Both species obtain almost all of their diet through excavating dead or dying wood (Table 1).

The genus *Picoides* (= *Dendrocopos* and *Picoides*) illustrates well the relationship between increasing ratios and pecking behavior. It is a large genus whose species show a great degree of variation in foraging behavior and rib ratios. In *Picoides* the ratio increases from species such as *P. canicapillus* ($\bar{x}$ = 10.3), which gleans, probes, pries, and excavates frequently but does no prolonged excavating (Ali and Ripley 1970, Short 1973), to those like *P. villosus* ($\bar{x}$ = 12.7), which frequently does prolonged and forceful excavating (Table 1), and the two three-toed woodpeckers. *Picoides scalaris* is intermediate in ratios and behavior, excavating less frequently and forcefully than *P. villosus* (Beal 1911, Short 1971c, Austin 1976).

The Red-headed, Lewis', and Red-bellied woodpeckers (*Melanerpes erythrocephalus, M. lewis,* and *M. carolinus,* respectively) excavate infrequently (Table 1). "It is interesting that *M. formicivorous* has a higher rib/femur ratio than *M. erythrocephalus* and *M. lewis* since it . . . excavates individually shaped holes for each intact acorn, rather than breaking up the acorns and storing them in pieces in existing (though sometimes enlarged) cracks" (C. E. Bock pers. comm.), as do the other two.

In the piculet subfamily, Picumninae, whose members have moderately high rib ratios ($\bar{x}$ = 7.8–11.6), *Picumnus cirrhatus* ($\bar{x}$ = 11.6) and *Sasia abnormis* ($\bar{x}$ = 9.9) do much excavating as well as gleaning and probing for food (Short 1970, 1973, 1978). *Nesoctites micromegas,* which has a lower ratio ($\bar{x}$ = 7.8), gleans and probes frequently and excavates infrequently in foraging (Short 1974b).

In *Sphyrapicus varius,* a discrepancy exists between the degree of rib modification and specialization of the skull for pounding; this species has a highly specialized skull structure yet has a rib ratio comparable to *Melanerpes formicivorus* ($\bar{x}$ = 8.6 and 8.4, respectively). Spring (1965) found that the blows delivered by *Sphyrapicus varius* produce less impact than those of *P. villosus* and *P. arcticus.* Grinnel and Storer (1924: 328) also noted that *S. varius* produces less forceful blows, observing that it "moves its head through a short arc, an inch or two at the most, giving but slight momentum to the blows." According to Spring (1965), *S. varius* delivers blows by using only its neck. *Picoides villosus* and *P. arcticus* deliver more powerful blows by employing a delivery stance that creates a greater distance between the body and the tree trunk for developing acceleration and by superimposing "lower body movements upon neck action" (Spring 1965: 467). In effect then, these woodpeckers accelerate greater mass through longer distances to produce more forceful impacts.

CONCLUSIONS

The force developed at the tip of the bill when a woodpecker pounds a trunk is transmitted through the vertebral column. The musculature associated with the modified ribs stabilizes the base of the neck against lateral and dorsal bending, and therefore a woodpecker that pounds harder and more frequently requires a better developed musculature at this point. The muscles connecting the anterior ribs and the 12th, 13th, and 14th vertebrae are in fact best developed in those woodpeckers that excavate frequently and forcefully to obtain food. Correlated with this increase in musculature is the broadening of the anterior ribs and their vertebral attachments to facilitate transmission of body motion or neck action into forceful pounding.

Burt (1930) showed that Picidae that excavate for burrowing prey as opposed to those that take primarily superficial prey have skulls that are highly modified for pounding. He found a continuum in skull structure from the least to the most specialized for pounding: *Colaptes auratus, Melanerpes lewis, M. erythrocephalus, M. formicivorus, M. carolinus, Dryocopus pileatus, Sphyrapicus varius, Picoides villosus, P. arcticus,* and *P. tridactylus* (the last two species showing the same amount of modification) that corresponds with an increase in pounding in the species' foraging behavior. The last four species had noticeably more specialized skulls than the others. With minor exceptions, the pattern of increasing rib ratios described here follows that of increasing skull specialization in the species described by Burt. This finding supports my contention that the widening in the first attached rib is related to more frequent and harder pounding during foraging.

The genera of woodpeckers showing greater modification in the anterior ribs also show greater modification in skull, pygostyle, and foot structure in adaptation to their pecking and climbing habits (Burt 1930, Richardson 1942, Bock and Miller 1959, Spring 1965). The broadened anterior rib complex, an adaptation to more frequent and harder pounding that reaches extreme development in those woodpeckers that excavate almost exclusively in foraging, enables the woodpecker to more fully specialize on the food resources of an arboreal environment.

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