CLIMBING AND PECKING ADAPTATIONS IN
SOME NORTH AMERICAN WOODPECKERS

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The majority of the studies of functional anatomy of birds deal with closely related species. Exemplifying this approach, workers such as Burt (1930), Miller (1937), Engels (1940), and Fisher (1946) have investigated adaptations in well-defined taxonomic complexes.

When substantial gradations of a particular action occur among closely related animals, comparisons of the anatomical parts involved may reveal significant variations correlated with the intensity, frequency, or other particulars of the action under consideration. But since a structure is involved in several actions, its configuration represents a compromise between two or more functional demands. In studying the anatomical modifications for a particular action, the use of closely related species offers the least variation in other actions affecting the structure. While closely related species may vary markedly in regard to a particular activity, they are more likely to be similar in the bulk of activities affecting the considered structure than would be distantly related species. The more closely related the species, the more likely it is that anatomical variations reflect differences of function.

While studies of convergences, as exemplified by Richardson (1942), may reveal much valuable information, it is my contention that this is not the most productive approach to functional anatomy. The first difficulty has already been stated. The second, which is rather closely related, concerns the concept of "multiple evolutionary pathways" recently discussed by Bock (1959). This concept implies that the anatomical differences which exist among species are not always explicable in terms of relative functional advantage. Bock (1960a) shows that the secondary jaw articulation of birds has probably developed independently as many as fifteen times and that the position of the articulation seems to vary randomly in regard to food-getting habits. In a particular species, the present position of the articulation was determined by where the elongating medial process of the mandible first contacted the basitemporal plate and not because a different position might have proved more advantageous at some later time in evolution.

Arguing from a purely functional viewpoint, one might say for a particular species or group that a different position of articulation would be more advantageous if less muscle, bone, and so on would be needed to achieve the same function. If this is so, one immediately faces the problem of why a particular species or group has not evolved another position of articulation. The most acceptable answer is that evolution from one adaptive condition toward the theoretically more advantageous one involved intermediate stages which had no selective advantage. While the end product of such a change would have been advantageous, the intermediate steps were impossible in a selective system operating on micromutations.

The concept of multiple evolutionary pathways is probably a factor of major importance in a functional study of convergent species. The worker studying convergent species is never really sure which differences among species are adaptive and which are expressions of the "opportunism" of former evolutionary history.

In keeping with the proposition that functional studies should employ closely related species, this study of the pecking and climbing adaptations in woodpeckers deals primarily with the genera *Sphyrapicus, Dendrocopos,* and *Picoides*. Representatives

of these genera were previously compared by Burt (1930) and represent the three most arboreal genera of the nine he studied. These three genera, on the basis of behavioral and morphological characters, might be considered as representative of a "more arboreal" subfamily of woodpeckers such as that proposed by Garrod (1873). Another subfamily proposed by Garrod includes the flickers (*Colaptes*), Lewis Woodpecker (*Asyndesmus lewis*), Red-headed and Acorn woodpeckers (*Melanerpes*), and the Red-bellied Woodpecker (*Centurus carolinus*). These so-called "ground woodpeckers" obtain the greater part of their food away from tree trunks (Burt, 1930:470), possess the accessory semitendinosus muscle (*op. cit.*:502), possess a perching-type foot (Bock and Miller, 1959), and have frontal bones which do not bulge anteriorly over the base of the upper bill (Burt, 1930:471). In contrast, the members of the "more arboreal" subfamily secure the greater part of their food by either pecking into wood or from the surfaces of tree trunks. They lack the accessory semitendinosus muscle, employ a "climbing" type foot, and possess frontal bones which bulge anteriorly over the base of the upper bill.

The genera *Sphyrapicus, Dendrocopos,* and *Picoides* as exemplified by the Yellow-bellied Sapsucker (*Sphyrapicus varius*), Hairy Woodpecker (*Dendrocopos villosus*), and the Black-backed Three-toed Woodpecker (*Picoides arcticus*) offer a wide range of adaptation in regard to the wood-pecking habit. On the basis of extensive stomach analyses (Beal, 1911), Burt (1930) has estimated that *Sphyrapicus varius* obtains 27 per cent of its food by wood pecking, *Dendrocopos villosus* obtains 45 per cent by this method, and *Picoides* (including *P. arcticus* and *P. tridactylus*) 85 per cent.

One question arising from these percentages is whether they reflect the relative force with which the different species deliver blows. While it may seem likely that there is a relationship, it cannot be initially assumed. The first section of the present paper will examine how the blows are delivered, the anatomical modifications for the different methods of delivery, and the effect that this has had upon other modes of environmental exploitation. The second section will evaluate a hypothesis originally suggested by Beecher (1953, 1962), that modifications of the cranial kinetic apparatus are involved in buffering the crania against heavy blows of the bill.

MATERIALS AND METHODS

Actions of woodpeckers were carefully observed in the field, in the laboratory,

and at Woodland Park Zoo in Seattle. The laboratory birds included four *Sphyrapicus varius* and two *Picoides arcticus* which were captured as nestlings and maintained for up to eleven months on a diet of mealworms and wet meal dog food. Motion pictures of pecking and climbing activities were taken at 64 frames per second with a 16 mm. Cine-Kodak Special No. 2 camera using Plus-X reversal and Tri-X reversal Kodak film; 16 mm. X-ray motion pictures were taken at 60 frames per second. All film footage was analyzed at slow speed using a Model K-160 Keystone 16 mm. projector with separate control box. Frame by frame tracings were obtained by projection onto a distortion free mirror inclined at a 45° angle so that the image could easily be traced.

Skeletal material of 13 species of woodpeckers was examined. Measurements were made to the nearest 0.1 mm., using vernier calipers. Among other measurements, the leg bones of all the woodpeckers represented in Burt's (1930) series were taken (because of a greater number of specimens, *Colaptes cafer* was used rather than *Colaptes auratus*). The greatest length of each bone was measured rather than the distance between articular surfaces. Thus, in the calculation of ratios, the "total limb length" is slightly greater than if the separate bones had been measured between articular surfaces.

Angles of kinesis were determined for 11 species as follows: the dried skull was placed in boiling water for one minute to loosen joints and connective tissue; the skull was then placed in a metal clamp and the arc of movement measured to the nearest degree on a protractor suspended at the side of the skull so that its center was adjacent to the nasofrontal hinge. Skulls missing parts of the kinetic mechanism or having other obvious imperfections were not measured. Three or more readings were taken for each skull and the results were averaged. In addition, skulls representing seven species of woodpeckers and six species of passerines were sectioned in the median sagittal plane and their frontal regions compared.

Preserved specimens of the Red-bellied (*Centurus carolinus*) and Red-headed (*Melanerpes erythrocephalus*) woodpeckers were dissected following Burt's (1930) description of the Pileated Woodpecker (*Dryocopus pileatus*). Finally, the cranial kinetic musculature was examined for nine species of woodpeckers and three species of nuthatches.

A device for recording the force of impact was constructed, but no data were collected. The woodpeckers tested refrained from hitting with full force any target with a recoil action, the working basis of the constructed device.

GENERAL FEATURES AND NATURAL HISTORY

The following is a brief review of certain aspects of the natural history of *Sphyrapicus varius*, *Dendrocopos villosus*, and *Picoides arcticus*, particularly in reference to food and feeding behavior. Food habits are a primary factor in the niche occupied by any species. These habits are not only reflected in the items taken and the methods of acquisition but also in territory size, habitat, and migratory traits.

In the evolutionary adjustment of a species to a particular niche, two factors are primarily instrumental in delimiting the boundaries of that niche: competition with species having similar ecological requirements and the so-called "time and energy budget." While natural selection has minimized interspecific competition by restricting niches, it has also "mediated" the exploitation habits of each species. For a species to maintain and perpetuate itself, the energy obtained through a particular exploitation pattern must be significantly greater than the energy required for that type of

exploitation. The data presented suggest how the three species exploit their environments so as to avoid competition while operating on a "time and energy budget" appropriate for self-maintenance and reproduction.

YELLOW-BELLIED SAPSUCKER

The two species of the genus *Sphyrapicus* are confined to North America. On the basis of "historical" considerations, Howell (1952) postulated that *Sphyrapicus* evolved from *Dendrocopos*. *Sphyrapicus* is unique in possessing morphological characters which are either absent or seldom occur in other genera. The horns of the hyoid apparatus are considerably shortened, and instead of curving over the top of the head and ending by the orbit or nostril, they reach no further than the occipital region. Also, the capital apterium is reduced (Burt, 1929), and the tip of the tongue is brushy rather than barbed.

Sphyrapicus varius is represented by four subspecies, two of which (*varius* and *nuchalis*) migrate extensively and two of which (*ruber* and *daggetti*) show more limited migratory movements. The wintering grounds of all subspecies lie generally within those areas having more than 180 frost-free days.

Although other species of woodpeckers have been reported to take sap, none has developed this habit to the extent found in the sapsuckers. Two chief methods are used in preparing drainage sites which are subsequently revisited several times: (1) rows of small holes may be excavated, or (2) patches of outer bark may be stripped off leaving one large wound.

Burt (1930) estimated that *Sphyrapicus varius* obtains 27 per cent of its food by pecking, 38 per cent on the surfaces of tree trunks, and 35 per cent from places other than tree trunks. Of the 27 per cent obtained by pecking, approximately 16 per cent is cambium. Beal's (1911) data omit the portion of sap in the diet. If both factors are taken into consideration, it is probable that not more than 10 per cent of the sapsucker's food consists of insects which must be excavated. The bulk of the food obtained by pecking probably lies in superficial positions which require minimal excavation. Accordingly, the drilling of sapsuckers is less vigorous than that of other species of woodpeckers. Grinnell and Storer's (1924) observations of *S. v. daggetti* correspond well with those of the author for *S. v. nuchalis*. They state (p. 328) that "the Sierra red-breasted sapsucker . . . does not ordinarily attract attention, as do the woodpeckers which are wont to pound noisily. The most vigorous drilling of the sapsucker will scarcely be heard more than a hundred feet away. The bird moves its head through a straight arc, an inch or two at the most, giving but slight momentum to the blows. The chips cut away are correspondingly small, mere sawdust as compared with the splinters or slabs chiseled off by other woodpeckers. The strokes are delivered in intermittent series, four or five within a second, then a pause of equal duration, then another short series, and so on." Also, the Yellow-bellied Sapsuckers I observed in the field engaged in generally longer vertical climbs than did the Hairy Woodpecker and more rapid climbs than the Black-backed Three-toed Woodpecker. The movements of the sapsucker are contrasted with those of the Hairy and Black-backed Three-toed woodpeckers in figure 1a.

Laboratory observations and motion pictures of sapsuckers on vertical surfaces show that most of the time the toes are held in the position described by Bock (in Bock and Miller, 1959) for the Hairy and Pileated woodpeckers. While the fourth toe is directed laterally at right angles to the trunk, the second and third toes are held anteriorly and the reduced hallux points down the trunk (fig. 1b). On horizontal

surfaces, the fourth toe is usually rotated to a position opposing the second and third toes. Such a position is typical of the permanently zygodactylous foot of the ground woodpeckers.

Howell (1952:247) has determined that the breeding territories of *Sphyrapicus varius* include an area within a 50- to 150-yard radius of the nesting site, the exact size depending on how heavily wooded the area is.

HAIRY WOODPECKER

Of the several species of *Dendrocopos* occurring in North America, *Dendrocopos villosus* has the widest distribution; it occurs from the northern tree limit to Panamá. Like other North American members of its genus, it is a year-round resident in all parts of its breeding range. Staebler (MS) examined the banding data of the Fish and Wildlife Service up to 1949 and found no evidence of migration for either the Hairy or the Downy woodpecker (*Dendrocopos pubescens*).

Burt (1930) estimated that 45 per cent of the Hairy Woodpecker's food is obtained by pecking, 30 per cent is obtained from trunk surfaces, and 25 per cent is obtained from places other than tree trunks. Of the food obtained by pecking, 31 per cent consisted of wood-boring larvae and 3 per cent of curculionid and engraver beetles—over three times as many wood-boring insects as utilized by *Sphyrapicus varius*.

Except at the northern and southern extremities of its range, the Hairy Woodpecker is sympatric with the Downy Woodpecker. The Downy Woodpecker hunts most of its food in brushy areas, in orchards, and on small branches and twigs, whereas the Hairy Woodpecker confines its activities mainly to the trunks and large branches of sizable trees. Staebler (MS) estimated that *D. pubescens* spends less than one-fourth of its time obtaining food in areas where *D. villosus* would also be expected to search.

Observations of Downy Woodpeckers leave the impression that they are more scansorial and active in their feeding than are Hairy Woodpeckers. Greater activity might be expected on the basis of studies by Gibb (1960), who found that feeding intensity for four species of passerines was inversely correlated with body size. Stomach analysis data probably reflect the more scansorial habits of the Downy Woodpecker; it obtains 5 per cent less food by pecking and 6 per cent more food from trunk surfaces. In both species, Beal (1911) notes an increase during the winter in the portion of diet consisting of wood-boring insects (a maximum December increase of 10 per cent for *D. villosus* and a maximum November increase of 6 per cent for *D. pubescens*).

The Hairy Woodpecker has a much larger nesting territory than either sapsuckers or the Downy Woodpecker. Although Staebler (MS) gives no definite territory size for either the Downy or Hairy woodpeckers, he reports that the Hairy Woodpecker ranges up to 1000 yards from its nest in search of food for nestlings. This wide foraging area is probably correlated with the rapidity with which it moves from tree to tree. Staebler watched a female *D. villosus* feeding from two to five feet above the ground. Working to a height of five feet, she spent from one-half to two minutes in each tree. Bent (1939) reports that Brasher followed a Hairy Woodpecker for four hours during which time it alighted "on 218 different trees, an average of nearly one tree a minute." On the basis of these observations the exploitation movements of the Hairy Woodpecker are suggested in figure 1*a*.

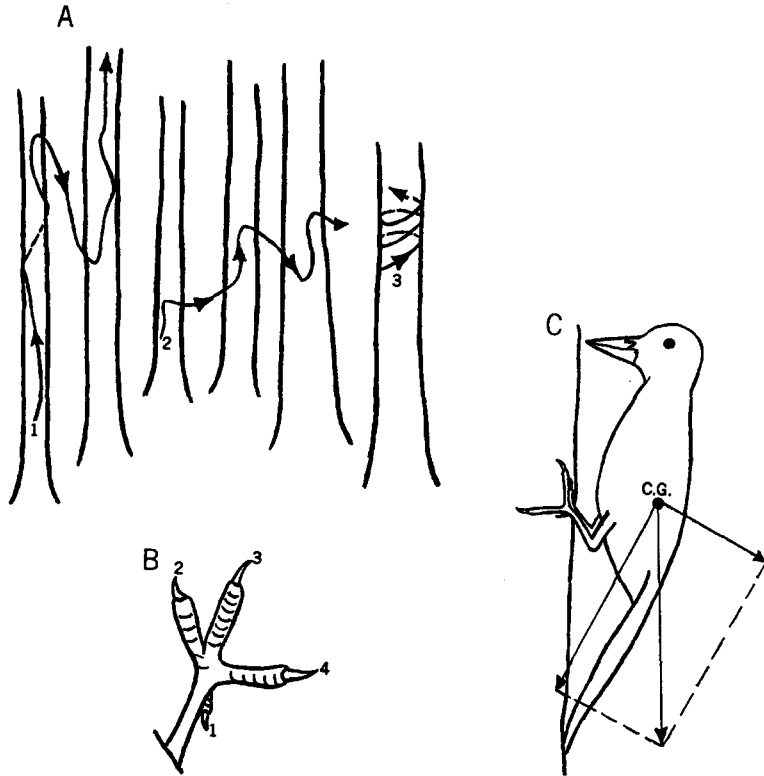From films of captive individuals, it has been determined that *Dendrocopos vil-*

Fig. 1. A. Climbing patterns of Yellow-bellied Sapsucker (1), Hairy Woodpecker (2), and
Black-backed Three-toed Woodpecker (3).

B. Dorsal view, right foot of Yellow-bellied Sapsucker or Hairy Woodpecker show-
ing toe arrangement usually seen on vertical surface.

C. Gravitational components acting on woodpecker (from Bock and Miller, 1959).

losus and *Dendrocopos pubescens* when on a tree trunk, usually hold their toes in the
same position as has been described above for the sapsucker.

BLACK-BACKED THREE-TOED WOODPECKER

Picoides arcticus is a resident of North America only. It ranges from the northern
tree limit into the northern United States and as far south in the western mountains
as central California. Over most of its range, it is sympatric with the Northern Three-
toed Woodpecker (*Picoides tridactylus*), a somewhat smaller species, although the
difference in size is not as great as that between *Dendrocopos pubescens* and *Den-
drocopos villosus*.

Both species nest largely in areas where there are numerous dead trees or stubs
such as may result from a fire, windfall, or insect infestation. In such habitats, both
species have been reported to nest close to one another. In the midwestern states and
provinces, *P. arcticus* shows a preference for tamarack swamps, "especially where
these have been burned over, leaving a few dead or dying trees" (Bent, 1939:106).

Burt calculated that both *Picoides arcticus* and *Picoides tridactylus* obtained 85
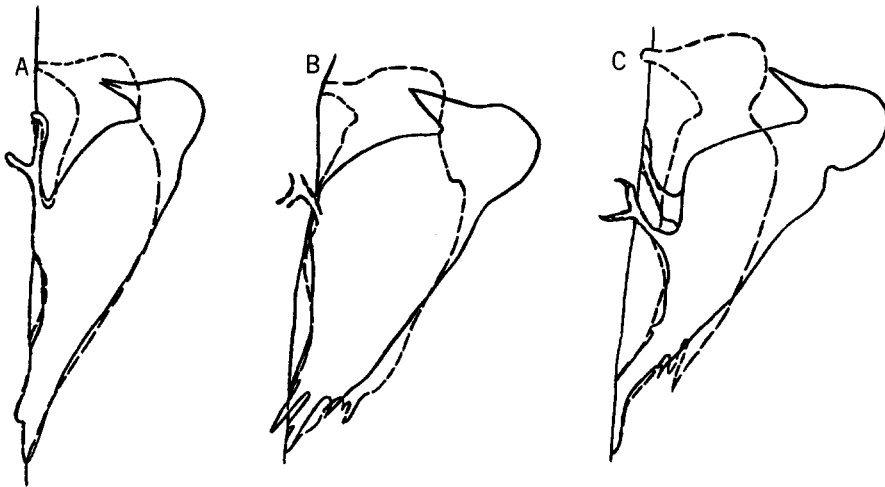
Fig. 2. Blow delivery in *Sphyrapicus varius* (A), *Dendrocopos villosus* (B), and *Picoides arcticus* (C). Solid line, "delivery stance"; broken line, three frames later when bird was solidly in contact with trunk.

per cent of their food by pecking, 10 per cent by gleaning surfaces of tree trunks, and 5 per cent from the ground. Beal's figures (1911) show that the portion of wood-boring larvae taken is 77 per cent for *P. arcticus* and 75 per cent for *P. tridactylus*.

Observers generally agree that Three-toed Woodpeckers are remarkably sedentary in their feeding. Pecking intently in the same area of trunk for long periods, they move only slowly up the tree and may circle it several times over a short vertical distance (fig. 1*a*). Both species are nonmigratory.

When on a vertical surface, the toes of *P. arcticus* (the hallux is lost) are usually held in the same position as those of *Sphyrapicus* and *Dendrocopos*. Also, as in *Sphyrapicus* and *Dendrocopos,* the fourth toe is rotated to a posterior position when the bird is on a horizontal surface.

In summary, the Yellow-bellied Sapsucker exploits primarily trunk surfaces—doing more climbing on fewer trees than the Hairy Woodpecker. The Black-backed Three-toed Woodpecker probably also requires fewer trees but is a slow climber. Data on breeding habitats and stomach analysis suggest that it exploits localities with large concentrations of wood-boring insects.

The migratory habits of *Sphyrapicus* are probably associated with surface feeding. *Sphyrapicus* is apparently unable to excavate efficiently the wood-boring insects which are so important to the other two genera in cold winter periods.

Both *Dendrocopos villosus* and *Picoides arcticus* are widely sympatrically with congeneric species. Although the means by which *D. villosus* and *D. pubescens* avoid competition are obvious, the mechanisms separating *P. arcticus* and *P. tridactylus* are obscure and await future ecological investigation.

Sphyrapicus varius, Dendrocopos villosus, and *Picoides arcticus* each possess characteristic climbing patterns although they all hold their toes in similar positions when on vertical and horizontal surfaces. The toe position is typical of the "more arboreal" subfamily of the Picidae and contrasts markedly with the zygodactylous arrangement which many authors have maintained to be the most efficient climbing foot.
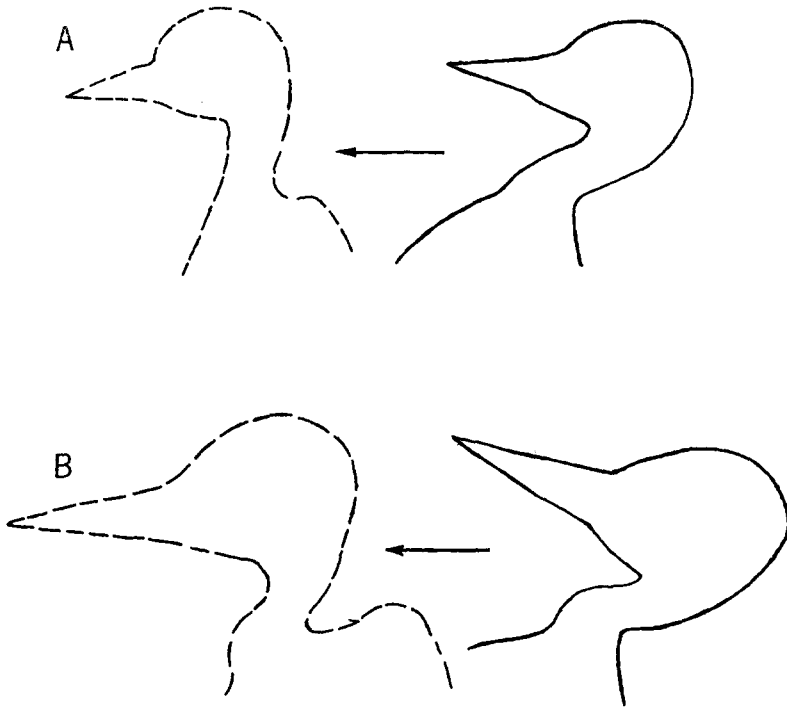
Fig. 3. Tracings of X-ray motion pictures showing neck curvature in *Sphyrapicus varius* (A) and *Picoides arcticus* (B). "Delivery stance" (solid line) and three frames later (broken line).

CHARACTERIZATION OF PECKING MOVEMENTS

Figure 2 contrasts the stances and pecking movements of *Sphyrapicus varius*, *Dendrocopos villosus*, and *Picoides arcticus*. Although there are interspecific overlaps in functional traits, it is possible to characterize clearly two of the species on the basis of existing film footage. *Sphyrapicus varius* and *P. arcticus* represent the extremes and *D. villosus* is intermediate.

YELLOW-BELLIED SAPSUCKER

Just prior to the delivery of a blow, the abdomen of the Yellow-bellied Sapsucker is held close to the vertical surface with the tarsus usually lying nearly parallel to and often in contact with the trunk. Tracings from both light and X-ray motion pictures reveal that the blow is delivered primarily by the neck (fig. 3). The lower body regions contribute little if any momentum. Although figure 2 shows that the foot is held more anteriorly in *S. varius* than in *P. arcticus*, this difference is not consistent. Measurements from 12 stance tracings of *S. varius* and eight of *P. arcticus* demonstrate more precisely the variation in the species (table 1).

Figure 4 traces in more detail a sequence for *S. varius* in which the bird is pecking into a deep hole. The action is relatively uncomplicated. The neck delivers the major portion of the momentum of blow. In this species and in all other woodpeckers filmed, the eyes are closed during the inward movement and are not opened until after impact. Displacement of the heel or tarsus is either slight or absent. In the heel action

FOOT POSITION IN *Sphyrapicus varius* AND *Picoides arcticus*
(Length[1] from most anterior toe to tip of tail as
percentage of distance from crown to tip of tail.)

Percentage	Sphyrapicus varius	Picoides arcticus
85–86	*	
83–84	*	
81–82	*	*
79–80		**
77–78	*	
75–76	**	*
73–74	**	*
71–72		
69–70	**	
67–68	*	
65–66		
63–64		*
61–62	*	
59–60		**

[1] Measured from tracings of birds in their "delivery stances."

seen, the main displacement of the heels and tarsi toward the trunk does not occur until after impact.

BLACK-BACKED THREE-TOED WOODPECKER

In contrast to *S. varius*, *P. arcticus* assumes a pecking posture in which the body is suspended significantly farther from the trunk. Calculations from ten stance tracings of *S. varius* and eight of *P. arcticus* reveal that the abdominal surface anterior to the tarsus is on the average over three times farther from the trunk in *P. arcticus* (table 2). Correspondingly, *P. arcticus'* center of gravity should lie more outward in relation to foot position.

Picoides arcticus delivers its blow by a combination of movements superimposed on one another. X-ray tracings (fig. 3) reveal that the curve of the neck just posterior to the foramen magnum is not straightened to the extent seen in *S. varius;* in fact, it may not straighten at all. Rather, the principle momentum is developed by the body. The thoracic portion of the back usually dorsiflexes prior to delivery and straightens during the inward movement. Also, the entire body is pitched forward as the pelvis rotates about the immobile femoral heads.

Figure 5 shows a detailed pecking sequence for *P. arcticus*. In assuming the "delivery stance" (the stance in the last frame before the bird begins its inward movement), the heels of the feet as well as the tarsi are displaced (levated) outward so that only the toenail tips are in contact with the trunk. Simultaneously, the back is arched. Both actions are reflected in a slight outward and downward tilting of the cranium. Figure 5 shows that as in *S. varius*, the tarsi and heels are not moved appreciably inward until the bill has contacted the trunk.

While the actions thus far described are characteristic in the delivery of hard blows, two actions are shown (fig. 5) which occur irregularly. The first (fig. 5, no. 5) is the slippage of one of the feet during blow delivery. This was not observed in
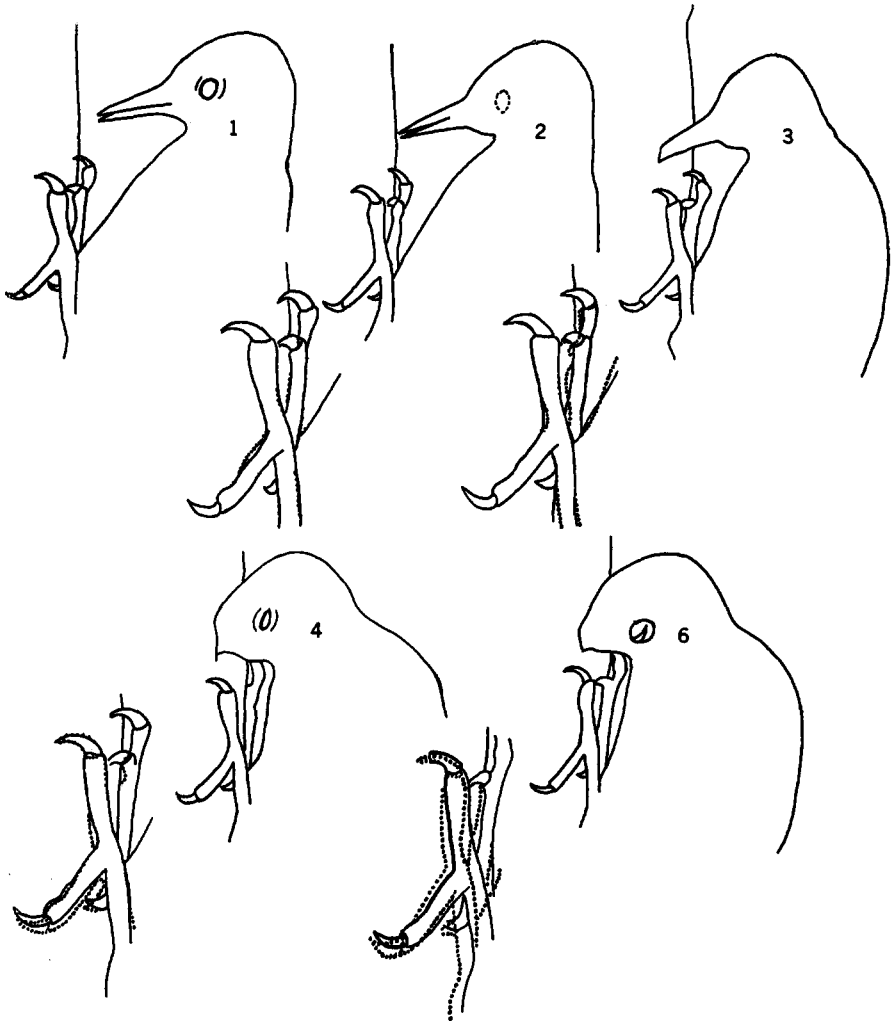
Fig. 4. Pecking sequence in *Sphyrapicus varius*. Successive tracings of tarsus and foot superimposed. Numbers denote frames in sequence (fifth frame omitted).

either *S. varius* or *D. villosus* and is probably accidental, being due to the precarious purchase of *P. arcticus* on the tips of its toenails. The second action, which occurs infrequently in all three species, is observed well after the initial impact. It consists of the tail leaving the vertical surface and staying suspended for several frames (up to 12 in one instance). The action appears to accompany a forceful inward push of the body on the point of bill contact.

HAIRY WOODPECKER

Film footage on *Dendrocopos villosus* was limited and no X-ray films were available. Also, there were few sequences in which the whole of the bird's body was clearly in profile. Consequently, the description of its pecking action is made with reservations.

TABLE 2

DISTANCE BETWEEN ABDOMEN AND TRUNK

(Shortest distance[1] between abdomen and trunk, anterior to point where leg meets ventral body line, expressed as a percentage of distance from crown to tip of tail.)

Sphyrapicus varius		Picoides arcticus	
Case no.	Per cent	Case no.	Per cent
1	0	1	3.6
2	0	2	4.8
3	0	3	6.3
4	1.5	4	6.7
5	1.6	5	7.2
6	2.0	6	7.7
7	2.1	7	9.5
8	3.1	8	10.2
9	3.7		
10	4.0	Mean	7.0
Mean	1.8		

[1] Measured from tracings of birds in their "delivery stances."

Prior to blow delivery, the abdomen lies close to the trunk in much the same position as in *S. varius*. However, the dorsal line of the back is generally farther from the trunk with the tail contacting it at an angle similar to that seen in *P. arcticus*.

As shown in figure 2, the body may contribute to momentum. However, in some blows the momentum appears to be mainly caused by neck action. Arching of the back was difficult to discern prior to blow delivery; I suspect that it could have been seen if good profile shots had been available. Probably *D. villosus* can deliver blows by essentially the same means employed by *P. arcticus* although back flexion and inward rotation of the body about the femoral heads is less pronounced.

In the details of its pecking sequence, *D. villosus* is similar to *S. varius*. The heels and tarsi are not appreciably displaced prior to blow delivery and, correspondingly, little or no noticeable inward displacement is observed at or after the time of bill contact.

SIGNIFICANCE OF FUNCTIONAL TRAITS CONCERNED IN BLOW DELIVERY

Film analysis and observation show clearly that there are significant differences in the maximum impacts delivered by *Sphyrapicus varius*, *Dendrocopos villosus*, and *Picoides arcticus*. In this functional series, increasing impact force is achieved by the superimposition of lower body movements upon neck action.

Since the force developed by a moving body is proportional to the product of its mass and acceleration, selection for harder blows might be expected to favor those means of delivery employing the larger mass. However, this would also depend upon the simultaneous development of sufficient means for the acceleration of that mass. *Picoides arcticus* and *Dendrocopos villosus* (probably to a lesser extent) have met this situation primarily in two ways. A delivery stance is employed which allows a longer distance for the development of acceleration and the means of delivery involving the less massive head and neck has been de-emphasized—thus increasing the distance available for acceleration of the more massive posterior regions.
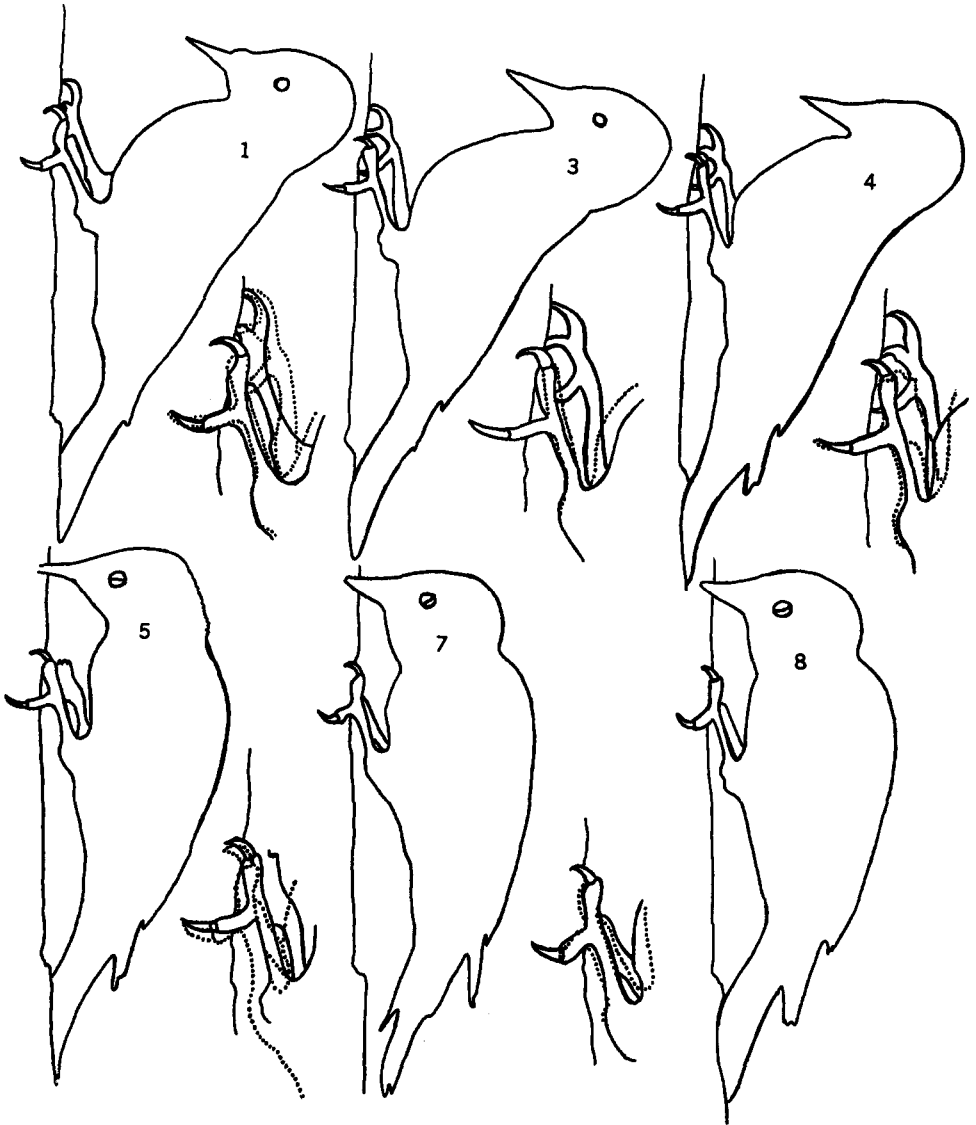
Fig. 5. Pecking sequence in *Picoides arcticus*. Successive tracings of tarsus and foot super-imposed.

In all three species, the tarsi and heels are inwardly displaced (depressed) at the conclusion rather than during blow delivery, although such displacements are more infrequent and less highly developed in *S. varius and D. villosus*. It is not known what part the femur and tibiotarsus may play. Probably the late timing of the action represents a relaxation that is possible only when the bill has made contact with the trunk. During the inward movement, outward pull on the feet would tend to keep the heels elevated so depression could occur only when the body had completed its inward movement.

As noted above, both straightening of back and rocking on the femoral heads are effectively superimposed to achieve maximum acceleration. The rocking motion in both *P. arcticus* and *D. villosus* is probably achieved in part through the contraction of the M. sartorius and the anterior portion of what Burt terms the M. gluteus primus (anterior extensor iliotibialis). The sartorius originates from the neural crests of the three vertebrae just anterior to the synsacrum and from the anterior lateral border of the ilium and inserts on the cnemial crest of the tibiotarsus (Burt, 1930:498). The anterior extensor iliotibialis originates from the anterior iliac crest and dorsal surface of the antitrochanter and inserts on the superior border of the cnemial crest (Burt, 1930:499). For these muscles to be effective in such an action would require that the tibiotarsus be fixed by other appendicular muscles.

The closure of the eyelids observed in all three species is doubtless an adaptation for protecting the eyes against the dust and flying wood chips which may accompany impacts. The few exceptions appeared during lightly delivered blows and even then the eyelids were drawn partly over the corneas.

ANATOMICAL MODIFICATIONS FOR BLOW DELIVERY

Schranke (1930) and Stolpe (1932) were the first to point out that posteriorly directed toes are functionally insignificant in woodpeckers climbing on vertical surfaces. Figure 1c illustrates the gravitational forces acting in such a situation. The longer gravitational component passes from the center of gravity through the rectrices to their point of trunk contact. The shorter component is directed at right angles to the first and represents the force tending to pull the bird outward. While the first component is effectively countered by anteriorly directed toes and minimal slippage of the tail, the second is countered by laterally directed toes oriented nearly at right angles to the trunk. The toe positions noted earlier for *S. varius, D. villosus,* and *P. arcticus* conform to a configuration that can effectively counteract these gravitational forces.

Bock (*in* Bock and Miller, 1959) has been the most recent to argue that the zygodactylous condition of ground woodpeckers (toes 2 and 3 directed anteriorly and toes 1 and 4 directed posteriorly) is basically a perching arrangement. A true scansorial foot is seen in the genera *Sphyrapicus, Dendrocopos, Picoides* in which the fourth toe can be rotated to a lateral position when on the tree trunk. In addition, the permanently posteriorly directed hallux is either reduced or lost. When present, as in *Sphyrapicus* and *Dendrocopos,* it can act on horizontal surfaces with toe 4 to oppose toes 2 and 3, thus providing a temporary perching arrangement.

In *P. arcticus,* the prominent inward and outward movements of the heel have been noted above. If the first toe were present, even in a reduced form, it is likely that it would impede heel movement. The loss of the hallux is probably one of *Picoides'* modifications for delivering maximum impact force.

Ratios calculated from measurements of limb segments include intramembral, functional, and limb-trunk. Intramembral ratios express the length of the tibiotarsus and tarsometatarsus as a percentage of femoral length; functional ratios express the length of each leg bone as a percentage of total leg length; limb-trunk ratios express separate leg bone lengths and total leg lengths as a percentage of an axial skeleton measurement (in this case, the dorsal median length of the four thoracic vertebrae just anterior to the synsacrum). The value of the limb-trunk ratio depends upon the assumption that in closely related birds, fixed distances along the dorsal skeleton are the least likely to vary adaptively from species to species and that limb segment dif-

TABLE 3

INTRAMEMBRAL RATIO

Species	No.	Tibiotarsus/Femur	Average deviation	Tarsometatarsus/Femur	Average deviation
Colaptes cafer	6	141.4	2.2	95.1	1.3
Asyndesmus lewis	7	151.5	1.4	98.1	1.2
Melanerpes erythrocephalus	10	148.8	2.0	97.3	1.3
Melanerpes formicivora	4	155.8	1.9	99.3	1.0
Centurus carolinus	12	144.9	1.2	94.4	1.3
Dryocopus pileatus	5	133.2	1.2	89.1	1.5
Sphyrapicus varius	13	151.6	1.6	105.5	2.2
Dendrocopos pubescens	7	152.1	0.8	101.0	0.5
Dendrocopos villosus	4	144.5	1.5	99.2	1.8
Picoides arcticus	5	136.8	1.7	96.5	1.5
Picoides tridactylus	4	137.7	1.7	94.9	1.1

ferences are likely to reflect absolute changes in skeletal proportions. Engels (1940) has discussed in detail various methods of handling such data. Because the samples were small, the significances of the differences between species were found by calculating the value for t as given in the formula in Simpson, Roe, and Lewontin (1960) and then reading the P value for each t from an appropriate table. The value of P was taken into consideration in the interpretation of the ratios.

When results from the three ratios are compared (tables 3, 4, and 5), certain trends are evident in the series consisting of *S. varius*, *D. villosus*, and *P. arcticus*. The femur undergoes no significant change in relative length from species to species. The tibiotarsus decreases significantly from *S. varius* to *D. villosus*. It also decreases from *D. villosus* to *P. arcticus* but to a lesser extent. The tarsometatarsus decreases significantly from *S. varius* to *D. villosus* but is approximately the same relative length in *D. villosus* and *P. arcticus*.

Engels (1940) noted a similar trend in comparing different species of the thrasher genus *Toxostoma*. In the longer-billed, more vigorous earth diggers, he found that the femur was relatively longer while the tibiotarsus and tarsometatarsus were relatively

TABLE 4

FUNCTIONAL RATIOS

Species	No.	Femur/TLL*	Average deviation	Tibiotarsus/TLL*	Average deviation	Tarsometatarsus/TLL*	Average deviation
Colaptes cafer	6	29.7	0.4	42.0	0.3	28.3	0.2
Asyndesmus lewis	7	28.6	0.1	43.3	0.2	28.1	0.2
Melanerpes erythrocephalus	10	28.9	0.2	43.0	0.3	28.1	0.2
Melanerpes formicivora	4	28.2	0.2	43.9	0.3	28.0	0.1
Centurus carolinus	12	29.5	0.2	42.7	0.2	27.8	0.3
Dryocopus pileatus	5	31.0	0.2	41.3	0.1	27.6	0.2
Sphyrapicus varius	13	28.0	0.3	42.5	0.2	29.5	0.3
Dendrocopos pubescens	7	28.3	0.2	43.1	0.2	28.6	0.2
Dendrocopos villosus	4	29.1	0.3	42.0	0.1	28.9	0.2
Picoides arcticus	5	30.0	0.3	41.0	0.3	29.0	0.2
Picoides tridactylus	4	30.1	0.0	41.4	0.2	28.6	0.2

*TLL = "Total Leg Length."

TABLE 5

LIMB-TRUNK RATIOS

Species	No.	Femur/4 Thoracic vertebrae	Average deviation	Tibiotarsus/4 Thoracic vertebrae	Average deviation
Colaptes cafer	6	183.0	3.3	258.9	8.1
Asyndesmus lewis	4	151.4	2.2	228.8	2.5
Melanerpes erythrocephalus	5	159.1	8.2	236.7	15.8
Melanerpes formicivora	2	158.2	1.2	249.0	1.0
Centurus carolinus	9	156.5	3.4	226.5	5.8
Dryocopus pileatus	4	167.7	2.7	222.7	4.2
Sphyrapicus varius	6	162.0	2.9	244.0	3.6
Dendrocopos pubescens	6	168.3	1.7	255.2	2.3
Dendrocopos villosus	3	160.3	3.6	231.1	3.5
Picoides arcticus	3	163.7	3.0	223.5	1.7
Picoides tridactylus	3	168.8	1.6	232.7	3.3

Species	No.	Tarsometatarsus/4 Thoracic vertebrae	Average deviation	"Total Leg Length"/4 Thoracic vertebrae	Average deviation
Colaptes cafer	6	174.0	5.2	615.9	16.3
Asyndesmus lewis	4	148.1	3.4	528.3	8.0
Melanerpes erythrocephalus	5	154.1	10.1	549.9	34.3
Melanerpes formicivora	2	157.2	0.5	564.4	0.4
Centurus carolinus	9	147.4	3.7	530.4	12.7
Dryocopus pileatus	4	148.8	3.6	539.2	10.0
Sphyrapicus varius	6	170.6	1.4	576.6	7.9
Dendrocopos pubescens	6	169.6	1.8	593.1	4.1
Dendrocopos villosus	3	158.1	1.7	549.5	7.9
Picoides arcticus	3	157.6	0.4	544.8	4.3
Picoides tridactylus	3	159.6	0.8	561.1	5.8

shorter. He suggested that the differences might be correlated with the more vigorous digging habits of the longer-billed forms.

The data thus presented suggest the probability that shortening of the distal leg bones is a modification for the delivery of harder blows. The exact advantage to blow delivery of a shortened tibiotarsus and tarsometatarsus is unclear. Possibly several factors are involved. The probability that certain muscles attaching to the anterior, proximal end of the tibiotarsus contribute to rocking the body has been noted. Generally, shortening of bones increases the effective power of muscles inserting on them while proportionally decreasing the speed of their action. Shortening of leg bones is one way in which the efficiency of fixation of the distal leg bones could be increased while the bird is pulling its body toward the tree.

Another modification is seen in the thoracic neural spines. Figure 6 illustrates the differences between *S. varius* and *P. arcticus*. The neural spines are relatively longer and more widely separated in *P. arcticus*. There is no consistent difference between *D. villosus* and *P. arcticus*. The increased length and spatial separation of the neural spines is probably a reflection of the degree of back flexion. Increased spine length may be indicative of increased muscular attachment on these processes. However, increased spatial separation is almost certainly a modification that prevents adjacent spines from contacting one another during back flexion. No comparable differences in neural spines are evident among the ground woodpeckers of Burt's series. All are
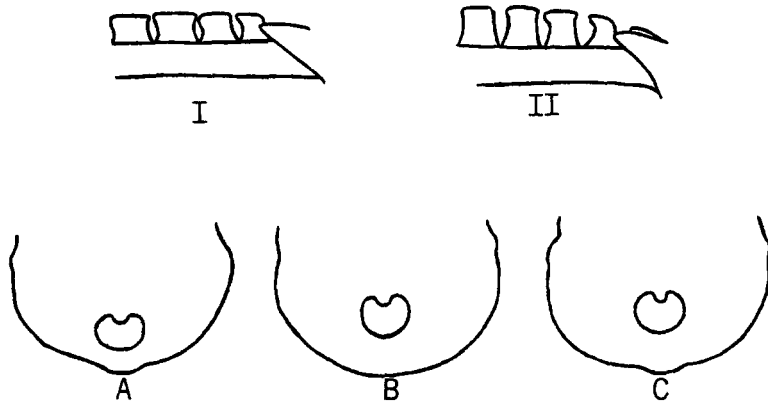
Fig. 6. Posterior thoracic vertebrae of *Sphyrapicus varius* (I) and *Picoides arcticus* (II). Ventral views of foramen magnums of *Sphyrapicus varius* (A), *Dendrocopos villosus* (B), and *Picoides arcticus* (C).

similar to *S. varius* and probably do not employ back flexion in their pecking actions.

Another apparent difference in the series is the position of the foramen magnum (fig. 6). In comparison to *S. varius,* the foramens of *D. villosus* and *P. arcticus* are more anterior to the occiput. (There is little or no difference between *D. villosus* and *P. arcticus.*) The position of the foramen magnum in *S. varius* corresponds to that in all the ground woodpeckers examined. A more anterior foramen magnum in those species delivering harder blows would increase the distance through which the tip of the bill would move to contact the tree. Conversely, having the foramen magnum close to the occiput should increase the reach of the bird so that less neck straightening would be required in picking up exposed food.

CLIMBING

Figures 7 and 8 trace the climbing cycles of *S. varius* and *P. arcticus.* Both species pull the body toward the trunk early in the upward lift. While *S. varius* pulls its body close to the trunk during upward progression, *P. arcticus* does not and progresses upward with its breast and abdomen well away from the trunk. While *S. varius* generally keeps the tail in contact with the trunk throughout the climbing motion, that of *P. arcticus* is usually flipped outward in the latter part of the movement when the feet extend upward to a new purchase.

All film footage of climbing movements was checked to estimate the frequency of the different tail actions, which were classified as follows: (1) tail in continuous or almost continuous contact with the trunk, and (2) tail not in continuous contact, tail leaves trunk in later part of climbing cycle. For 30 climbing movements in each species, the tail stayed in continuous or almost continuous contact with the trunk 93 per cent of the time in *S. varius* and 13 per cent of the time in *P. arcticus.* The tail left the trunk in the later part of the climbing cycle 7 per cent of the time in *S. varius* and 87 per cent of the time in *P. arcticus.* Only four climbing movements were observed in *D. villosus* and these were assigned to the type in which the tail leaves the trunk in the later part of the climbing cycle, although I feel only one of the outward tail flippings was of the magnitude characteristic of *P. arcticus.*

Inward hitching of the body early in the climbing movement is probably charac-

Fig. 7.   Climbing in *Sphyrapicus varius*. Numbers denote frames in sequence.

teristic of most birds which progress straight upward on vertical surfaces. In woodpeckers, this action obviously decreases that component of gravity tending to pull the bird off the trunk. If the bird is able to maintain or even accentuate this position until the feet are extended upward, there will be a minimal tendency to fall outward while the feet are moving to their new purchase point. *Picoides arcticus* must flip its tail outward to compensate for the tendency to fall backward before the feet achieve contact.

The ability to deliver hard blows thus appears to be inversely correlated with the "smoothness" of climbing. This is not to say that *P. arcticus* is unable to climb straight upward but that it does so with less grace and a greater expenditure of energy than does *S. varius*. *Sphyrapicus varius* climbs more efficiently but is able to deliver only light blows. Hence, the arrangement of muscles, tendons, and bones associated with an outward purchase, maximum body rocking, and pronounced heel displacements before and after blow delivery is an arrangement which appears to be poorly adapted for pulling the body inward and maintaining it close to the trunk during upward progression. Possibly, the trend in shortening of the tibiotarsus and tarsometatarsus is associated with poorer climbing ability.

Fig. 8. Climbing in *Picoides arcticus*. Numbers denote frames in sequence.

Limited film footage of pecking and climbing was obtained for *Dendrocopos pubescens*. The blows were delivered in much the same manner as was suggested for *Dendrocopos villosus* (fig. 9). The thoracic portion of the back was often arched prior to blow delivery with the inward movement involving both straightening of back and a forward rocking on the femoral heads. Some of the blows appeared to consist mainly of neck action. The eyelids were closed during delivery and a slight inward movement of the foot and tarsus was sometimes apparent at the moment of impact. However, in contrast to the other species, *D. pubescens* maintained a relatively constant foot purchase with the contact point high on the trunk. Consequently, the tarsus was usually parallel and often in contact with the vertical surface. In the three climbing cycles available, the tail left the trunk in the later part of the cycle.

The leg bones of *D. pubescens* and *P. tridactylus* were measured and the results expressed in terms of intramembral, functional, and limb-trunk ratios (tables 3, 4, and 5). The figures for *D. villosus* and *D. pubescens* suggest that the leg is relatively longer in *D. pubescens* and that the increased length involves significant increases in all three leg bones. The leg of *D. pubescens* is approximately 8 per cent longer than that of *D. villosus* and 3 per cent longer than that of *S. varius*.

The above differences between *D. villosus* and *D. pubescens* are probably related to the more anterior foot position of the latter. Possibly, longer legs allow *D. pubescens* more easily to extend the feet to encircle small limbs or trunks and obtain a

Fig. 9. "Delivery stance" (solid line) and stance three frames later (broken line) for *Dendrocopos pubescens*.

more solid purchase for climbing and blow delivery. A more anterior foot purchase would increase the relative length of each limb extension for *D. pubescens* when it is climbing. As noted earlier, *D. pubescens* forages more on trunk surfaces than does *D. villosus*. If the ratios for *P. arcticus* and *P. tridactylus* are compared, a similar relative lengthening of all leg bones is evident, but the differences are not as great as those between *D. villosus* and *D. pubescens* (also, the P values for ratios comparing the two species are all less than 0.98). Possibly, the smaller species of *Picoides*, like the smaller species of *Dendrocopos*, feeds on smaller limbs and trunks and is a better climber.

One of the most interesting comparisons of ratios is that between *D. pubescens* and *P. tridactylus*. The femur is the same relative length in both species but the two lower leg bones are significantly shorter in *P. tridactylus*. Except for shortening in relative tibiotarsal length, these are the same types of differences as those noted above between *P. arcticus* and *D. villosus*.

DISCUSSION OF DELIVERY OF BLOWS AND CLIMBING

It is postulated that *S. varius, D. villosus,* and *P. arcticus* each select and exploit habitats in such a way that maximum energy is obtained for that which is expended in the feeding process. Anatomical adaptations for pecking and climbing can best be interpreted in terms of what the woodpecker does most efficiently and not by what is impossible for it to do. While *P. arcticus* is capable of vertical climbing, it does so clumsily and with a higher expenditure of energy than that necessary for *D. villosus* or *S. varius*.

It is evident that *P. arcticus* possesses a feeding pattern which employs a minimum of vertical climbing and a maximum of stationary feeding on trunks where the primary source of food is wood-boring insects. Where such insects are available in high concentrations, *P. arcticus* should be competitively superior to *D. villosus* which is not as well adapted to deliver hard blows but is a better climber. Thus *P. arcticus* is not a "fugitive species" in the sense proposed by Hutchinson (1951), where one
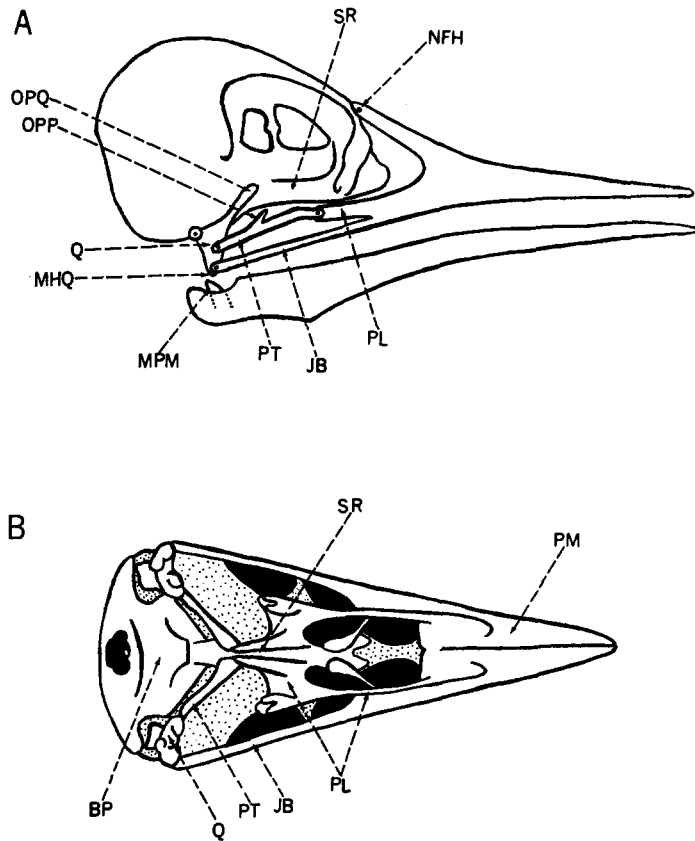
Fig. 10. A. Diagrammatic lateral view of cranial kinetic apparatus (modified from Engels, 1940).

B. Ventral view of *Corvus* skull (from Bock, 1960*b*).

Abbreviations:

BP — Basitemporal plate
JB — Jugal bar
MHQ — Mandibular head of quadrate
MPM — Medial process of mandible
NFH — Nasofrontal hinge
OPP — Orbital process of pterygoid
OPQ — Orbital process of quadrate
PL — Palatine
PM — Premaxilla
PT — Pterygoid
Q — Quadrate
SR — Sphenoidal rostrum

of two similar species is competitively superior and the inferior or fugitive species must rely upon more effective means of dispersal to occupy newly arisen habitats where food is temporarily in superabundance.

Each species appears to exploit its environment in such a manner that its niche is largely separate from those of the other two species. Each niche can be described in

terms of behavioral, habitational, and energetic factors. All these factors are inter-related and attempts to describe the niches in terms of any one particular set of factors only partly describes the true situation.

Anatomical and functional changes associated with decreasing climbing ability in the series consisting of *S. varius, D. villosus,* and *P. arcticus* are at least partly different from those associated with the suggested decrease in climbing ability between *D. pubescens* and *D. villosus* and between *P. tridactylus* and *P. arcticus.* The fact that climbing ability is inversely correlated with the ability to deliver harder blows is clearly apparent in *S. varius, D. villosus,* and *P. arcticus.* But on the basis of present data, a difference in blow delivery cannot be proposed between *D. pubescens* and *D. villosus,* or between *P. tridactylus* and *P. arcticus.*

In the "more arboreal" species of woodpeckers studied, correlations are evident between the method by which a particular species clings to the tree and its particular feeding method. The more open the delivery stance and the farther the bird from the trunk, the more the posterior region of the body is used in the development of blow momentum. Another interesting stance was noted by Bock (Bock and Miller, 1959: 22–23) in the Ivory-billed Woodpecker (*Campephilus principalis*) in which the feet are directed diagonally upward and sidewise so that the long axis of the lower leg forms approximately a 45° angle with the horizontal plane. On the basis of photographs, Bock thought that the tarsus was pressed against the tree trunk.

Allen and Kellogg (1937), Tanner (1942), and Dennis (1948) have referred to the bark-scaling habits of ivory-bills. Allen and Kellogg report that the birds which they watched in Louisiana spent more time knocking off bark and looking for what was beneath it than in drilling deeply for wood-boring insects.

The stance employed by *Campephilus* is most advantageous for peeling bark. With the feet spread far apart in an anterior position, the widest possible base and greatest stability is provided for the delivery of sidewise blows. What effect this stance has on climbing ability is not clear. While Bock argues that the stance is very efficient for clinging and climbing, I have some doubts as to the advantage in vertical climbing. To advance vertically the leg muscles of the Ivory-billed Woodpecker must shorten in a direction which is not parallel to the line of progression.

MECHANICS OF CRANIAL KINESIS

Cranial kinesis, a mechanism which permits the upper bill to move independently with respect to the brain case, is generally recognized as characteristic of most living birds. While Moller (1931) gives a detailed account of its mechanism, Beecher's (1962) and Bock's (1964) discussions are probably the best in the English language. Muscular forces acting on bones which connect either directly or by intermediate bones to the premaxillae produce upward and downward movements of the tip of the upper bill (figs. 10 and 11). These actions are facilitated by a dorsally situated nasofrontal hinge and by two ventral bony linkages connecting the premaxillae to the quadrates. Upward (protraction) and downward (retraction) movements of the bill about the nasofrontal hinge are coordinated with rocking of the quadrates on their cranial articulations.

Some muscles act directly on the quadrates and effect upper bill movements; other muscles attach more anteriorly on the pterygoids and palatines which form one of the connecting links between the premaxillae and quadrates. The palatine, which is fused anteriorly to the premaxilla, and the pterygoid, which articulates posteriorly with the quadrate, meet along the sphenoidal rostrum. At their point of union, they
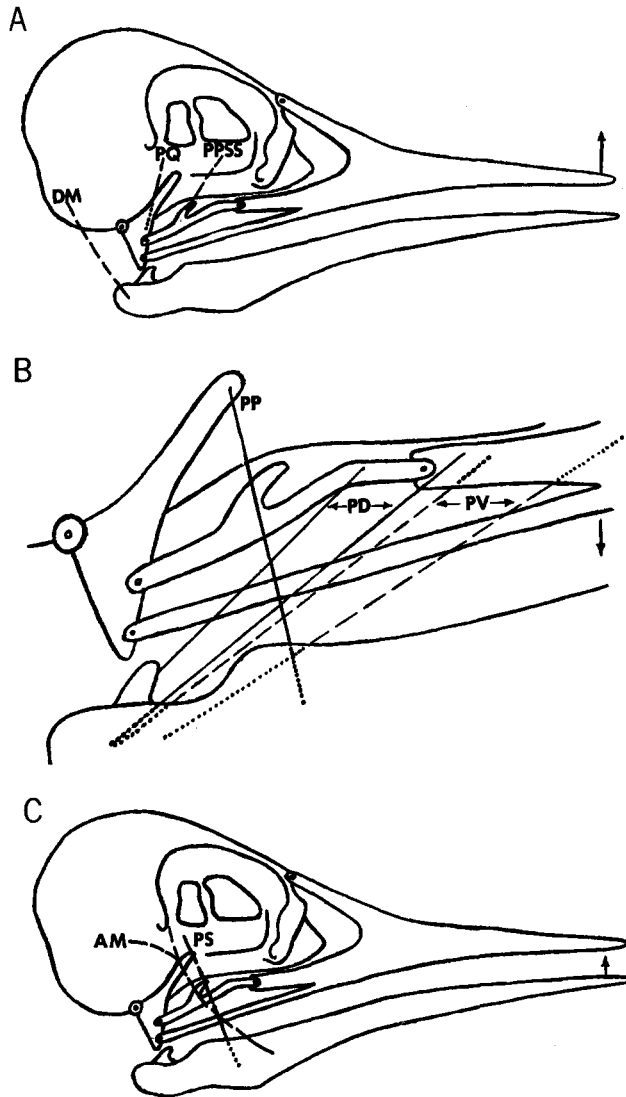
Fig. 11. Diagrammatic scheme showing major courses of cranial kinetic muscles.

    A. Protractors of upper bill:
         DM   — M. depressor mandibulae
         PPSS   — M. protractor pterygoidei (*sensu stricto*)
         PQ   — M. protractor quadrati
    B. Primary retractors of upper bill; also elevate mandible:
         PP   — M. pseudotemporalis profundus
         PD   — M. pterygoideus dorsalis
         PV   — M. pterygoideus ventralis
    C. Primary elevators of mandible; also retract upper bill:
         AM   — M. adductor mandibulae
         PS   — M. pseudotemporalis superficialis

form a flattened plate which slides along the rostrum—anteriorly during bill protraction and posteriorly during retraction. The other linkage between the premaxillae and quadrates is via the laterally situated jugal bars. The bones forming this linkage are thin and, in freshly killed birds, the bar is usually rather flexible.

The general orientations of the muscles responsible for protraction and retraction of the upper bill, and elevation and depression of the mandible are shown in figure 11. Most of these muscles are capable of causing two actions either simultaneously or at different times in their contraction. For instance, the M. depressor mandibulae by pushing the mandibular head of the quadrate forward can protract the upper bill while simultaneously depressing the mandible. The major protractor of the upper bill, the M. protractor pterygoidei, can be divided into two portions. The more rostral part—the M. protractor pterygoidei, sensu stricto (Lakjer, 1926)—inserts on the orbital process of the pterygoid. The more caudal M. protractor quadrati inserts on the medial face of the quadrate.

The primary retractors are the M. pseudotemporalis profundus, M. pterygoideus dorsalis, and M. pterygoideus ventralis, all of which also effect mandibular elevation. The M. pseudotemporalis superficialis and M. adductor mandibulae primarily elevate the mandible but can cause upper bill retraction—the adductor mandibulae via slips inserting on the body of the quadrate and both muscles by producing posteriorly directed pressure on the mandibular head of the quadrate.

SKULLS OF THE PICIDAE

The skulls of the species investigated show a number of modifications which are correlated with the pecking habit. Figure 12 compares the skull of the Brewer Blackbird (*Euphagus cyanocephalus*), an omnivorous passerine, with that of *Dendrocopos villosus*. In woodpeckers the interorbital septum is well ossified and if a fenestra is present, it is generally smaller than in other birds; the union of the pterygoids and palatines is located posteriorly on the sphenoidal rostrum and lies close to the basitemporal plate, suggesting that retraction is limited in this region; the basitemporal plate is relatively expansive; the pterygoids bear well-developed orbital processes; the opisthotic process of the quadrate articulates very solidly with the cranium, and the body of the quadrate does not project as far below the brain case as in most other birds; except for *Colaptes,* the orbital process of the quadrate is elongated, suggesting an emphasis upon power rather than speed during retraction of the upper bill.

Median sagittal sections were made of the skulls of several species including those of *Sphyrapicus varius, Dendrocopos villosus,* and *Picoides tridactylus* (fig. 13). Burt (1930) previously pointed out the bulging of the frontal bones over the base of the upper bill which occurs in these genera. The bulge is best developed in *Sphyrapicus varius* and *Dendrocopos villosus.* It is primarily an empty space with scattered bony struts. In *Sphyrapicus varius* and *Dendrocopos villosus,* the struts are more concentrated in the median line and form a perforated bony plate. Ventral to the base of the bill is a network of sagittally oriented interconnected struts that pass posteriorly between the twin plates of the interorbital septum. Thus, the medial portion of the upper bill posterior to the nasofrontal hinge is reinforced by a meshwork of bony struts. Inward pressure in this region is countered directly by the ventral struts and by the dorsal plate distributing the force as tension to the anterior wall of the frontal bulge.

Burt (1930) indicated a number of cranial trends in his functional-anatomical series, some of them largely subjective, others based upon ratios calculated from skel-
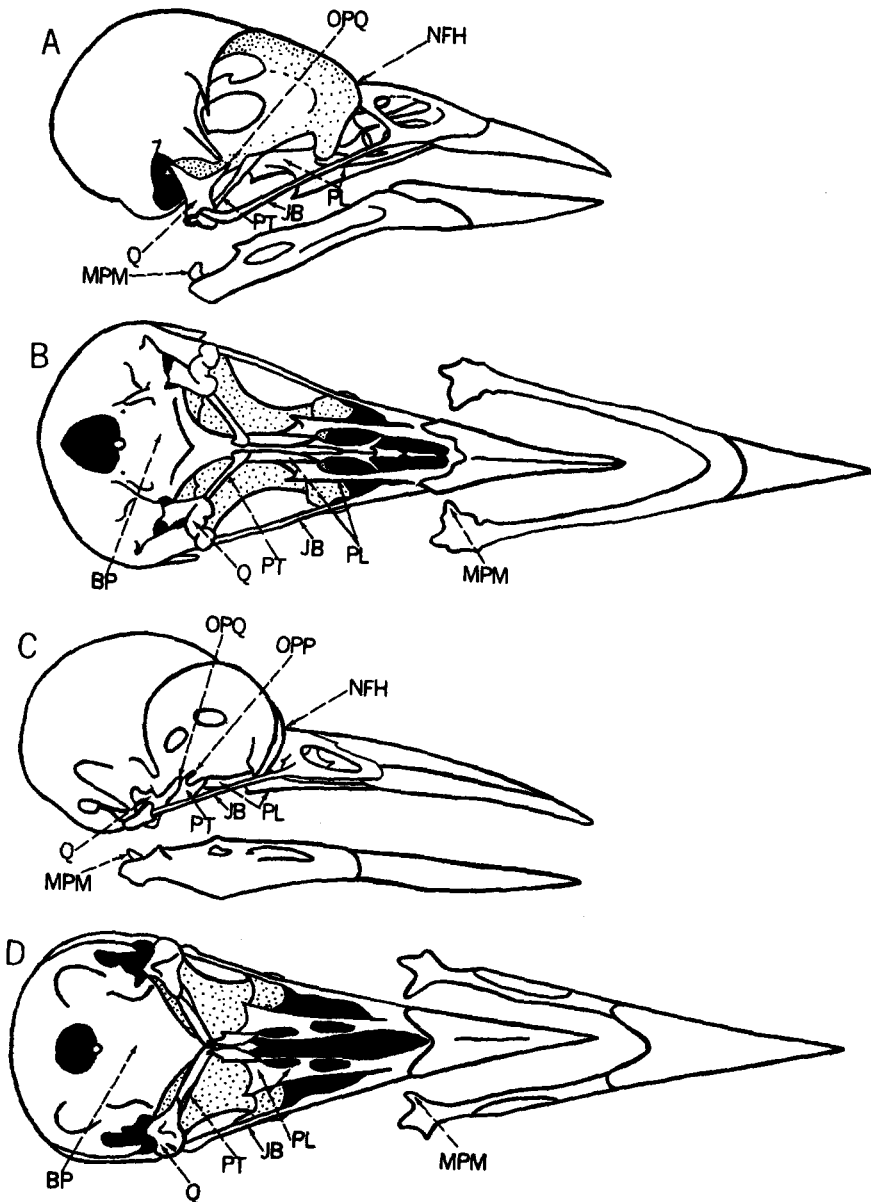
Fig. 12. Skulls of *Euphagus cyanocephalus* (A and B) and *Dendrocopos villosus* (C and D). Lateral and ventral views. Abbreviations the same as in figure 11.

etal measurements. His cranial measurements were expressed as a percentage of the tibiotarsal length. Since it is evident that the tibiotarsus undergoes significant changes in relative length and that the femur is more constant, femoral length should serve as a better standard of comparison. Recalculation of Burt's data based on femoral length showed that although the quantitative differences between species were
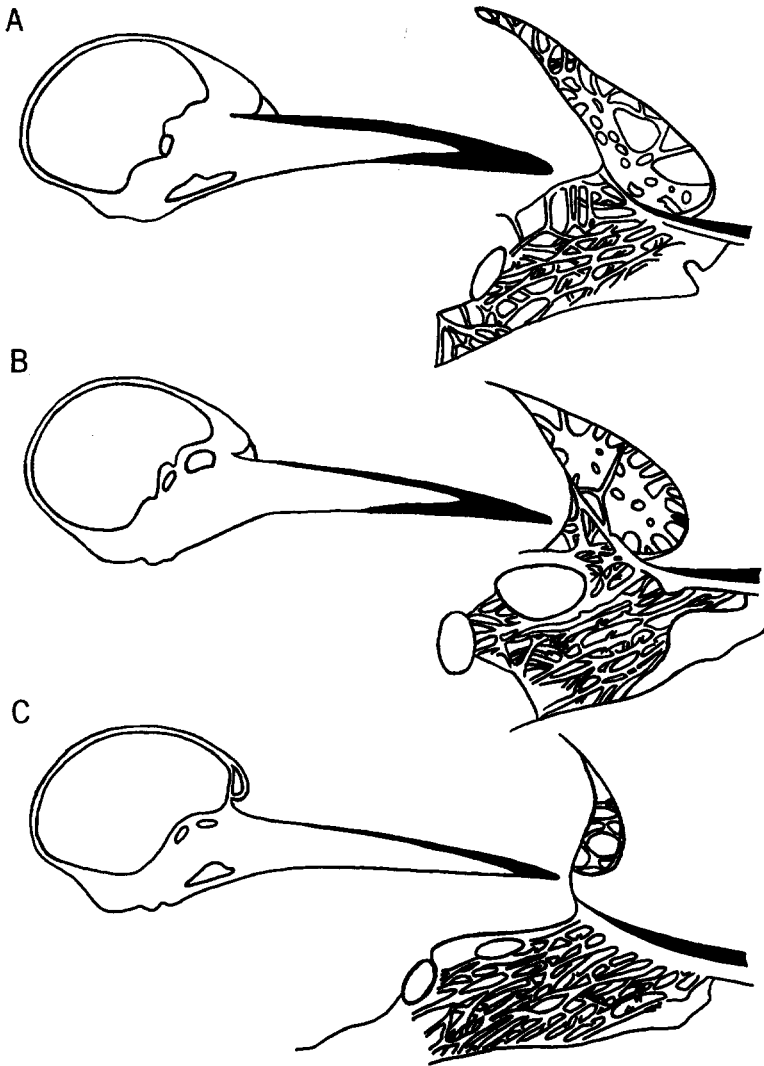
Fig. 13. Median sagittal sections of *Sphyrapicus varius* (A), *Dendrocopos villosus* (B), and *Picoides tridactylus* (C). Details of frontal region at right. The rhamphotheca is shown in black.

changed, the general trends remained the same. The cranium becomes relatively wider, the interorbital septum relatively thicker, the relative width of the maxillae increases, and the relative length of the mandibular symphysis increases.

CRANIAL KINETIC BUFFERING MECHANISMS

Burt (1930) asserted that the skulls of woodpeckers were akinetic. However, Beecher (1953) has shown that woodpecker skulls are kinetic and proposed that their characteristic cranial kinetic musculature is involved in a shock-absorbing mechanism. He writes (p. 294): "The Picidae have a good expression of both palatine retractors
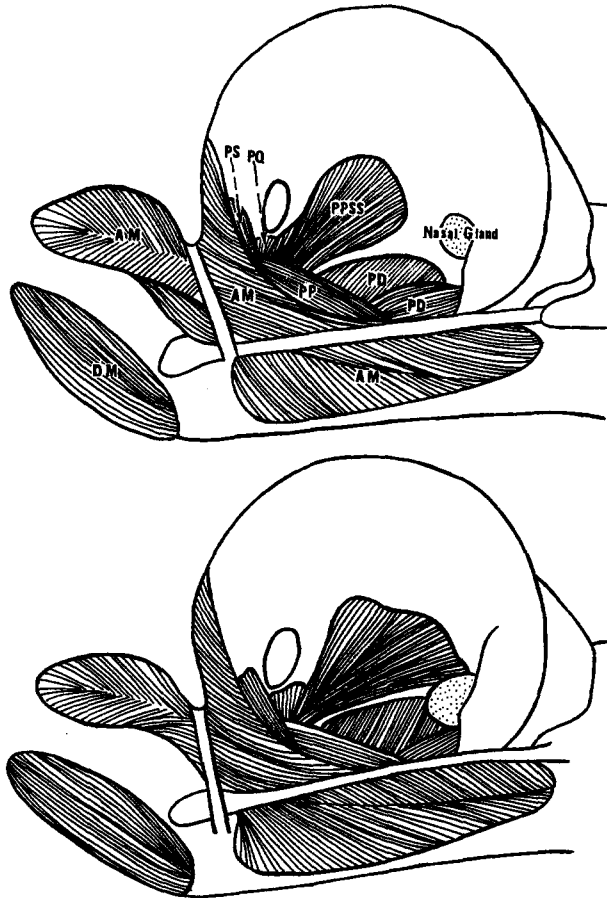
Fig. 14. Cranial kinetic muscles in *Melanerpes erythrocephalus* (above) and, *Centurus carolinus* (below). Abbreviations the same as in figure 12.

and adductors but are outstanding for the extreme emphasis on the protractors of the mandibles, M. depressor mandibulae and M. protractor quadrati. This is especially so in the latter, which originates over most of the area of the interorbital septum. . . . This arrangement, which is met in the piculets as well as in the more highly-adapted woodpeckers, is also found among passerines in the nuthatch, *Sitta*. Its effectiveness in prying is evident and it is seen (with the M. protractor quadrati less well expressed) in numerous species of prying birds (Beecher, 1950, 1951 *a* and *b*); but in woodpeckers it probably serves as part of an interesting shock-absorbing mechanism."

Elaborating on the shock-absorbing mechanism (p. 295) Beecher states that "in the shock-absorbing mechanism of woodpeckers and nuthatches, the antagonistic action of the enormous M. protractor quadrati against the retraction of the pterygoid musculature probably holds the bill in a state of resilient rigidity as it rains its blows on the tree trunk."

Bock (1964) has proposed a theory very similar to Beecher's but with one main exception. He believes that the entire jaw apparatus is protracted at the moment of
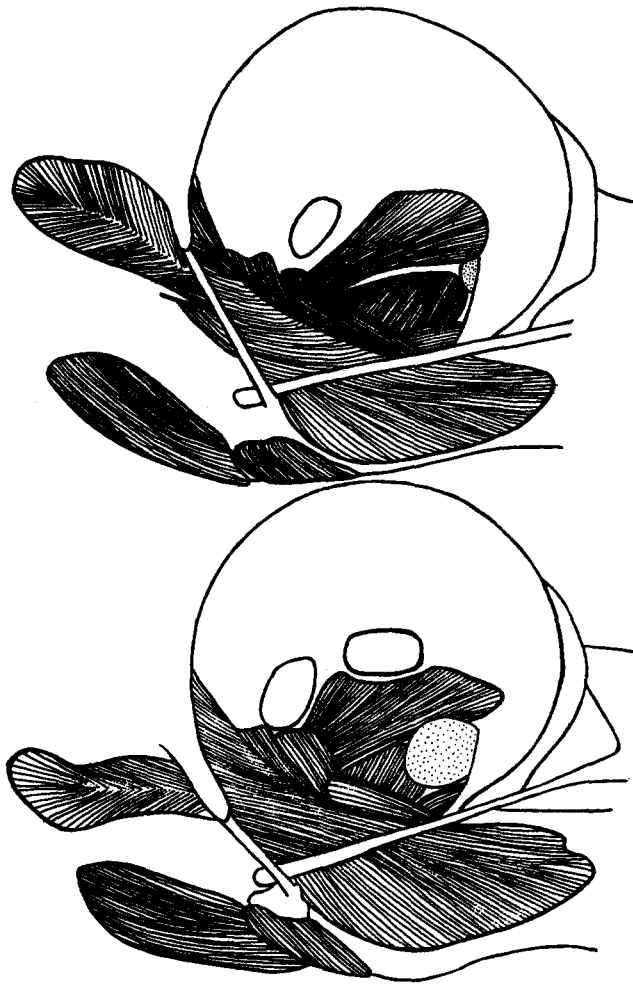
Fig. 15. Cranial kinetic muscles of *Sphyrapicus varius* (above) and *Dendrocopos villosus* (below). Compare with figure 14.

impact. In this position the main protractor is supposed to act as the shock absorber —it being stretched at the moment of impact.

My dissections of the cranial musculature of woodpeckers and nuthatches agree with Beecher's description. The protractor originating on the interorbital septum is massively developed. However, his description would be more accurate if he had been consistent in following Lakjer's (1926) nomenclature. According to my dissections, almost all of what Beecher figures as the "protractor quadrati" in the Red-headed Woodpecker is the protractor pterygoidei (*sensu stricto*). The protractor quadrati portion is largely obscured by overlying muscles. In *Melanerpes,* and in the other species dissected, the protractor pterygoidei (*sensu stricto*) comprised the more massive portion of the protractor pterygoidei (Figs. 14, 15). Obviously, it accounts for the strong development of the orbital process of the pterygoid in all Picidae skulls
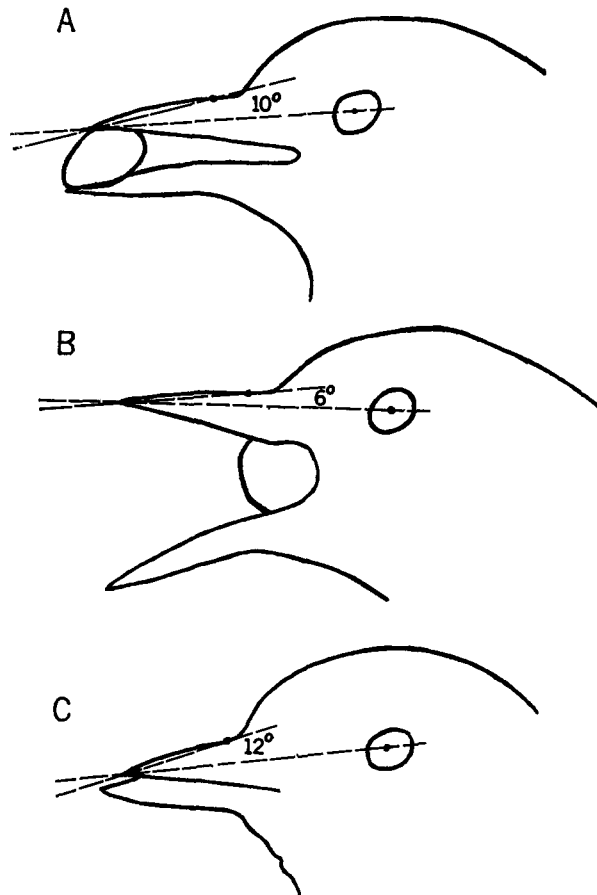
Fig. 16. *Sphyrapicus varius* attempting to swallow a large piece of food. A. Food at tip of bill. B. Food in angle of mouth. C. Just having dropped food. Lines drawn and angles measured to demonstrate that upper bill is actually protracted in swallowing attempt. Three points chosen in drawing lines: tip of upper bill, center of eye, and point on culmen one inch from the tip of upper bill.

examined. Beecher was not the first to note the development of the protractor pterygoidei in woodpeckers. Fiedler (1951) characterized both portions of it as being well developed in *Dendrocopos villosus*.

I believe it is unlikely that the protractor pterygoidei and bill retractors buffer the cranium by holding the bill in a state of "resilient rigidity" as suggested by Beecher (1953, 1962). The term "resilient rigidity" is itself a paradox, because the terms represent opposite conditions. While there are intermediary stages, rigidity is gained only at the expense of resiliency. At a particular moment, an object or mechanism cannot be both resilient and rigid. The most efficient system for the delivery of blows would be one in which all of the energy expended appeared as force upon the trunk and not partly as a stretching of those muscles holding the bill in place. Selection should favor cranial kinetic mechanisms which held the bill as tightly fixed as pos-

TABLE 6

ANGLES OF KINESIS

Species	No. of skulls measured	Readings in degrees	Means
Colaptes cafer	4	17, 24, 25, 25	23
Colaptes auratus	1	24	24
Asyndesmus lewis	4	28, 31, 32, 34	31
Melanerpes erythrocephalus	2	23, 23	23
Melanerpes formicivora	1	21	21
Centurus carolinus	3	20, 25, 26	24
Dryocopos pileatus	6	13, 13, 13, 14, 14, 16	14
Sphyrapicus varius	2	22, 24	23
Dendrocopos villosus	2	22, 24	23
Picoides arcticus	2	15, 18	17
Picoides tridactylus	1	15	15

sible, provided that significant cranial protection was achieved by the same mechanism.

The presence of kinesis in birds in general suggests that in woodpeckers it serves more than just a protective function. Obviously it can be of value in increasing the size of the gape. In *Sphyrapicus varius,* this seems to be true as shown in tracings of an individual attempting to swallow a large chunk of food (fig. 16).

Moller (1931) has suggested that cranial kinesis is a means of preserving the axis of the bill during capture of prey since the upper bill is generally elevated when the mandible is depressed. Actually, the increase in gape that would be provided by such an arrangement might also be of advantage during capture of prey. The higher cranial kinetic readings (table 6) of *Asyndesmus lewis* suggest that greater kinesis is here associated with the capture of flying prey. More than any other woodpecker, *Asyndesmus lewis* is known for its flycatching behavior (Bent, 1939).

Frazzetta (1962), in a study of lizard cranial kinesis, has suggested another feature which may well be applicable to birds: that kinesis would permit the bird to engage its food with both mandibles simultaneously, thus decreasing the risk of food deflection before the mandibles secure a positive grip.

In postulating a cranial kinetic buffering mechanism for woodpeckers, I have considered several factors. As Beecher (1953) has stated, the retractors and protractors are well developed. Of the protractors, the M. protractor pterygoidei is outstanding in its development; a comparable development is seen only in the Sittidae. In woodpeckers, it is the rostral portion of the protractor pterygoidei which is best developed (figs. 14, 15), but in *Dendrocopos villosus* and *Picoides tridactylus* the protractor quadrati is also greatly developed. In addition, cranial kinesis is substantially reduced in *Picoides tridactylus* (table 6). Thus, maximum blow force appears to be correlated with a reduction of kinesis and an increase in the relative size of M. protractor quadrati. Both of these developments are prominent in the Pileated Woodpecker which also delivers very forceful blows.

Laboratory-filmed observations show that woodpeckers hit the trunk with an essentially straight inward blow. At impact, the nasofrontal hinge is above the line of force through the tip of the bill and one might expect much of the force to react as pressure tending to retract the kinetic mechanism.

If the impact force tends to retract the bill, the protractor pterygoidei is the only

muscle in a position to counter the action. By remaining isometrically contracted, it would serve to distribute the reactive force of the impact to its expansive insertion on the interorbital septum while simultaneously holding the bill in its steadiest possible state.

This idea differs from Bock's (1964) proposal that the protractor absorbs the force by being stretched at the moment of impact. As noted above, this means that a part of the energy expended in blow delivery appears as a stretching of muscle rather than impact force upon the trunk. Presumably the more the muscle was stretched, the greater the degree of protection. Probably both transmission of force and stretching of the muscle takes place at impact. But, I feel that force transmission is the much more important of the two events.

It is significant that it is the rostral portion of the protractor pterygoidei which is so tremendously enlarged in all woodpeckers. Inserting on the orbital process of the pterygoid, the protractor pterygoidei (*sensu stricto*) is in a most advantageous position to intercept retractile forces and prevent pressure on the quadrate's cranial articulation. It is not surprising that with increasing impact forces, as seen in *Dendrocopos villosus* and *Picoides tridactylus*, the more caudal portion of the protractor pterygoidei which inserts on the quadrate is more strongly emphasized while the anterior portion continues to retain the expansiveness of *Sphyrapicus varius*. If the force of impact increases without a commensurate increase in the size of the protractor pterygoidei (*sensu stricto*), the bill can be held steady only by increasing the size of the protractor quadrati. With more of the blow's force appearing at the quadrate-cranial articulation, there would be an increased tendency for the cranial kinetic apparatus to undergo retractile movements—a tendency which could be countered only by increasing the size of the protractor quadrati once the upper limit of development for the protractor pterygoidei (*sensu stricto*) had been reached. An increased area of origin would also increase the force distribution potential of the protractor quadrati. The decreased kinesis of *Picoides* is probably an adaptation for even more forceful blows. If both portions of the protractor pterygoidei reach their maximum development, the bill can probably be held rigid only by decreasing the potential range of retractile bill movements so that those bones and ligaments tending to restrict kinesis may be used to steady the bill at the moment of impact.

While pressure on the tip of the upper bill would tend to retract it, pressure on the tip of the lower bill would tend to push the mandible posteriorly creating pressure on its articulation with the quadrate. This pressure would tend to rock the quadrate in a retractile direction—a pressure which could be countered by both portions of the protractor pterygoidei distributing that force as tension on the interorbital septum. Occasionally, one of the woodpeckers in the laboratory would break away the tip of the upper bill leaving the tip of the lower bill protruding forward as much as one-eighth of an inch. Nevertheless, the birds appeared to deliver just as hard blows as when both tips were even.

SUMMARY

Pecking and climbing adaptations of the Yellow-bellied Sapsucker (*Sphyrapicus varius*), Hairy Woodpecker (*Dendrocopos villosus*), Black-backed Three-toed Woodpecker (*Picoides arcticus*), and related forms are described and contrasted on the basis of field and laboratory observations, analysis of high speed motion pictures, dissections of musculature, and osteological measurements, from which several ratios are constructed and compared. Functional modifications for the delivery of hard blows

include: a pecking stance in which the whole body is held far from the tree trunk, a decrease in the contribution of the neck to blow delivery, and the development of blow momentum by the regions of the body posterior to the neck. Anatomical modifications for the delivery of more forceful blows include a shortening in the relative length of the distal leg bones, a heightening and wider spacing of the thoracic neural spines, an anterior shift in the position of the foramen magnum, and the loss of the hallux in *Picoides*. *Dendrocopos pubescens* and *Picoides tridactylus* possess relatively longer legs than the larger members of their respective genera and this probably correlates with greater climbing ability in the smaller species. The ability to deliver forceful blows is inversely correlated with the smoothness and energetic efficiency of climbing. This inverse correlation is reflected in the methods by which the different species exploit their habitats so that maximum energy is obtained for that which is expended.

Some cranial adaptations of woodpeckers are described. Particular attention is given to the cranial kinetic buffering mechanism proposed by Beecher (1953, 1962). Dissections of woodpeckers' cranial kinetic musculature reaffirm the tremendous development of the M. protractor pterygoidei, particularly its rostral portion. Modifications for increasing blow force include increased development of the caudal portion of the M. protractor pterygoidei and a decrease in the angle of cranial kinesis. While these modifications may steady the bill's kinetic mechanism at the moment of impact, the hyperdevelopment of the M. protractor pterygoidei seems important in the distribution of shock as tension on the interorbital septum.

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