VARIATION IN THE POSTERIOR BORDER OF THE STERNUM IN SOME TREE-TRUNK FORAGING BIRDS

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THE posterior border of the avian sternum varies considerably in various taxa but no one to date has been able to offer a convincing correlation between form and function of this complex character. Those correlations of sternal anatomy with functions which have been attempted and which have some credence are summarized by Heimerdinger and Ames (1967), but all are tenuous at best. This paper examines the form and possible function of the posterior border of the sternum in several unrelated groups of birds which are comprised both of forms which forage by creeping up vertical surfaces, and those which forage from the normal perching fashion.

THE STERNUM IN OVENBIRDS AND WOODHEWERS

Woodhewers (Dendrocolaptidae) (tree-trunk foragers) and ovenbirds (Furnariidae) ("normal foragers") are very closely related, and therefore offer the opportunity to discover specific adaptations associated with the tree-trunk foraging habit.

The variation in the notches of the posterior border of the sternum in oscine and suboscine passerine birds has been reported by Heimerdinger and Ames (1967). They examined almost a thousand specimens and divided the sternal types into six categories (see Fig. 1), grading from those with no notches (type 1), to those with four complete notches (type 6). Heimerdinger and Ames (op. cit.) discovered the greatest amount of variability within the Dendrocolaptidae, and found that of 173 specimens in nine genera, the majority possessed two-notched (type 3) sterna; types 2, 3, and 4 were sometimes found in the same species, but no specimens were described as possessing type 5 or 6. Woodhewers possess rather solid sterna, with one specimen of *Xiphocolaptes promeropirhynchus* having a sternum devoid of any perforations (type 1).

Ovenbirds typically possess a two-notched (type 3) sternum, but some specimens exhibit the more perforate types. Heimerdinger and Ames (op. cit.) discovered type 5 sterna (with a lateral notch and a large medial fenestra on each side) in five of 199 specimens examined, including certain specimens of *Xenops rutilans*, *Pygarrhichas albogularis*, *Sclerurus rufigularis*, and *S. guatamalensis*.
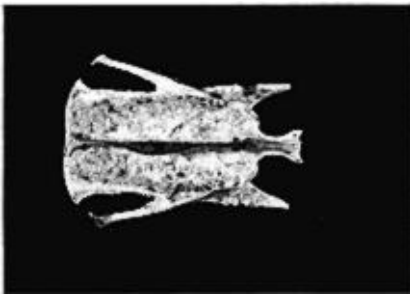
I have attempted to show general trends in the sternum by condensing data from Heimerdinger and Ames (1967) in tabular form (Table 1). When the data are presented in such a manner certain things become apparent. The
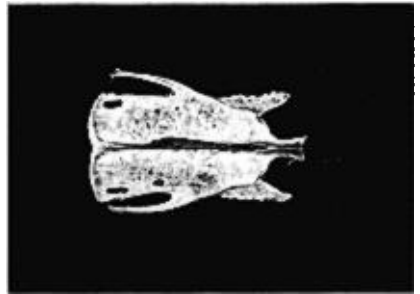
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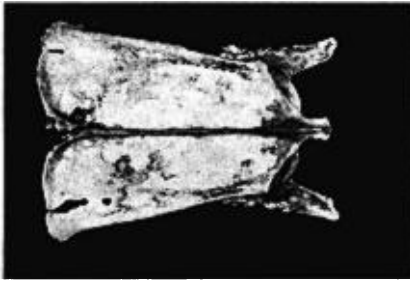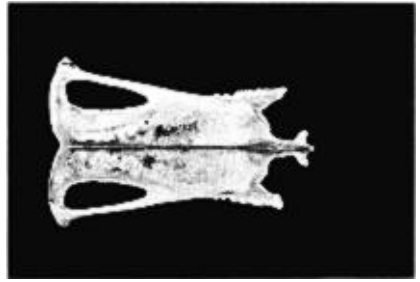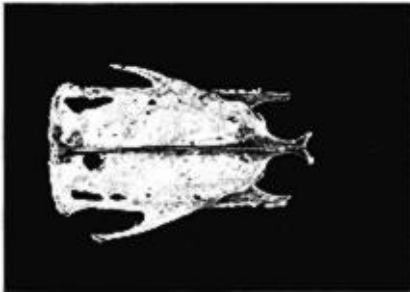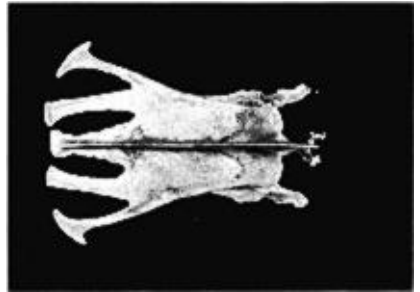
FIG. 1. Photographs of the sternal notch types: A, *Xiphocolaptes promeropirhynchus*: Dendrocolaptidae (type 1 approaching type 2); B, *Xiphorhynchus guttatus*: Dendrocolaptidae (type 2); C, *Automolus ochrolaemus*: Furnariidae (type 3); *Cinclodes fuscus*: Furnariidae (type 4 approaching type 5); E, *Sclerurus guatemalensis*: Furnariidae (type 5); F, *Dendrocopus villosus*: Picidae (type 6). Photographs made to approximately same scale.

TABLE 1

DISTRIBUTION OF STERNAL NOTCH TYPES FOUND WITHIN OVENBIRDS AND WOODHEWERS.
(Data primarily from Heimerdinger and Ames, 1967).

The numbers under each sternal type represent the number of specimens examined within each genus. The species within each genus may be found in Heimerdinger and Ames (op. cit.).

	Sternal Notch Types							
	1	2	2–3	3	3–4	4	4–5	5
Geositta				5	1	2		
Upucerthia				7	1			
Ochetorhynchus				2		1		
Eremobius				1				
Cinclodes				7	3	4	1	
Furnarius				15				
Sylviothorhynchus				1				
Aphrastura				4		2		
Phleocryptes				1	1			
Leptasthenura				6				
Schizoeaca				1				
Schoeniophylax				2				
Synallaxis				34	1			
Certhiaxis				2				
Cranioleuca				5				
Asthenes				11				
Phacellodomus				3				
Coryphistera				3				
Anumbius				2				
Margarornis				7		1		
Premnoplex				2	1	2		
Pseudocolaptes				3				
Pseudoseisura				4		2		
Hyloctistes				2				
Syndactyla				3				
Anabacerthia				8		1		
Philydor				4				
Automolus				12	1			
Hylocryptus				2				
Xenops				7				1
Pygarrhichas						2		1
Sclerurus								3
Lochmias						1		

TABLE 1
Continued

	1	2	2–3	3	3–4	4	4–5	5
				Sternal Notch Types				
Dendrocincla				8	1			
Deconychura				3				
Sittasomus				18		1		
Glyphorhynchus				10				
Xiphocolaptes	1	3	1	5				
Dendrocolaptes		1	1	8	3	1		
Xiphorhynchus		10	4	37	5	3		
Lepidocolaptes		7	1	34		2		
Campylorhamphus				4				
Dendrexetastes				1				

ovenbirds and woodhewers possess a basic sternal type, which is type 3. These type 3 sterna tend to be more open (to the left-hand side of table 1), or more closed (to the right-hand side of table 1), than typical type 3 sterna. When they are more open they become types 3–4, 4, 4–5, and 5, and when they are more closed they become types 2–3, 2, and 1. The ovenbirds tend to have type 3 sterna, but with a considerable degree of opening; whereas, the woodhewers are the only forms which show closure. In fact, the only genera which show closure are *Xiphocolaptes, Dendrocolaptes, Xiphorhynchus*, and *Lepidocolaptes*. These data indicated to me the possibility that closure of the posterior border of the sternum might be associated with the tree-trunk foraging habit.

It is of interest here to note that the four woodhewer genera which are somewhat intermediate between the Furnariidae and Dendrocolaptidae in many anatomical characters, *Dendrocincla, Sittasomus, Deconychura*, and *Glyphorhynchus*, show the sternal pattern of the ovenbirds with no tendency towards closure of the posterior border. *Dendrocincla* forages in a variety of postures (including creeping), while *Sittasomus, Deconychura*, and *Glyphorhynchus* creep up tree trunks like other woodhewers. I have shown elsewhere (Feduccia, 1969) that the above genera possess many primitive characters within the woodhewer assemblage, and it is possible that some may represent separate ovenbird offshoots which have reached the dendrocolaptid "grade" of anatomical organization. *Dendrocincla* even possesses the hemoglobin characteristic of the family Furnariidae. Thus, if sternal ossification is occurring with tree-trunk foraging, the lack of sternal closure in the above genera would not be surprising.

It should also be noted here that there are several ovenbirds which may
at times forage like the woodhewers by hitching up tree trunks; however, all
of these forms, which include *Margarornis, Premnornis, Premnoplex, Cranio-
leuca, Pseudocolaptes, Xenops, Automolus*, and *Pygarrhichas*, forage in a
variety of manners, and hitch up tree trunks only as alternatives to other pos-
sible foraging postures. Oscines which creep up tree trunks show the same
sternal pattern as non-creeping forms. As Heimerdinger and Ames (1967)
have pointed out, "Oscines which have a specialized form of locomotion
such as creeping on vertical surfaces *(Certhia, Sitta)*, or which are partially
terrestrial *(Eremophila, Cinclus)*, have exactly the same sternal characters
as the more typical oscines. It is also true, however, that many of these spe-
cialized species are migratory; the importance of certain regular, but short-
time, activities during the life span may override a tendency toward adapta-
tion for the daily type of locomotion."

THE STERNUM IN THE PICIFORMES

If it is expected that closure of sternal notches occurs with the evolution of
tree-trunk foraging behavior, then one should be able to find a similar con-
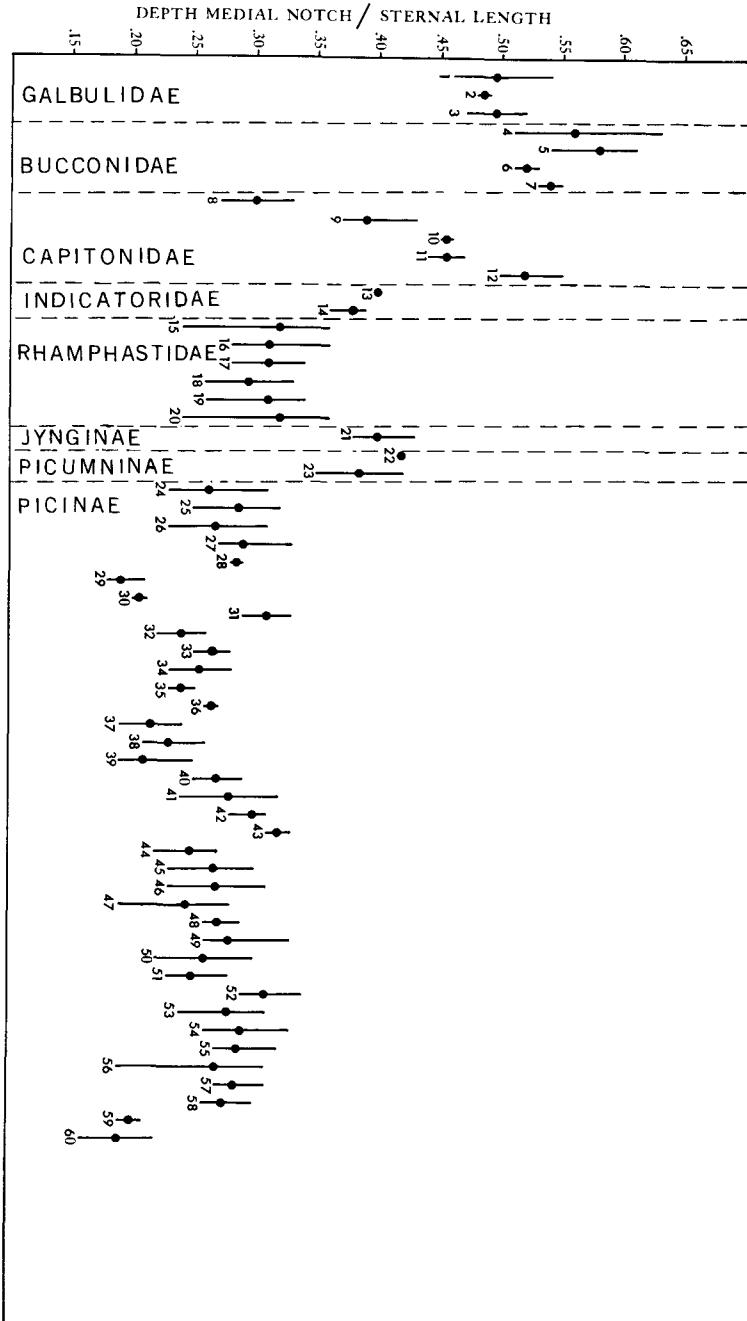dition in other climbing birds.

In order to test the hypothesis that closure in the posterior border of the
sternum is a result of selection pressures for stronger sterna associated with
tree-trunk foraging, I turned to the diverse order Piciformes. Unlike the
ovenbirds and woodhewers which possess diverse sternal types, making com-
parisons very difficult, all of the piciform birds that I examined possessed
type 6 sterna (four notches). Within the order Piciformes are found both
trunk-foragers and perching types. If trunk foraging is associated with sternal
closure then it should be obvious in piciform birds. In order to compare
various piciform birds with respect to sternal closure I have taken the ratio
of depth of median notch of the sternum to the total sternal length. The
means and ranges from these data are shown in Figure 2. Small sample size
for most species prohibits elaborate statistical testing, but certain trends are
obvious within the diagram. The most important point is that the tree-trunk
foraging piciform birds (nos. 24–60) show, in general, more sternal closure
than the non-trunk foraging piciforms (nos. 1–23). However, when one views
the diagram in segments one finds many interesting points. The Galbulidae
(nos. 1–3) seem to form a cohesive group as do the Bucconidae (nos. 4–7).
However, the Capitonidae (nos. 8–12) are tremendously variable. Why
Capito niger (no. 8) should show great closure of the sternal border is an
enigma. The species of the Indicatoridae (nos. 13–14) seem to be very homog-
eneous. The Ramphastidae (nos. 15–20) are of great interest, for although
they form a cohesive group, they clearly show more sternal notch closure

than the other perching piciform birds. The Jynginae (no. 21), and the Picumninae (nos. 22–23), as expected from the hypothesis, have relatively open sterna as compared to other members of the Picidae. The large wood-peckers, *Dryocopus pileatus* and *D. lineatus* (nos. 38–39), and *Phloeoceastes guatemalensis* and *P. rubicollis* (nos. 59–60), are towards the bottom of the woodpeckers with respect to sternal closure, but the medium-sized wood-peckers, *Piculus simplex* and *P. flavigula* (nos. 29–30), and *Meiglyptes tukki* (no. 37), show equally closed sterna.

If the trend towards closure of the posterior sternal border were truly invari-able, then one might expect to see some trend in closure corresponding to the relative amount of time that the forms spend on tree trunks. Thus, the series might go from *Colaptes* to *Asyndesmus* to *Melanerpes* (see Burt, 1930; and Spring, 1965). However, no such trend appears to be evident. Therefore, I feel that the tendency towards closure (as was the case for the woodhewers) should be stated as a general trend, not as a strict anatomical law. As in the case of the woodhewers, there is a general trend towards closure of the poste-

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FIG. 2. Means and ranges for the ratio of depth of medial notch of sternum to total length of sternum for the following piciform birds: Family Galbulidae: no. 1, *Galbula ruficauda* (4 specimens), no. 2, *G. galbula* (2), no. 3, *G. dea* (2) ; Family Bucconidae: no. 4, *Malacoptila panamensis* (3), no. 5, *Notharchus macrorhynchos* (5), no. 6, *Monasa atra* (2), no. 7, *Chelidoptera tenebrosa* (3) ; Family Capitonidae: no. 8, *Capito niger* (2), no. 9, *Semnornis rhamphastinus* (3), no. 10, *Tricholaema lachrymosum* (2), no. 11, *T. diadematum* (2), no. 12, *Trachyphonus darnaudi* (3) ; Family Indicatoridae no. 13, *Indicator variegatus* (2), no. 14, *I. indicator* (3) ; Family Ramphastidae: no. 15, *Pteroglossus torquatus* (5), no. 16, *P. castanotis* (8), no. 17, *P. aracari* (3), no. 18, *Ramphastos swainsonii* (5), no. 19, *R. toco* (5), no. 20, *R. sulfuratus* (6) ; Family Picidae: Subfamily Jynginae: no. 21, *Jynx torquata* (3) ; Subfamily Picumninae: no. 22, *Picumnus temminckii* (2), no. 23, *P. minutissimus* (4) ; Subfamily Picinae: no. 24, *Colaptes cafer* (6), no. 25, *C. auratus* (11), no. 26, *C. campestris* (4), no. 27, *C. melanochloros* (3), no. 28, *C. punctigula* (2), no. 29, *Piculus simplex* (3), no. 30, *P. flavigula* (2), no. 31, *Campethera nubica* (3), no. 32, *C. abingoni* (2), no. 33, *Celeus elegans* (2), no. 34, *C. undatus* (2), no. 35, *C. flavus* (2), no. 36, *Picus viridis* (2), no. 37, *Meiglyptes tukki* (2), no. 38, *Dryocopus pileatus* (7), no. 39, *D. lineatus* (5), no. 40, *Asyndesmus lewis* (2), no. 41, *Melanerpes erythrocephalus* (8), no. 42, *M. formicivorus* (5), no. 43, *M. carolinus* (5), no. 44, *M. uropygialis* (6), no. 45, *M. aurifrons* (9), no. 46, *M. chrysogenys* (3), no. 47, *M. pucherani* (4), no. 48, *Leuconerpes candidus* (3), no. 49, *Sphyrapicus varius* (11), no. 50, *Veniliornis fumigatus* (3), no. 51, *V. spilogaster* (3), no. 52, *Dendrocopus major* (3), no. 53, *D. villosus* (18), no. 54, *D. pubescens* (11), no. 55, *D. borealis* (6), no. 56, *D. scalaris* (6), no. 57, *Picoides tridactylus* (5), no. 58, *P. arcticus* (5), no. 59, *Phloeoceastes guatemalensis* (3), no. 60, *P. rubicollis* (3). All of the above piciform birds possess type 6 sterna with the exception of *Celeus elegans*, which has the median notches open, but with one large perforation laterally on each side of the sternum. *Celeus undatus* and *C. flavus* both possess normal type 6 sterna.

DEPTH MEDIAL NOTCH / STERNAL LENGTH

.15 .20 .25 .30 .35 .40 .45 .50 .55 .60 .65

GALBULIDAE

BUCCONIDAE

CAPITONIDAE

INDICATORIDAE

RHAMPHASTIDAE

JYNGINAE

PICUMNINAE

PICINAE

rior border of the sternum, but closure may only occur where it does not interfere with other sternal functions which may be necessary at sometime during the life history of the organism, but which are under opposing selection forces.

Short's (1971) paper on the evolution of terrestrial woodpeckers points to the fact that though there are as many as twelve species of terrestrial or semi-terrestrial woodpeckers, they tend to spend part of their life histories on tree trunks or vertical surfaces. These forms might therefore be under selection forces for maintaining adaptations associated with tree-trunk foraging. Even the most terrestrial form, the Andean Flicker (*Colaptes rupicola*), roosts commonly in excavated holes in vertical surfaces (Short, op. cit., Fig. 11). As Short (op. cit., p. 15) also points out, "Arboreal woodpeckers . . . may vary greatly in the use of their legs during climbing, and structural parallelism may result between terrestrial and certain arboreal woodpeckers even though their legs function differently in locomotion." "The tail too is apt to be utilized diversely in woodpeckers . . . so that clear-cut differences between ground woodpeckers and typically arboreal woodpeckers are not apparent." The foregoing might at least partially explain the lack of clear-cut differences in sternal form between partially terrestrial woodpeckers (species of *Colaptes*; nos. 24–28, and *Picus viridis*, no. 36, Fig. 2), and totally arboreal picine species.

HOOPOES AND WOODHOOPOES

In an attempt to discover other groups in which there is a tendency to ossify the posterior border of the sternum with the tree-trunk foraging habit, I examined the hoopoes (Upupidae), which do not hitch up tree trunks, and the woodhoopoes (Phoeniculidae), which forage in a variety of postures, but also by hitching up tree trunks (personal observation; and Clancy, 1964, and McLachlan and Liversidge, 1957). *Upupa epops* (Upupidae), and *Phoeniculus purpurescens* and *Rhinopomastos cyanomelas* (Phoeniculidae) possess type 3 (two notched) sterna. The ratio of depth of sternal notch to total sternal length is given in Figure 3, which graphically illustrates the more open sternum of *Upupa*, as compared with *Rhinopomastos* and *Phoeniculus*. Again, small sample size prohibits meaningful statistical testing, but at least *Upupa* is clearly significantly different from *Phoeniculus*. Furthermore, one specimen of *Phoeniculus purpurescens* possessed a type 2 sternum (with two lateral fenestrae), showing even additional closure, much in the same manner as the woodhewers. Therefore, in general, woodhoopoes appear to show the same general tendency towards closure of the posterior border of the sternum associated with tree-trunk foraging as observed in the woodhewers, and begin with the same sternal ancestry, a type 3 sternum.
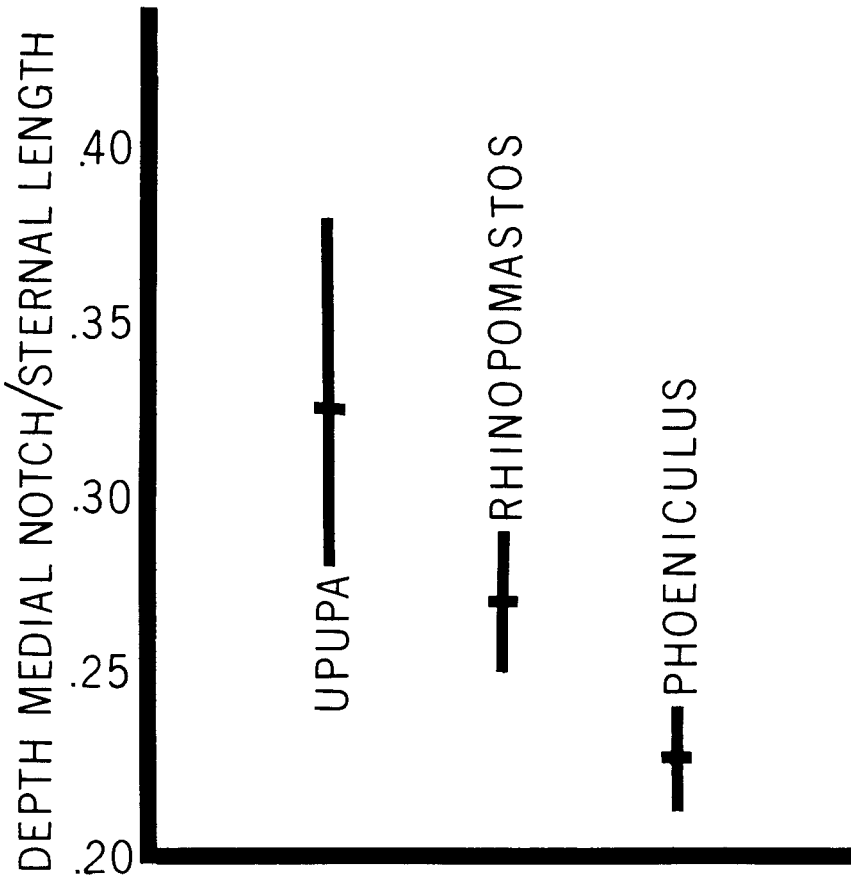
FIG. 3. Means and ranges for the ratio of depth of medial notch of sternum to total length for *Upupa epops* (n = 7), *Rhinopomastos cyanomelas* (n = 3), and *Phoeniculus purpurescens* (n = 5).

POSSIBLE FUNCTION OF THE POSTERIOR BORDER

So far I have merely established a correlation between closure of the posterior border of the sternum with the tree-trunk foraging habit, without elaborating on the possible functional reason for the closure.

The avian sternum provides attachment for two major sets of muscles. Lindsay (1885) pointed out that the outline of the posterior border of the sternum should in some way reflect the resultant of the forces of these two opposing sets of muscles. In the case of the birds under consideration in this paper, the relative powers of flight would not appear to vary greatly from one group to another. Thus, flight would not be an obvious place to look for
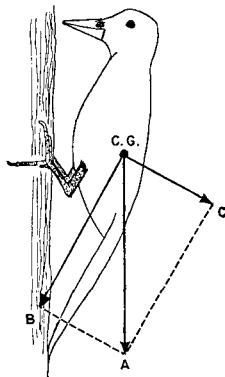
THE WILSON BULLETIN

FIG. 4. Diagram (from Stolpe, 1932) to show the forces acting on the climbing bird. A downward and inward force, B, and an outward force, C, constitute the two components of the gravitational pull, A.

functional correlates to explain the form of the posterior border of the sternum. However, if one considers the posture of a tree-trunk foraging bird on the trunk (Fig. 4), with the forces acting on a climbing bird, then one should be able to postulate the manners in which the bird could counteract the gravitational forces which act to pull the bird downward. Figure 4 is taken from Stolpe (1932), and was used by Bock and Miller (1959) to explain the functioning woodpecker foot. As Bock and Miller pointed out, the gravitational force, A, is divided into two component forces, B, and C. They further point out, "Force B, which is the larger of the two components, is directed downward and inward along the axis of the tail. The tail and fore toes (two and three) act together to counterbalance force B; the tail provides the greatest support. The outward force C tends to pull the woodpecker away from the tree trunk. This force is overcome by a combined action of the fore toes and the laterally directed fourth toes, of which the latter are probably the most important." However, while the fore toes and tail are of paramount importance in counteracting the gravitational forces, certain muscles must also function in this capacity. The most obvious set of muscles which might counteract the outward component force (C) are the abdominal muscles, and indeed, it is this set of muscles which attaches to the posterior border of the sternum. The main muscles involved are the M. obliquus externus abdominis, M. rectus abdominis, and M. transversus abdominis, all of which originate along the posterior border of the sternum (see Burt, 1930). I would postulate that the outward component force C is additionally counteracted by increasing the forces exerted by the abdominal muscles, thereby necessitating an increase in the strength of the posterior border of the sternum. Although

I have not had the opportunity to examine the abdominal muscles of creeping and non-creeping piciforms, I have examined these muscles in an ovenbird and woodhewer of approximately the same size (*Autumolus ochrolaemus* and *Xiphorhynchus guttatus*). My qualitative observations clearly showed that the woodhewer possesses much more mass in all of the abdominal muscles. Quantification of these types of comparisons will be necessary to fully test this hypothesis; until then it may at least bear the name of a strong hypothesis.

Though I have attempted to outline a general functional anatomical reason for an increase in sternal ossification in the posterior border of the sternum in tree-trunk foraging birds, there may be other factors involved. Short (1971) emphasizes what he calls the attribute of "toughness" of woodpeckers. Such undefinable attributes associated with climbing and tree-trunk foraging habits probably account for the fact that (Short, op. cit., p. 21), ". . . woodpeckers are remarkably thick-skinned, tough birds that are tenacious of life . . ." The same general attributes are assignable to woodhewers as well, and may be assessed, though poorly understood, as having to do with tree-trunk foraging adaptations.

PHYLOGENETIC ALTERNATIVES

Bock (1967:67) introduced the term paradaptation to apply to "Those aspects of a feature that are dependent upon, resulting from, or under the control of chance-based evolutionary mechanisms . . ." He used as his example the evolution of perching feet in birds. Anisodactyl, syndactyl, zygodactyl, and heterodactyl feet have evolved in birds as multiple evolutionary pathways for efficient perching mechanisms. As Bock (op. cit.) pointed out, ". . . each represents a different adaptation to the selection force for a more efficient perching foot because each is an adaptive advance for perching as compared to the ancestral foot." The perching foot types are therefore "paradaptive" because of their chance-based evolution, but are also adaptive in the sense that each type has been accepted by selection as an efficient perching foot.

A modified form of Bock's concept of paradaption (see also Bock, 1969; and previous emphasis of the role of accident in evolution by Mayr, 1962) appears to me to be useful in renewed emphasis. However, I do not feel the necessity for the introduction of a new term, nor do I feel that the term "mechanism" should be used in this context, as it carries a connotation of mutationism or macroevolutionary mechanism. However, it is true that phyletic lines begin their evolution with different structural forms which when placed under similar selection forces may result in different modifications to achieve similar goals. Thus, I used the term "phylogenetic alternatives" instead of paradaptation, emphasizing differences in phylogenetic background,
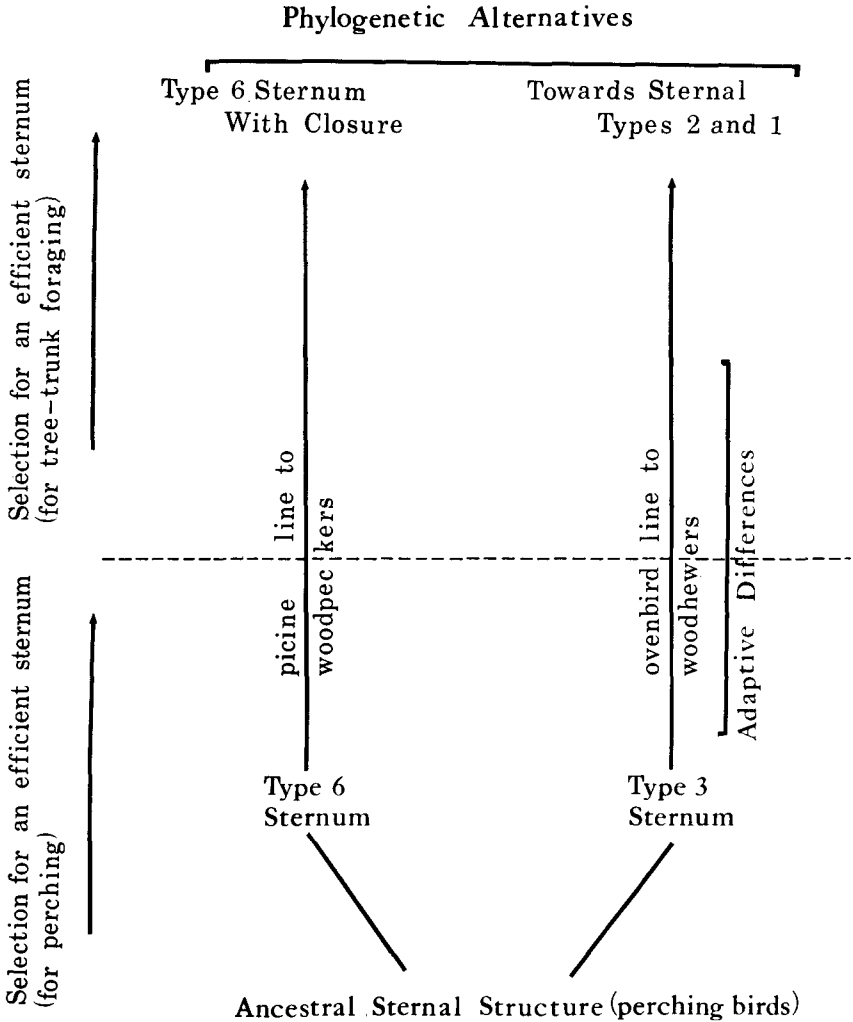
FIG. 5. Schematic diagram (following Bock, 1967) to show multiple evolutionary pathways of the sternal types of woodpeckers and woodhewers. The two ancestral sternal types (6 and 3) were first under the same selection force for a more efficient sternal type for perching, later under the same selection force for tree-trunk foraging. Vertical differences are adaptive; horizontal differences are owing to the ancestral character state.

but not as a macroevolutionary mechanism; these are simply aspects of evolutionary opportunism. In Figure 5, I have attempted to show how this concept might apply to the posterior border of the sternum, following the diagram given by Bock (1967) for the evolution or foot types in birds. In this case,

there are multiple pathways of evolution. Type 6 sterna evolve in early picines and type 3 sterna in the ovenbird ancestors of woodhewers, both under similar selection forces for a more efficient sternum for perching; but "evolutionary background" provided each group with different, but perhaps equally efficient, sternal types. When tree-trunk foraging groups evolve from each evolutionary line, the selection force changes to produce an efficient sternum for tree-trunk foraging. However, with the different evolutionary backgrounds in each group, a slightly different solution to the problem is found in each case. In the woodpeckers, the solution is apparently to increase closure of the border of the sternum by ossification; in the woodhewers, the number of notches becomes reduced.

SUMMARY

The evolution of the posterior border of the sternum in unrelated groups of tree-trunk foraging birds may be characterized, in general, by a tendency to increase the ossification of the border. In woodpeckers, which possess a four-notched sternum (type 6), there is an increase in the amount of closure of the notches. In woodhewers and woodhoopoes, which possess basically a two-notched sternum (type 3), there is a tendency to reduce the notches, resulting in some species in type 2 (with lateral fenestrae), and even type 1 (with no notches) in one species. Increasing the ossification of the posterior border of the sternum in the Dendrocolaptidae, Picidae, and Phoeniculidae is probably associated with increasing the strength of the sternum for tree-trunk foraging.

ACKNOWLEDGMENTS

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ANNOUNCEMENT

The Proceedings of the First Conference on the Status of the North American Osprey are expected to be available for distribution in late summer. This conference met in February 1962 at the College of William and Mary, under the chairmanship of Mitchell A. Byrd. Eighty persons attended the three-day affair. Copies of the Proceedings may be obtained by writing Dr. Mitchell A. Byrd, Department of Biology, College of William and Mary, Williamsburg, Virginia 23185. A bill will be sent at the time the order is filled, and no money need accompany the order. The price is expected to be no more than $2.