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The Scansorial Foot of the Woodpeckers, with Comments on the Evolution of Perching and Climbing Feet in Birds

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FOREWORD

The present study is based on a manuscript left by Waldron DeW. Miller at the time of his death in 1929. Although the work was done as long ago as 1915, and the results were first presented at the 1916 meeting of the American Ornithologists' Union, the manuscript was apparently never submitted for publication and was deposited with the rest of Miller's papers in the Department of Birds of the American Museum of Natural History. In the spring of 1956 Dr. Dean Amadon asked me if I would examine this manuscript and edit the parts suitable for publication. This task led to the reading of several papers on the structure of the woodpecker foot, all of which were published after Miller's death, and to a rather extensive review of the past work on the structure and evolution of the avian foot. Some of Miller's findings and conclusions have been anticipated and discussed in these papers, but his major discovery (the structure and function of the foot of the ivory-billed woodpecker) has not lost any of its importance during the 40 years that separate their discovery and the publication of

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this paper. However, the results of these later papers made it necessary to rewrite Miller's manuscript completely. Hence the responsibility of presenting the material is mine, and the first person singular pronouns throughout the text refer, of course, to me. But the credit of discovering the peculiar nature of the foot of the ivory-billed woodpecker and determining its functional significance belongs solely to W. DeW. Miller. I limit the discussion to a descriptive and comparative functional anatomy of the woodpecker foot, with special emphasis on that of the ivory-billed woodpecker. In the original manuscript, Miller had included some remarks on the relationships of the woodpeckers possessing the "ivory-billed woodpecker" foot structure and on the evolution of the woodpecker foot; these are outdated and have been omitted. My views on the relationships of these genera of woodpeckers, which differ radically from those of Miller, are being prepared for separate publication; however, a brief summary of the evolution of the woodpecker foot is given.

Two other manuscripts, one on the history of the various classifications advanced for the woodpeckers and the second on a new classification of the "Campephilinae," were also among W. DeW. Miller's papers. These manuscripts were read but were regarded outdated and unsuitable for publication. It should be mentined that J. L. Peters had access to the latter manuscript and based the grouping of the campephiline woodpeckers in the classification of the woodpeckers presented in volume 6 of his "Check-list" on the conclusions of that study. All three manuscripts have been returned to the American Museum of Natural History and have been placed with the rest of Miller's papers.

Acknowledgments

I am indebted to Dr. Dean Amadon for allowing me to examine W. DeW. Miller's papers and for permission to publish any part that I thought suitable for publication. Drs. Ernst Mayr and Dean Amadon have kindly read the manuscript and offered many helpful criticisms for which I am most grateful. Determination of the position of the toes of the climbing bird in several genera of woodpeckers was possible only through the kindness of several people. My thanks are extended to Drs. A. A. Allen and J. T. Tanner who lent me several photographs of the ivory-billed woodpecker, to Dr. S. F. Hoyt who showed me a motion picture of the pileated woodpecker made during the course of her husband's study of that species, and to Mr. Lester Short who allowed me to observe his captive flickers. This study was done while I was working under a National Science Foundation Predoctoral Fellowship.

WALTER J. BOCK

INTRODUCTION

One of the characteristic features of the Order Pici is the zygodactyl, or yoke-shaped, foot, in which the first and fourth toes point backward and oppose the second and third toes. Such an arrangement of toes had evolved from the ancestral anisodactyl foot and is a strict adaptation for perching, not for climbing. Yet the zygodactyl foot is believed by most ornithologists to be an adaptation for climbing on vertical surfaces as well as for perching on branches, a typical statement being (Beecher, 1953, p. 298): "This arrangement of toes [zygodactyl] is particularly advantageous for birds climbing about on tree trunks as barbets and woodpeckers do or for perching." Similar statements with perhaps more emphasis on the supposed scansorial function of the zygodactyl foot can be found in Grassé (1950, pp. 175–178, 943–946), Wallace (1955, p. 59), and Wing (1956, p. 19, fig. 1·12, pp. 47–48). Only a small minority of workers state definitely that the zygodactyl foot is not an adaptation for scansorial habits, as, for example, Stresemann (1927–1934, p. 550), who cites the results of the several German publications that are discussed below in this paper. A brief comparison of the foot structure and the habits of some perching and climbing birds is sufficient to refute the belief that the zygodactyl foot is an adaptation for climbing.

A permanent "yoke arrangement" of the toes, the zygodactyl or heterodactyl foot, is found in all the Pici, the Psittaci, the Cuculidae, and the Trogones, and a temporary or reversible yoke arrangement is present in the Pandionidae, the Musophagidae, and the Striges. With the exception of the Picinae, *Micropsitta*, and perhaps a few others, these birds are perching birds and do not climb on vertical surfaces. There is no reason to believe that the ancestors of these yoke-toed families were anything but perching birds. Consequently, it can be concluded that the zygodactyl and heterodactyl foot is an adaptation for perching. On the other hand, many excellent climbers, such as the Dendrocolaptinae, the Sittidae, the Certhiidae, and *Mniotilta* of the Parulidae, have a typical anisodactyl foot. Other forms that are specialized for clinging to vertical surfaces, such as the Apodidae and the Coliidae, usually have all four toes pointing forward—the pamprodactyl foot. The Coliidae possess a temporary pamprodactyl foot, and the hallux and the fourth toe can be directed either forward or backward, depending on whether the bird is clinging to a vertical surface or perching on a branch. Although all woodpeckers are said to have a zygodactyl foot, this arrangement of toes serves as the functional foot only in the Jynginae, the Picumninae, and the most unspecialized members of the Picinae (e.g., *Colaptes*) when they are climbing. This toe arrangement is also seen in all the Picinae when they are hopping on the ground or perching on a branch. However, the zygodactyl foot has been lost as the functional scansorial foot in the more specialized climbing woodpeckers and has been replaced by a different type of foot, one that is a true scansorial foot. Similarly, *Micropsitta* has no longer the zygodactyl foot of the parrots, but a foot structure like that of the specialized swifts or the mouse-birds. Thus, from these brief remarks, we can conclude that the zygodactyl foot is an adaptation not for climbing, but for perching. If a bird with a zygodactyl foot acquires scansorial habits, the zygodactyl foot must be replaced by some other type of foot, if the bird is to become a specialized climber. The question before us is, How was the zygodactyl foot of the ancestral Picidae converted into the scansorial foot of the woodpeckers?

In the original manuscript of Miller, the structure and function of the foot of the ivory-billed woodpecker were described first and then were compared to those of the foot of the less specialized woodpeckers. I, however, adopt another method of presentation. The structural adaptations found in the foot of the ivory-billed woodpecker are the culmination of a long series of modifications beginning with the generalized piciform foot. Comprehension of the structure and function of such an extreme specialization as the foot of the ivory-billed woodpecker is greatly facilitated if these modifications are traced stepwise through a series of increasingly specialized woodpeckers. The series here presented is not to be interpreted as an evolutionary series; it is a morphological series showing increasing specialization, no more and no less. It begins with *Jynx* and is followed by *Picumnus*, and then by *Colaptes*. After the level of specialization shown by *Colaptes*, two lines of adaptation appear, the dichotomy being brought about by differences in the length of the hallux. In the short-hallux line, I trace the modifications in the foot structure through *Dendrocopos*, in which the hallux is small and functionless, to *Picoïdes*, in which the hallux has been lost. Returning to *Colaptes*, I trace the long-hallux line through *Dryocopus* to *Campephilus*, in which the lengthened hallux is retained as a functional part of the foot. Whenever possible, the structure or its modification is related to its functional significance, but in many places the function is assigned with doubt. I have not had the opportunity to observe some of the important forms such as the primitive subfamilies (Jynginae and Picumninae) and the ivory-billed woodpecker in life, so that my knowledge of their habits is quite limited. Here may be the best place to enter a plea for observations on the method of climbing used by woodpeckers (and the other climbers discussed below in this paper) and especially the position of the toes when the bird is climbing. These observations are especially desirable for birds of tropical areas. In the present discussion, I limit myself to the external features of the foot.

Finally, a general discussion of perching and climbing feet and their evolution is given; this section was not part of Miller's original manuscript and was added as a somewhat lengthy postscript to prove conclusively that the zygodactyl foot evolved as an adaptation for perching.

Earlier Works

Waldron DeW. Miller was able to proceed directly into the description of the foot of the ivory-billed woodpecker without having to refer to earlier works on the functional anatomy of the woodpecker foot; there were none at his time. Since his death, however, several important contributions to our knowledge of the morphology and function of the woodpecker foot have appeared and have established a firm foundation on which we can build a comparative analysis of the climbing modifications in the foot of the different genera of woodpeckers. Unfortunately, because they were published in German, the results of these papers have not penetrated fully into the general English literature. For this reason, I briefly summarize the conclusions of those papers that are pertinent to this study.

Burt (1929, 1930) analyzed and compared the climbing modifications of a number of structures in North American woodpeckers. Although he was not specifically concerned with the structure of the foot, he did study the osteology and myology of the hind limb and thus contributed greatly to the eventual understanding of the comparative functional anatomy of woodpecker feet. Burt was the only worker to undertake a comparative study of the climbing adaptations within the woodpeckers and has arranged the North American genera in a sequence of increasing arboreal specialization. Unfortunately, he was unable to study the ivory-billed woodpecker and hence did not realize that there are several alternate ways in which a woodpecker can adapt to a highly arboreal mode of life. Peters' (1948) arrangement of the picine genera follows closely the sequence of increasing arboreal specialization set down by Burt.

Scharnke (1930) investigated the arrangement of the toes and underlying osteology and myology in several genera of woodpeckers with special emphasis on *Picus mineaceus* (called *Callolaphus miniatus* in his paper) and *Dendrocopos* [*Dryobates*] *minor*. He is apparently the first worker to stress the fact that, in at least certain genera of woodpeckers, when the bird is clinging to a tree trunk, the reversed fourth toe no longer points backward and opposes the fore toes but is directed laterally. Thus when the woodpecker (e.g., *Dendrocopos minor*) is climbing, the second and third toes point forward and support the bird against downward forces, while the fourth toe is held to the side and in this way braces the woodpecker against lateral and backward forces. The hallux generally lies on its side along the fourth toe and is functionless. Scharnke points out that the first and fourth toes do not have to oppose the fore toes, that is, the foot does not have to function as a pincer or a clasper. The tail, which is braced against the tree trunk, acts as a prop and aids the fore toes in supporting the bird against the pull of gravity. Scharnke believed the extreme rotation of the fourth toe to be in a right-angle position to the fore toes (pp. 310–311). Unfortunately, he was unable to observe any of the "ivory-billed woodpeckers" in life and could not realize that the extreme possible rotation of the fourth toe is when it points forward. In the rest of the paper, Scharnke described the arrangement of the trochlea, muscles, and tendons which permit the reversed position of the fourth toe and its movement back to a lateral position. He believed that the lateral rotation of the fourth toe is produced by an inward turning of the tarsometatarsus; this was, however, shown to be incorrect by later workers. Rotation of the fourth toe is produced by the action of the muscles inserting on it. In a later paper (1931), Scharnke emphasized that in most woodpeckers the first toe is not needed and can be lost without injury to the woodpecker's ability to climb on vertical surfaces.

Stolpe (1932) correlated the structure of the hind limb to its function in a number of different types of birds—runners, swimmers, perchers, and climbers. In describing the action of the woodpecker leg, Stolpe was particularly concerned with the effect of gravitational forces on the woodpecker while it is climbing on a vertical surface. He divided the force of gravity into two components and showed that the tail served as a brace against the major downward force and that the feet held against the force tending to pull the bird away from the tree trunk (see fig. 4A). Stolpe supported Scharnke's major conclusions and emphasized the importance of the lateral position of the fourth toe and the fact that the hallux is not necessary for the proper functioning of the foot. He stated that the lateral position of the toe is an important adaptation to counteract the outward component of the gravitational pull; the fourth toes of the two feet act together to grasp the tree trunk in the manner of a pincer. Stolpe pointed out that the extreme rotation theoretically possible for the fourth toe is when it points forward, but said that he never observed this condition. In all his observations, the fourth toe was extended to the side, with the maximum rotation being when it was at right angle to the anterior toes. However, Stolpe did not have the opportunity to observe any member of the "ivory-billed woodpecker" group. Yet Stolpe's chief contribution to our understanding of the morphology of the woodpecker hind limb was not his discussion of the foot or the tail, but his interpretation of the variation in the hind limb musculature. He showed that in all perching and running birds, the pull of gravity tends to close (i.e., flex) the joints of the leg. Thus in these forms, the muscles that overcome gravity are the extensors of the segments of the limb. In the woodpeckers, which have evolved from perching birds, the reverse is true; gravity tends to open or extend the joints of the leg (i.e., pull the woodpecker away from the tree trunk). Hence the important limb muscles in the woodpeckers are the flexors (fig. 4B). Stolpe pointed out that, in the woodpeckers, the extensors are relatively weak, while the flexors are well developed. This conclusion agrees with Burt's findings that the more specialized genera of North American woodpeckers have the most highly developed flexors of the hind limb in the family.

Steinbacher (1935) studied the morphology of the foot, both the osteology and the myology, of those birds having a reversed or reversible toe. Aside from correcting a few of Scharnke's minor mistakes, he did not add anything new to our knowledge of the woodpecker foot. However, his general conclusions are of the greatest importance to the general results of the present paper. Steinbacher points out that none of the different foot types (e.g., zygodactyl, heterodactyl) has only one function distinct from the functions of the other foot types. Rather, each foot type allows a great variety of functions with relatively minor morphological changes from its basic or generalized structure. The possible functions of the different foot types may overlap, as, for example, the ability to perch or to run on the ground is possible with the zygodactyl foot of the Pici, the Psittaci, and the Cuculidae. From those observations, Steinbacher draws his main conclusion (translation, p. 281): "That the differences between the several foot types cannot be explained on functional grounds, but appear to be the result of phylogenetic divergence and thus are of great systematic value." This conclusion is discussed below in more detail in the section on the evolution of the perching and climbing foot types. The most pertinent of Steinbacher's conclusions for the following comparison of the foot of the different genera of woodpeckers is that profound functional changes may be accompanied by only slight morphological ones. Thus in comparing "primitive" and "specialized" woodpeckers, we may discover a radical change in function (from a perching to a highly specialized climbing foot), with little change in structure.

Richardson (1942) was not primarily concerned with comparative adaptations within the woodpeckers, but with the adaptive modifications for climbing in different groups of birds, namely, woodpeckers (*Dendrocops*), nuthatches (*Sitta*), and creepers (*Certhia*). Although he did not contribute any new information to our knowledge of the functional anatomy of the woodpecker foot, Richardson did introduce the results of the above-mentioned studies into the English literature. Unfortunately, their spread stopped here. Richardson compared the climbing adaptations of these three genera of birds in an attempt to ascertain the indispensable climbing modifications in birds. However, although he cited Steinbacher's major conclusion, as follows (p. 307): "Steinbacher's work (1935), correlating structure and function in the feet of birds, is significant in demonstrating that different structural types can adapt to the same use, or that the same structural type can adapt to several uses," he failed to realize that Steinbacher also implied that if birds possessing different foot types acquired the same mode of life, i.e., climbing on vertical surfaces, they would not necessarily acquire the same structural modifications for this new way of life. Richardson's conclusions (p. 365) on the climbing modifications in birds are rather vague and meaningless, and he missed the most important one of the scansorial adaptations, namely, the position of the toes. Nevertheless, Richardson's work clearly emphasizes the fact that a climbing foot does not have to be a zygodactyl foot.

Since the appearance of Richardson's paper, nothing of pertinence to our knowledge and understanding of the foot structure of the woodpeckers has been published.

COMPARISON OF THE FOOT IN DIFFERENT TYPES OF WOODPECKERS

SUBFAMILY JYNGINAE

WRYNECK (*Jynx torquilla*)

The arrangement of the toes is zygodactyl in study skins and presumably always so in life. The first and fourth toes lie on each side of the midline of the tarsus and have no connection with each other; a heavy pad on the distal end of the tarsus separates them. Although the hallux is relatively long, it is very slender and appears to have little importance in opposing the fore toes. In fact, the opposed third and fourth toes, which are subequal in size, are about twice as large as the second and first toes. As in all woodpeckers and indeed in all the Pici, the basal phalanges of the second and third digits are bound together by a common sheath of skin. These basal phalanges are relatively long, slightly longer than the second phalanges of these toes—the condition that is found in other families of the Pici. The broad plantar surfaces of the toes are covered with small rounded scales and are subdivided by creases into pads (tylari) which correspond to the phalanges. The tarsus is long and slender. Its plantar surface is rounded or even angular in cross section and is covered with a single row of large rectangular scales—the holaspidean condition. The claws are small, weak, and only slightly curved. The main features of the wryneck foot can be seen in figure 1A, which illustrates the foot of *Pteroglossus* of the Ramphastidae, a foot rather similar to that of the wryneck.

The wryneck, although it is a member of the Picidae, spends most of its time crawling about branches or hopping on the ground. It does cling to tree trunks occasionally, but usually without using its soft tail as a prop. Witherby *et al.* (1953, p. 292) describe the wryneck as "looking in field much more like a Passerine bird than relative of woodpeckers." Hence, from a knowledge of its habits, we can conclude that the wryneck is a perching bird and that its foot structure must be suitable for perching on branches and for hopping on the ground. A glance at the foot of the wryneck shows that it is a perching foot, and indeed it is more similar to the perching foot of the Bucconidae or the Ramphastidae than to the foot of the climbing members of the Picidae. I here assume that the perching foot of the wryneck represents the ancestral woodpecker foot and that any modifications from the wryneck condition in the foot structure of the more specialized woodpeckers is an adaptation for climbing. (It is possible that the wryneck has secondarily acquired perching habits and that its foot is secondarily modified for perching. This possibility must be considered if one is investigating the evolution of the woodpeckers, but it does not seriously affect the conclusions of this study, for I am regarding the feet of the different genera as morphological types in a strict sense.) However, I shall outline the functional significance of certain features of the wryneck foot in order to emphasize the climbing modifications in the specialized woodpeckers.

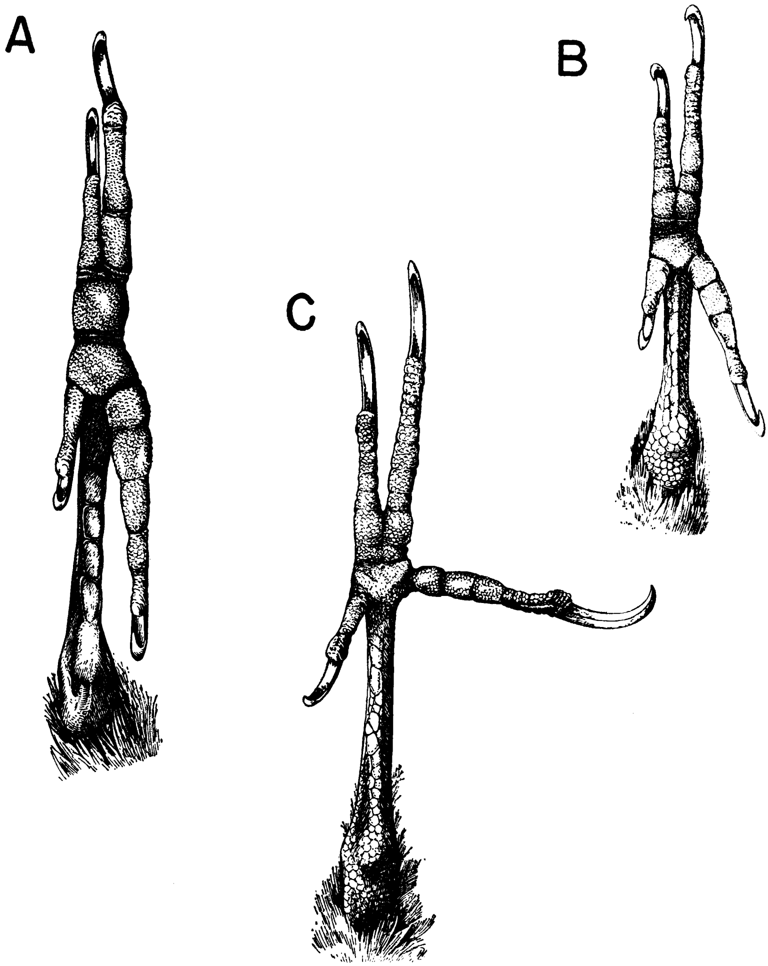

FIG. 1. Plantar surface of the foot. A. *Pteroglossus* of the Ramphastidae (perching foot). B. *Celeus elegans* (perching and climbing foot). C. *Dryocopus pileatus* (climbing foot). The toes have been drawn in their normal functional position.

The most prominent clasping features in the wryneck foot are the zygodactyl arrangement of the toes and the small, slightly curved claws. The outer pair of opposed toes, the third and fourth, are longer and thicker than the inner pair, the first and second, and probably assume the major role in clasping the branch. The reason for the shortened second digit is unknown, but, although the decrease in the second toe is most likely an adaptation for perching, it has been retained in most of the climbing woodpeckers. The relatively great length of the joined basal phalanges of toes two and three prevent these toes from spreading. Parallel toes are an advantage to perching birds in that all of the force of flexion is directed against the branch. All perching families of the Pici have conjoined basal phalanges of the second and third toes. The syndactyl foot of the Coraciae, in which the anterior toes are joined together for a lesser or greater distance and hence are parallel to one another, clearly illustrates the advantage of parallel toes in a clasping foot. In the extremely specialized clasping foot of the African chameleons, the toes of the opposed sets are bound together by a common sheath of skin; thus they are held parallel and act as a single unit (Gadow, 1901, pp. 567–568).

SUBFAMILY PICUMNINAE

PICULETS (*Picumnus innominatus*)

The piculets are similar to the wrynecks in that they do not climb on vertical tree trunks. They are, however, more arboreal than the wryneck and do not hunt for food on the ground, but confine their activities to branches of trees. In all respects, the structure of the piculet foot is similar to that of the wryneck and does not require a separate description. Of interest is the length of the fourth toe, which has become equal or even longer than the third toe—a modification for a stronger clasping foot. The fact that the piculets have a longer fourth toe than the wryneck is correlated with the more arboreal habits of the piculets. Loss of the hallux in one genus, *Sasia* (fig. 2A), is of interest, but not of great importance. This toe is degenerate and

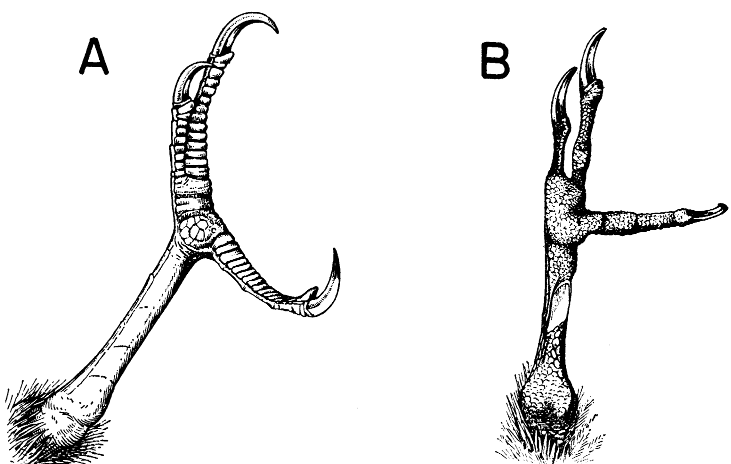

FIG. 2. Plantar surface of the foot. A. *Sasia* (perching foot). B. *Gecinulus viridis* (climbing foot).

practically useless in many genera of the perching families of the Pici. In the genus *Brachygalba* of the Galbulidae, the hallux is exceedingly small, and it is wholly wanting in the closely related and probably congeneric *Jacamaralcyon tridactyla*. Obviously the first toe is now functionless and can be lost without harming the perching ability of the bird.

SUBFAMILY PICINAE

FLICKER (*Colaptes auratus*)

The arrangement of the toes in flickers as seen in study skins is zygodactyl; the first and fourth toes lie on each side of the midline of the tarsus and are not associated with each other. The relative proportions of the toes are roughly the same as in the wryneck. The conjoined basal phalanges of the second and third digits are still relatively long. On their plantar side, the conjoined phalanges form a conspicuous pad which is not subdivided by a longitudinal groove separating the two digits. The plantar surface of the toes is broad, covered with small circular scales, and subdivided by creases into pads corresponding to the phalanges. The tarsus is still relatively long, but is thicker than that of the wryneck. Its plantar surface bears two rows of rectangular scales and, as in the wryneck, is angular when seen in cross section. The "heel" is normal in that it does not bear a heavy, horny callus. The claws are large and more curved than those of the wryneck. These features can be seen in figure 1B, which pictures the foot of *Celeus elegans* which is very similar to that of the flicker.

The flicker represents a group of woodpeckers that are often referred to as ground woodpeckers. They obtain most of their food from the ground and confine their "woodworking" activities to the excavation of their nesting holes. Yet in spite of the fact that the flicker chisels out its nesting hole and does much other climbing and has acquired some of the typical climbing adaptations of the woodpeckers, notably a stiffened tail and strongly curved claws, its foot has not changed radically from that of the wryneck. There is no indication that the fourth toe of the flicker is directed laterally when the bird is climbing on tree trunks. In all my observations on captive flickers, the toes were held in a zygodactyl position while the bird was climbing on a vertical surface. The fourth toe was never held closer than 45 degrees to the horizontal. The hallux was always kept on the inside of the foot. The position of the toes in the diagram given by Richardson (1942, p. 322) is typical for a climbing flicker. It is not certain whether or not the flicker sometimes extends its fourth toe to the side when climbing, as has been reported for the structurally similar green woodpecker, *Picus* (Scharnke, 1930). Nevertheless, when the bird is hopping on the ground, the toes are in a zygodactyl position. Because most of the flicker's food is obtained from the ground, selection will favor the zygodactyl arrangement of the toes and may actually hamper the development of a more efficient scansorial arrangement of the toes. The large and strongly curved claws of the flicker are an adaptation for climbing. As has been shown by Aehmichen (*in* Grassé, 1950, pp. 175–178), strongly curved claws are necessary to allow the tip of the claw to penetrate into the bark of the tree trunk when the flexors of the toes contract (see fig. 5). Another scansorial modification in the foot of the flicker is the shortened basal phalanges of the second and third toes. This shortening permits a greater spreading of the fore toes, more than in the wryneck, but not so much as in the more specialized woodpeckers. A spreading of the fore toes gives them a firmer purchase on the bark.

The structure of the flicker foot is important, for it proves that the zygodactyl foot can serve as a climbing foot albeit a poor one. There is so little difference between the feet of the wryneck and those of the flicker that we must conclude that the foot of the flicker is essentially a perching foot, not a climbing foot. In other words, the arrangement of the flicker's toes do not show any scansorial modifications. The flicker does possess several other scansorial modifications, namely, the stiffened tail, the strongly curved claws, and the slightly shortened basal phalanges of digits two and three. These specializations can be easily developed from the wryneck condition. The wryneck clings to tree trunks and occasionally uses its tail as a brace. A stiffer tail and stronger claws could be selected for in a woodpecker-like bird, if the proper genetical modifications appeared. This selection force did not have to be associated with obtaining food from tree trunks, but could have been associated with the excavation of the nesting hole. The ancestral woodpeckers were hole-nesters and depended on natural cavities for nest sites; consequently their numbers would be limited by the availability of suitable nesting holes. The ability to dig their own nesting holes would be of great advantage and perhaps the key to the success of the woodpeckers. It is well known that the population density of hole-nesting passerines is limited by the number of nesting holes available and that it can be greatly increased by saturating the woods with nesting boxes. Once the basic climbing modifications were developed (in connection with digging the nesting hole), the woodpeckers could invade a new feeding habitat (the tree trunks) and further modify the foot and other structures towards more efficient climbing structures.

The barbets (Capitonidae) provide additional evidence in support of the above discussion. These birds are typical perching birds except that they cling to vertical tree trunks while they are digging their nesting hole (e.g., Chapin, 1939, p. 496). They are the only family of the Order Pici other than the woodpeckers that dig their own nesting hole (excluding the bank-nesting forms) and are the second largest family in the order, which illustrates the success associated with the ability to excavate a nesting hole. The barbets may be considered as providing an analogous example to the ancestral group of woodpeckers.

It is of interest, then, to determine the scansorial modifications, if any, of the barbets. In study skins, the toes are arranged in a typical zygodactyl fashion. There is no indication that the fourth toe is ever directed laterally in life. A search through the literature failed to uncover any description of the arrangement of the toes when the barbet is clinging to the tree trunk. Most likely, the toes of the barbet are zygodactyl when it is climbing, which is assumed to be true in the absence of any contradictory evidence. Thus the arrangement of the toes in the barbet does not show any scansorial modifications. Furthermore, other than the claws, which may be more curved than expected, the barbets have no obvious modifications for climbing. This is not surprising, for the barbets are essentially perching birds and cling to tree trunks only when digging at their nesting hole which is usually located in the soft wood of a dead tree. However, the important point is that the barbets were able to cling to the vertical trunk and excavate their nesting hole before they had acquired any scansorial modifications. The zygodactyl foot is apparently sufficient for short periods of clinging while the bird is working at its nesting hole or for other brief periods of climbing (e.g., drumming in the flicker). This is true for both the barbets and the flickers. Therefore it is incorrect to say that a bird with a zygodactyl foot cannot cling to a vertical surface. It can, but not very well. Yet this does not prove that the zygodactyl foot is an adaptation for climbing. It is not. Furthermore, if a bird possessing a zygodactyl foot is to become a specialized climber, the foot structure must be modified to provide better support against the pull of gravity. These changes are described in the next section.

Hairy Woodpecker (*Dendrocopos villosus*)

The toes appear to be zygodactyl in study skins, but quite often the fourth toe is directed more or less laterally. As in the flicker, the first and fourth toes lie on each side of the tarsus and appear to have no connection with each other. The major change from the flicker foot has been a change in the proportions of the toes; the fourth toe has become longer, the hallux shorter, and the second toe almost as long as the third toe. The basal phalanges of the second and third toes are still joined together, but they have become shorter in respect to the length of these toes. There is a shallow crease dividing the pad of the united basal phalanges into halves corresponding to the digits. The plantar surface of the toes shows less subdivision into pads, corresponding to the phalanges. In addition, the plantar surface on the distal end of the digits has become compressed laterally and has lost its smooth covering of small rounded scales. Instead, this part of the plantar surface is covered with rows of rough scales which are separated by strong transverse grooves. (These grooves do not appear in fig. 3.) The scales on the plantar surface of the tarsus are beginning to break up into smaller scales, but one longitudinal row of large rectangular scales still exists. This would correspond to the taxaspidean condition of the podotheca. The plantar surface is still rounded when viewed in cross section. The "heel" is normal and lacks a horny callus. Claws are large and strongly curved. The foot of the hairy woodpecker is shown in figure 3; the left foot illustrates the normal arrangement of the toes in

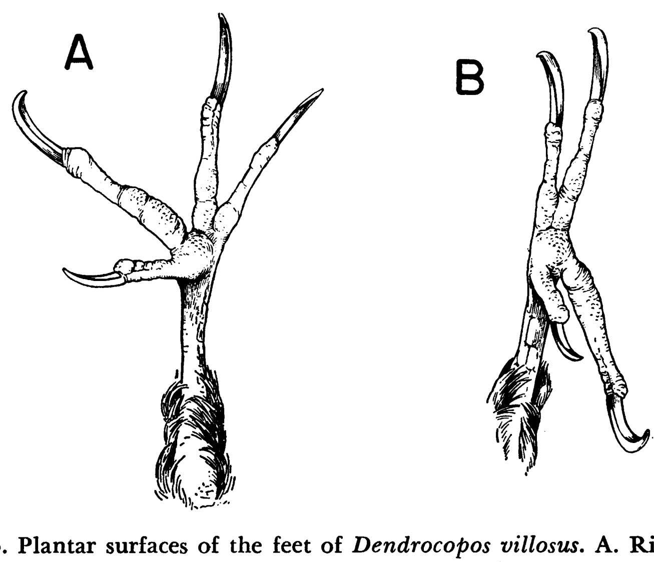

FIG. 3. Plantar surfaces of the feet of *Dendrocopos villosus*. A. Right foot. B. Left foot. The toes of the left foot are natural. Of the right foot the hallux and fourth toe have been pulled to the lateral side of the foot to show the position of the toes when the bird is climbing.

the study skin; the right foot has been arranged to show the approximate position of the toes when the bird is climbing.

The hairy woodpecker was chosen because it is typical of the majority of the picine genera; it obtains most of its food by drilling and shows all the adaptive modifications of the woodpeckers. The position of the toes of the birds in this genus while they are climbing has been discussed previously by Scharnke (1930). My observations agree completely with his. He has shown that, when the bird is climbing, the zygodactyl arrangement of the toes is lost and is replaced by another arrangement. In the scansorial foot of the hairy woodpecker, the fore toes (two and three) still point forward, but are somewhat spread apart. The decrease in the length of the conjoined basal phalanges of digits two and three allows these toes to spread; the angle between the toes is from 15 degrees to 25 degrees. The fourth toe no longer points backward, but is thrust out to the side so that it is held approximately at right angles to the fore toes. The hallux generally points laterally rather than medially and can quite often be seen lying on its side under the distal end of the tarsometatarsus. Figure 4C illustrates the position of the toes in a climbing woodpecker. The hallux and fourth toe are apparently bound together basally in some fashion, for they appear to move as a unit when the toes are manipulated in a freshly killed bird, as was done in the right foot in figure 3. Perhaps the ligament running from the base of the hallux to the base of the fourth toe (see Scharnke, 1931) is responsible for the "common movement" of these toes. Although the claw on the hallux may sometimes be hooked into the bark, the hallux more commonly lies on its side and hence is of no help in holding the bird to the tree trunk. If a woodpecker is climbing on a thin branch, the toes may encircle the twig with toes three, four, and one pointing laterally and only the second toe pointing forward.

The function of the toes can best be explained with the aid of a diagram showing the forces acting on a climbing woodpecker (fig. 4A). This diagram has been taken from Stolpe (1932, fig. 37). The force of gravity, A, can be divided into two component forces, B and C. 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. The fourth toes of the two feet act together as a pincer to hold the bird fast to the tree. Any toe pointing down the

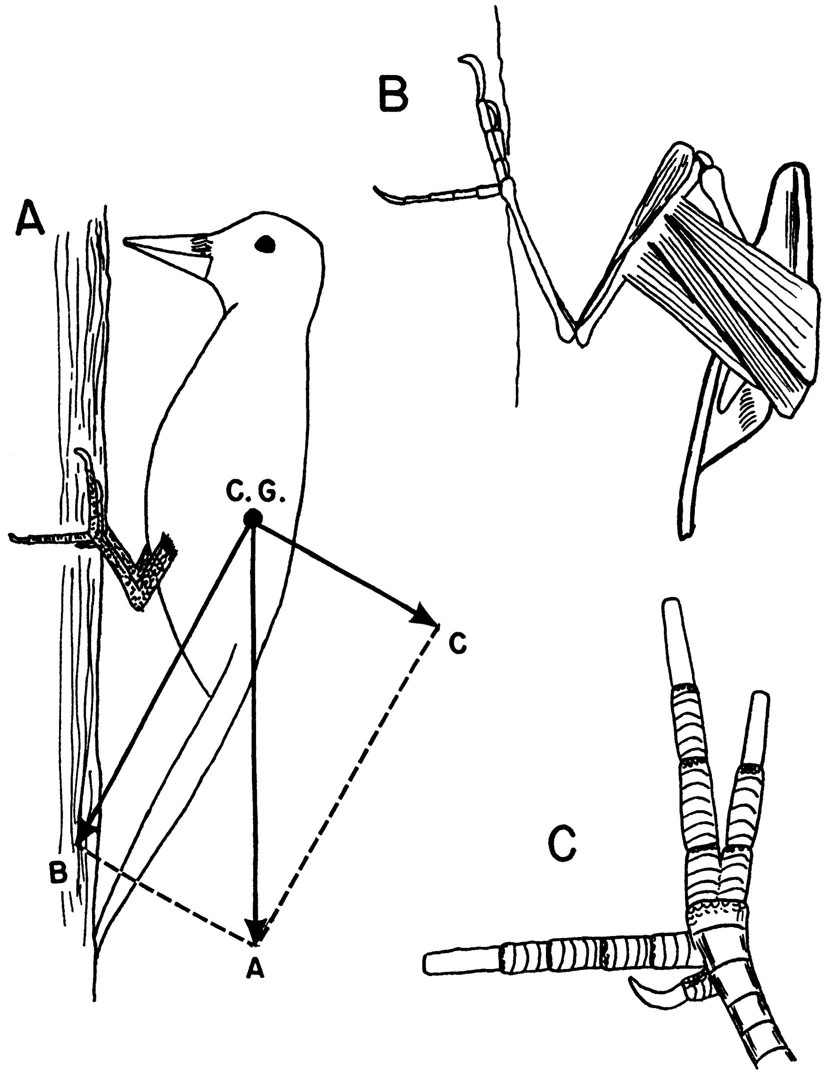

FIG. 4. Some factors associated with climbing in woodpeckers. A. Forces acting on a climbing woodpecker. The pull of gravity, A, is divided into its two components, the downward and inward force, B, and the outward force, C. The forces originate from the center of gravity, C. G., of the bird. B. The pelvic girdle and hind limb of a woodpecker to show the muscles that are important in flexing the segments of the leg. They are the flexors of the tibia (M. biceps femoris, M. semitendinosus, and M. semimembranosus) and the flexor of the tarsus (M. tibialis anterior). The flexors of the toes are not shown. There are no important flexors of the femor. C. Dorsal surface of the foot, showing the typical position of the toes when the woodpecker (e.g., *Dendrocopos*) is climbing.

tree trunk is of no value, for it does not counterbalance any force acting on the woodpecker; thus there is no need for a zygodactyl arrangement of the toes. In other words, the toes of the woodpecker, speaking about one foot at a time, need not grasp the tree in the manner of a pincer, as is commonly believed (e.g., Richardson, 1942, p. 322; Grassé, 1950).

The forces acting on a woodpecker can be more easily understood if the following two analogies are used. The first is that of a man climbing a tree or a pole. His feet with climbing irons correspond to the woodpecker's tail and serve to brace him against the large downward component of the gravitational force. The strap about the tree trunk against which the climber can lean serves the same function as the woodpecker's foot; it prevents the climber from falling backward. The lateral position of the fourth toe can best be explained by reference to a mountain climber. If one is standing on a narrow ledge, the most secure hold is maintained when the arms are spread out to the sides and the body is held close to the cliff. This reduces the outward component and increases the downward component, which can be

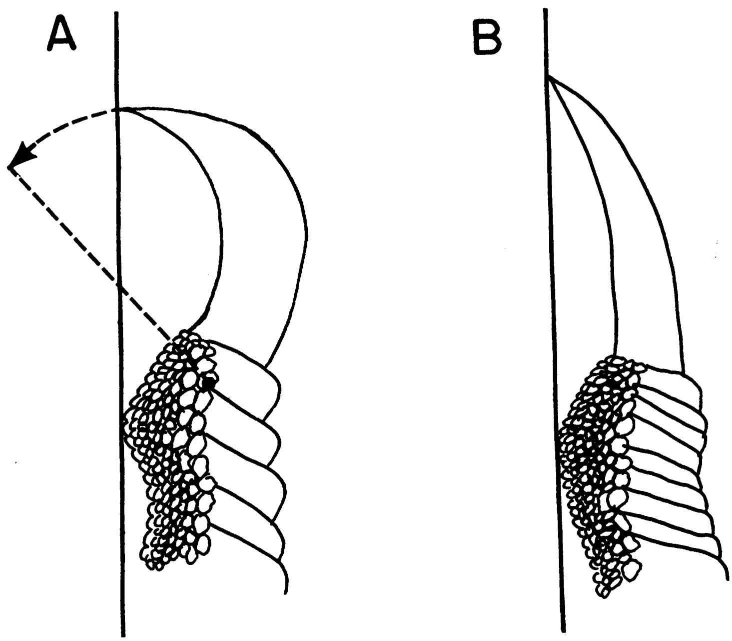

FIG. 5. A. Strongly curved claw of a climbing bird. B. Relatively straight claw of a non-climbing bird. When the foot is placed against a tree trunk, only the strongly curved claw is able to penetrate the bark.

easily overcome by the feet, and at the same time this position permits the greatest possible leverage of the arms. If the arms are doubled up beneath the body, the muscles pull close to the fulcrum point of a long lever arm and thereby lose most of their force. However, if the arms are extended to the sides, the pull of the muscles is along the longitudional axis of the bones and thus at their greatest mechanical advantage. Also when the arm is extended to the side, the muscle is at the beginning of its contraction cycle and hence able to contract with more force than when the arm is doubled up beneath the body and the muscle already partly contracted.

Three-toed Woodpecker (*Picoïdes tridactylus*)

The foot of the three-toed woodpecker is similar to that of the hairy woodpecker except for the loss of the hallux (see fig. 2B). The remaining toes are held in the same position and have the same function as the corresponding toes of the hairy woodpecker. I pointed out above that in the hairy woodpecker the hallux, as in most of the picine genera in which it is short, is largely functionless and can degenerate without detriment to the climbing ability of the woodpecker. Final loss of the hallux has occurred in the genera *Picoïdes, Dinopium,* and *Gecinulus.* Scharnke (1931) has shown that the metatarsus of digit one is important as a point of attachment for a tendinous stop (*Sperrvorrichtung*) running from the trochlea of the second toe to the base of the fourth toe. This tendinous stop is apparently of such importance to the proper functioning of the foot that it does not permit the hallux and its metatarsus to degenerate beyond a certain point. Even in the three-toed woodpeckers, in which there is no external evidence of the hallux, the metatarsus and a nubbin of bone representing the hallux remain (as first pointed out by Forbes, 1882b) and still serve as the point of attachment for the tendinous stop running between the second and third toes.

Pileated Woodpecker (*Dryocopus pileatus*)

The foot of the pileated woodpecker is quite similar to that of the flicker. It is zygodactyl, with toes one and four lying on each side of the tarsus and having no connection with each other. The relative lengths of the toes are about the same as in the flicker, but the claws are larger and more strongly curved. The claw on the hallux is especially well developed and strongly curved, although the hallux itself is relatively short. The united basal phalanges of the second and third digits are as long as in the flicker, and the pad on their plantar surface is divided by a slight groove separating the digits. Again as in the flicker, the plantar surface of the toes is of uniform width throughout the length of the toes, covered with small rounded scales and divided into tylari. However, the tarsus is relatively shorter and broader than that of the flicker, and its plantar surface is covered with small hexagonal scales approaching the pycnaspidean condition. There is no callus on the "heel." The foot of the pileated woodpecker is illustrated in figure 1C.

The pileated woodpecker does more drilling than the flicker and commonly cuts large troughs in pine trees to obtain carpenter ants that are boring in the wood. However, a large part of its food is obtained from rotting logs or from the ground (Burt, 1930, p. 464). It is difficult to judge the degree of specialization in the foot of the pileated woodpecker because of the varied habits of the bird. The pileated woodpeckers seen in Hoyt's film always thrust the fourth toe out to the side while they climb (also reported for the black woodpecker, *Dryocopus martius,* Scharnke, 1930). On the other hand, the foot is most likely zygodactyl when the bird is on the ground or on fallen and decaying logs. Morphologically, the foot of the pileated woodpecker is very similar to that of the flicker. The only major change towards a more efficient scansorial foot is the rotation of the fourth toe to the lateral side of the foot which is not reflected in its structure. While the pileated woodpecker is obviously somewhat specialized for climbing, it is safe to assume that it is not a highly specialized climbing woodpecker. It may well be one of the most unspecialized of the truly arboreal woodpeckers. One interesting feature in the foot of the pileated woodpecker is the shortness of the hallux. In the two species of *Dryocopus* examined, the hallux was quite short, even relatively shorter than the hallux of *Dendrocopos villosus.* The important question is whether the hallux of these species of *Dryocopus* is important for the functioning of the foot. I was unable to see the hallux of the birds shown in the film and thus cannot answer this question at the present time. However, I postulate that some form of *Dryocopus* or woodpecker similar to it had a hallux which remained long and functional —the ancestral foot from which the foot of the ivory-billed woodpecker evolved.

Ivory-billed Woodpecker (*Campephilus principalis*)

The foot of the ivory-billed woodpecker presents a striking contrast to the foot of the flicker or of the pileated woodpecker, yet the morphological changes are relatively minor. The hind toes, both the first and fourth, have rotated to the outer side of the foot until in the extreme condition all four toes point forward—a "pamprodactyl" foot. Thus the zygodactyl condition of the foot is completely lost, and there is no opposability of the digits. Furthermore, the hallux has lost all connection with the second toe and has actually shifted from its inside position towards the outer edge of the tarsus, to lie on the outer side of the foot next to the fourth toe. The base of the hallux and the fourth toe are connected, so that they move as a single unit in much the same way as in the hairy woodpecker. Perhaps the toes are joined by the ligament running from the base of the fourth toe to the base of the second toe (see above, p. 16). This secondary pamprodactyl foot is markedly different from the pamprodactyl foot of the swifts or the mouse-birds. In the ivory-billed woodpecker, all four toes are in one plane, but not in the plane of the tarsometatarsus. The anterior toes have rotated on their longitudinal axis so that their plantar surfaces face obliquely inward, while the reversed toes (one and four) have also been twisted in a similar manner until their plantar surfaces lie in nearly the same plane as that of the anterior toes. The fourth toe is the longest toe in the foot and is relatively longer than the fourth toe in any other woodpecker. Similarly, the hallux is relatively longer than that of any other picine woodpecker and reaches the same relative length as the hallux of the wryneck. However, the hallux of the ivory-billed woodpecker is thicker, and its claw is long and strongly curved. The basal phalanges of the second and third toes are still united by a common sheath of skin, but they are proportionally shorter than in any other woodpecker. A deep longitudinal groove divides the pad on the plantar surface of these conjoined phalanges. The plantar surface of the toes has lost its covering of smooth, rounded scales on the distal two-thirds of the digit. Instead, the plantar surface is compressed laterally and is covered with rows of rough scales which are separated by transverse grooves. The tarsus is of about the same relative length as that of the flicker and is decidedly longer than that of the pileated woodpecker, but is much broader than the tarsus of either form. Its plantar surface is reticulated or covered with small rounded scutes—the pycnaspidean condition. When viewed in cross section, the plantar surface of the tarsus is flatter than that of all other woodpeckers. A well-developed callus is present on the plantar side of the proximal end (the "heel") of the tarsus. The foot of the ivory-billed woodpecker is illustrated in figure 6.

The structural differences of the ivory-billed woodpecker foot make it appear markedly different from the foot of the flicker or that of the pileated woodpecker. However, its appearance in life is even more

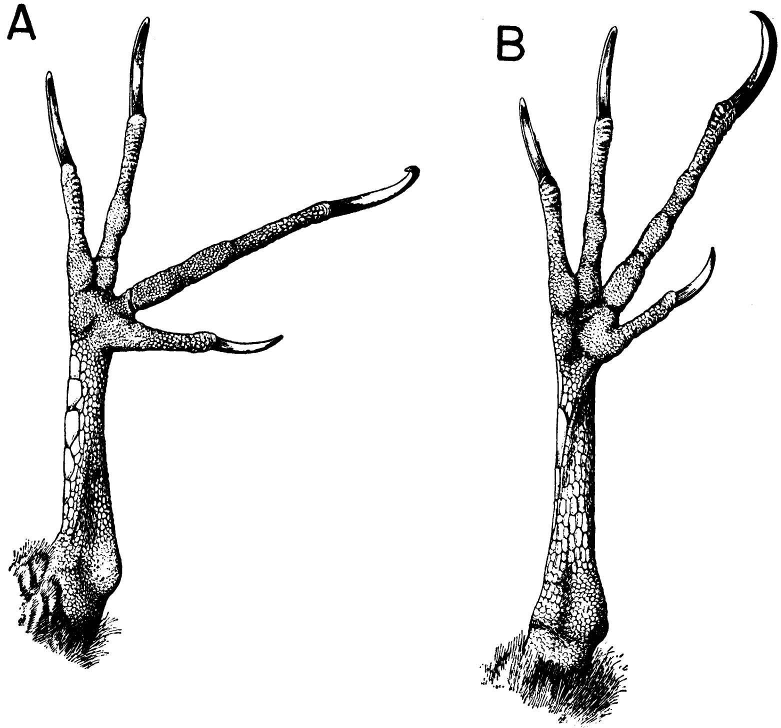

FIG. 6. Plantar surface of the foot to show the moderate and extreme rotation of the fourth toe and the hallux in the ivory-billed woodpeckers. A. *Phloeoceastes melanoleucos*. B. *Phloeoceastes rubricollis*.

remarkable. Waldron DeW. Miller writes in the original manuscript: "In life, as observed in the Guatemalan Ivory-billed (*Phloeoceastes guatemalensis*) in its native haunts, the position of the toes is very striking. They possess great mobility, and the long fourth toe can be thrust out at right angles to the anterior digits, and again may be directed as strongly forward as in the ordinary anisodactyl foot. Frequently, as when ascending a vertical limb, the toes are all directed forward, a pamprodactyl arrangement of a unique kind."

The arrangement of the toes in a climbing ivory-billed woodpecker can be seen in the bird illustrated by Tanner (1942, pl. 13).[1] The feet are held to the side of the body and are directed diagonally upward

[1] The following remarks on the arrangement of the toes in the ivory-billed woodpecker are based on the position of the toes seen in the several photographs presented by Tanner (1942) and several photographs lent to me by Dr. A. A. Allen and Dr. J. T. Tanner to whom I am very grateful.

and sidewise. Usually the angle between the tarsus and the horizontal plane is 45 degrees or less. All four toes are spread wide apart; the shortness of the conjoined basal phalanges of toes two and three makes possible the spreading of these toes. Generally the three longest toes are held forward and the hallux laterally, or the second and third toes are directed forward and the fourth and first toes to the side. When the three longest toes are held forward, they are spread widely; the angle between the longitudinal axes of toes two and four is from 90 degrees to 120 degrees. This arrangement of the toes provides a very firm support against both the downward and outward components of gravity. Miller states that the plantar surface of the tarsus is pressed against the tree trunk, but does not say whether he observed this in life. In all the photographs of the ivory-billed woodpecker that I have seen, the tarsus seems to be pressed against the tree trunk, but I do not have direct proof of this fact. In all other woodpeckers, the tarsus is held away from the tree trunk. In these woodpeckers, the hallux lies under the distal end of the tarsus and thus prevents it from lying against the tree trunk. In the ivory-bill, the hallux has shifted from the medial side of the tarsus to the lateral side, so that it does not prevent the tarsus from being pressed against the supporting surface. The callus on the "heel" of the tarsus protects it from abrasion when it is pressed against the tree trunk.

The specialized modifications in the highly arboreal ivory-billed woodpecker are not so much in the structure of the toes as in the position of the legs. The action of the toes is similar to that of the hairy woodpecker with the addition of the functional hallux. However, in most woodpeckers, as, for example, the pileated woodpecker, the legs are held more or less beneath the body, the joints are doubled up, and the tarsus is held away from the tree trunk. This position of the legs is disadvantageous for the bird, because the body is held away from the tree trunk and the muscles of the leg are working at a mechanical disadvantage; the analogy is to the mountain climber who is standing on a narrow ledge with hand holds only beneath his chest. In the ivory-billed woodpecker, the legs are directed away from the center of the body, and the tarsus is pressed against the tree trunk. This method allows the body to be held close to the tree, with the joints of the leg extended. Hence the leg muscles have a mechanical advantage, because they are at the beginning of their contraction cycle and are acting along the length of the segments of the leg. When the body is held close to the trunk, it not only decreases the outward component of gravity but allows the tail feathers to be applied to the supporting surface for a greater distance from their tips. If the bird is climbing on smaller limbs, the feet can encircle the limb and thus obtain better support. However, no matter what size the limb is, the disposition of the legs and the spreading of the toes of the ivory-billed woodpecker furnish direct and powerful resistance to both the lateral and backward motions of the woodpecker when it is at work and, with the tail, furnish a tripodal base of great strength against the pull of gravity.

When the ivory-billed woodpecker is sitting on the ground and presumably when it is perching on horizontal limbs, the toes assume the typical zygodactyl arrangement. This can be seen in plates 17 and 18 of Tanner's study of the ivory-bill (1942).

A foot structure quite similar to that described for the ivory-billed woodpecker is found in the following genera: *Blythipicus*, *Chrysocolaptes*, *Phloeoceastes*, and *Campephilus*, which have been placed together by Peters at the end of his list of woodpeckers and considered by him to be the most highly specialized genera of woodpeckers.

SUMMARY OF THE CLIMBING MODIFICATIONS IN THE WOODPECKER FOOT

The modifications that are described in detail above can be briefly summarized in a comparison of the major changes between the three main types of picine woodpeckers. I do not consider the perching foot of the wryneck and the piculets, as there are only minor changes between their foot structure and that of the flicker.

Ground Woodpeckers

In study skins and in life when the bird is climbing, the toes are typically zygodactyl. Both the hallux and the fourth toe are directed backward, but the fourth toe may sometimes (rarely?) be held to the side. These toes are not associated with one another. The anterior toes are nearly parallel, the result of the relatively great length of the joined basal phalanges of these toes. These woodpeckers spend much time on the ground, during which time the toes are zygodactyl.

Short-Hallux Line

In life, the long fourth toe usually projects outward or even obliquely forward. The weak hallux lies on the outer side of the foot, sometimes at right angles to the fore toes, but almost always lies on its side or in some other cramped position. In study skins, the feet are usually zygodactyl, but the reversed fourth toe often projects more or less outward but never forward of a right angle to the anterior digits. The fore toes are spread somewhat more than in the ground woodpeckers because of the reduction in the length of the conjoined basal phalanges. The hallux is short and functionless and has become degenerate or even lost in several genera, *Picoïdes, Dinopium,* and *Gecinulus.* In these genera, the position and function of the remaining toes are the same as those of the corresponding toes in the other genera of this group.

Long-Hallux Line

In life, the well-developed hallux and the very long fourth toe, which are bound together basally, are habitually directed forward or at least at right angles to the anterior toes. This arrangement of the toes is usually retained in study skins. The fore toes are widely divergent, which is permitted by the extremely short but still conjoined basal phalanges of the second and third toes. The feet of these woodpeckers are held to the side of the body, while the tarsus is pressed against the tree trunk, thus permitting the body to be held close to the tree.

Thus in the woodpeckers, an unmodified zygodactyl foot is present only in the most generalized scansorial genera or those that obtain their food from the ground. A zygodactyl arrangement of the toes is perfectly suitable for locomotion on the ground, the outstanding example being the road runner (*Geococcyx*) which is among the fastest running birds and has retained the typical cuculid zygodactyl foot. All woodpeckers, even the most specialized climbers, hold their toes in a zygodactyl position when hopping on the ground. However, although the most generalized picine woodpeckers hold their toes in a zygodactyl arrangement when they are climbing, a more efficient climbing foot has evolved in the more specialized woodpeckers. The major change from the zygodactyl foot in the development of this new foot type was an outward rotation of the fourth toe to a lateral position in most woodpeckers or to an anterior position in few highly specialized genera; whether the hallux is short and functionless or long and functional is of lesser importance. For this reason, W. DeW. Miller had suggested the term "ectropodactyl" (turning-out-of-the-way toe) for the functional scansorial woodpecker foot. Adoption and use of this term would help emphasize the fact that the functional climbing foot of the woodpeckers is not a zygodactyl foot, but a true scansorial foot—the ectoropodactyl foot.

THE FOOT STRUCTURE OF *MICROPSITTA*

The small parrots of the genus *Micropsitta* of New Guinea and surrounding islands obtain their food by climbing on tree trunks and picking fungus off the bark (Steinbacher, 1935, pp. 271–272; Sibley, 1951, p. 86). Their tail feathers have stiffened shafts and are used to brace the tiny parrot in the same way as does the tail of the woodpeckers. The foot structure of the Psittacidae is zygodactyl, one that is rather similar to the zygodactyl foot of the perching families of the Pici. The important question is whether *Micropsitta* has retained the zygodactyl foot of the parrots or if its foot has become modified in some way. Fortunately Steinbacher (1935, p. 272) has pictured the foot of *Micropsitta*. In this genus, the fourth toe has rotated to the front of the foot on the lateral side and lies next to the third toe, while the hallux has rotated to the front of the foot on the medial side and lies next to the second toe. All four toes point forward, which signifies a pamprodactyl foot but one that is similar to the pamprodactyl foot of the Coliidae, not to the foot of the ivory-billed woodpecker. Thus in one genus of parrots that has acquired scansorial habits, the zygodactyl foot was converted into a typical pamprodactyl foot.

EVOLUTION OF PERCHING AND CLIMBING FEET IN BIRDS

The Problem

The fact that the zygodactyl foot is not a climbing foot but a perching foot has, I believe, been established beyond any reasonable doubt. The functional scansorial foot of the woodpeckers is not a zygodactyl foot, but an ectropodactyl foot, that is, a true climbing foot which has evolved from the zygodactyl foot. These facts are clear, but if one attempts to align them with what is known about the evolution of perching and climbing feet in birds, the picture becomes most confused. Steinbacher's work (1935) is still the most thorough as well as the most recent study of this problem, yet it leaves many unsolved questions. His major conclusion was that the differences between the various arrangements of the toes cannot be explained on functional grounds, but that these morphological differences are "phylogenetic" in origin. This conclusion does not seem to be quite correct, for it has just been shown that the zygodactyl foot differs functionally as well as morphologically from the ectropodactyl foot, the former being a perching foot while the latter is a climbing foot. Yet Steinbacher's argument in support of this conclusion is perfectly correct, for he points out, first, that a specific foot type such as the zygodactyl foot may be used for several quite different modes of locomotion, with only very small structural modifications from the basic morphological type, and, second, that several different foot types may be equally suitable for one particular function. However, from Steinbacher's conclusion, it is impossible to determine if he also implied that the different arrangements of the toes evolved not because of functional needs (i.e., the accumulation of genetical factors by natural selection) but rather by some other method. He did claim that the foot types evolved before their functions became similar, which implies that they did not evolve because of functional demands but rather had appeared and were then made use of by the birds. These ambiguous conclusions on the evolution of the foot types are the result of Steinbacher's confusion of two quite important principles of evolution, namely, that a structure may evolve for one purpose and once evolved can function in several other ways, and that there is more than one way of achieving the same functional goal (for a discussion of the latter point, see Simpson, 1953, pp. 179–181). It must be remembered that Steinbacher was chiefly interested in the adaptive modifications of the internal structure of the foot, which he studied in great detail, and only secondarily interested in the evolutionary history of the several foot types.

But the dilemma remains. Can the evolution of the several foot types be the result of functional needs, if their morphological differences cannot be explained on functional grounds? I attempt to solve this problem by first establishing the basic functional requirements of the perching foot and of the climbing or clinging foot, from which the selection forces controlling their evolution may be determined. From the knowledge of these selection forces and of the structure of the ancestral foot structure, the evolutionary histories of the different arrangements of the toes can be deduced. Although many workers, including Steinbacher, have discussed the function and evolution of the hind foot in birds, a study of the causal factors and the evolution of the different perching and climbing feet in birds has never been attempted. The only paper dealing with the foot in the entire class of birds is by Reichenow (1871). It contains much information but is long out of date. In the present discussion, I am concerned only with the arrangement of the toes as it can be observed in the living bird or in a study skin; the variation in the internal morphology of the hind limb is not considered. It is believed that a comparison of the internal morphology would not contribute significantly more at this time to a better understanding of the evolution of the foot types than can be obtained from a comparison of the arrangements of the toes, but would only confuse the over-all picture with needless detail. Study of the internal morphology of the foot is needed to provide additional evidence for the determination of the validity of the conclusions drawn below and to provide the details necessary for a knowledge of the finer points of the evolution of the foot.

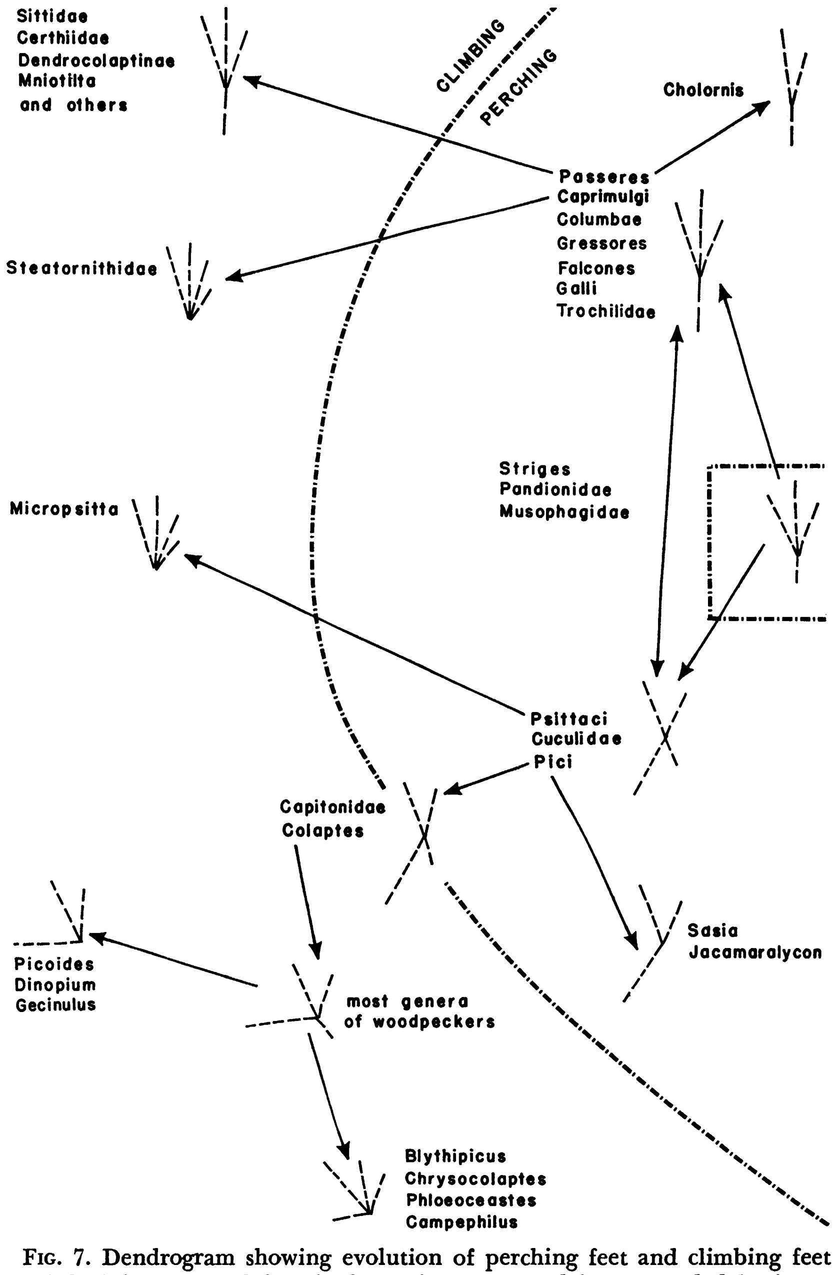

FIG. 7. Dendrogram showing evolution of perching feet and climbing feet in birds. The ancestral foot is shown in center and is surrounded by inner ring of perching feet which in turn is surrounded by outer ring of climbing feet. See text.

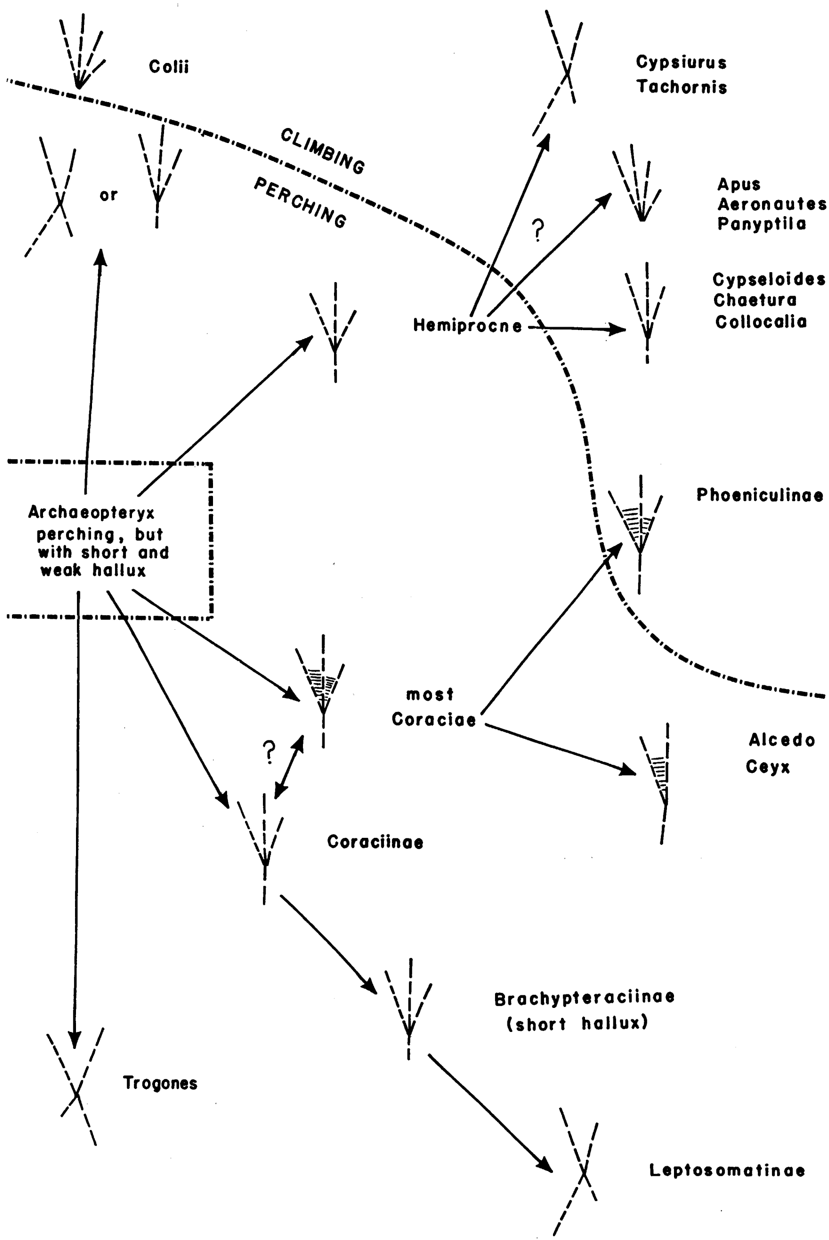

FIG. 7. (*continued*). (For legend, see opposite page.)

I assume that the perching-foot types evolved first and then gave rise to the several types of climbing feet. There are many clear examples of the evolution of climbing feet from perching feet, but no case of a distinct type of climbing foot that gave rise to a perching foot, although there may be cases in which a climbing bird reverted to a perching way of life with the necessary changes in foot structure. The over-all picture of the evolution of the foot types is shown in figure 7. In this dendrogram, unrelated birds are occasionally grouped together if they have the same foot structure. Thus this figure does not necessarily indicate relationships between those birds placed together or show the exact number of times that a particular foot type has evolved. For example, only one evolution of the zygodactyl foot from the ancestral anisodactyl foot is shown, but there is little doubt that the Pici, the Psittaci, and the Cuculidae have all acquired their zygodactyl foot independently of one another.

In these discussions, running or swimming feet are not considered, because no really distinct arrangement of toes has evolved for running or swimming. Rather, the ancestral anisodactyl arrangement was kept with modifications in the claws, the development of lobes or webs between the digits, or perhaps the loss of a toe, usually the hallux. There is good evidence in support of the hypothesis that the six arrangements of the toes found in birds evolved in response to the selection forces associated with perching or climbing. Although the perching-foot types are suitable for locomotion on the ground as well as for perching in trees, the terrestrial way of life developed after the perching-foot type had evolved, so that the cursorial function of the foot must be regarded as a secondary function, not as the primary function responsible for the origin of the particular foot type.

Foot Types

Six major arrangements of the toes can be defined, as follows:

1. Anisodactyl: Hallux posterior (to the tarsometatarsus) and usually long; second, third, and fourth toes anterior.
2. Syndactyl: Hallux posterior and usually long; second, third, and fourth toes anterior and partly encased by a common sheath of skin.
3. Zygodactyl: Hallux and fourth toe posterior; second and third toes anterior; hallux usually short.
4. Heterodactyl: Hallux and second toe posterior; third and fourth toes anterior; hallux usually short.
5. Pamprodactyl: All four toes anterior; the hallux lies on the inside of the foot and next to the second toe.
6. Ectropodactyl: Second and third toes anterior; fourth toe either lateral, at

right angles to the second and third toes, or anterior; hallux usually lateral or rarely anterior, but, if so, it lies next to the fourth toe, not the second.

In most birds, the arrangement of the toes is permanent in life, but in some groups, one or more of the toes can be moved from one position to another. Birds that have a movable toe usually have two different methods of locomotion, for instance, climbing on trees and hopping on the ground as in some woodpeckers, and can change the arrangement of the toes to meet the functional demands of the type of locomotion. In any case, the functional position of the toes, not necessarily the arrangement seen in the study skins, is correlated with the habits of the bird.

Ancestral Foot Structure

The reptiles ancestral to the birds, the pseudosuchians, had a pamprodactyl foot, with all five digits present. In the course of the evolution of the avian foot, the fifth digit was lost and the hallux rotated to the posterior side of the foot to oppose the remaining fore toes. The functional basis for the loss of the fifth toe is obscure, but the reversal of the hallux was an adaptation to the arboreal habits of the first birds. Thus *Archaeopteryx* possessed an anisodactyl foot, but one in which the hallux is relatively short. De Beer (1954, p. 33) gives the following measurements for the specimen in London: hallux, total length, 20 mm.; second toe, total length, 31.5 mm.; third toe, total length, 46 mm. These measurements show that the hallux was decidedly shorter than the anterior toes. In the modern passerines, the hallux is usually longer than the second toe and approaches the length of the third toe. More significant, however, is the fact that the hallux of *Archaeopteryx* appears to be slightly elevated above the plane of the anterior toes, which would further reduce its effectiveness as an opposable toe. Therefore, although it is quite safe to assume that *Archaeopteryx* was an arboreal bird, its foot was not a very effective perching foot. Because *Archaeopteryx* lived in the Jurassic, it cannot be considered as directly ancestral to the modern orders of birds which probably arose in the late Cretaceous or early in the Tertiary, but I assume that the immediate ancestral avian foot was similar to that of *Archaeopteryx*. If the ancestral avian group, or groups, from which the modern orders of perching birds evolved had a well-developed hallux and consequently an efficient perching foot, then there would be no reason for the other types of perching feet to evolve. This last bit of reasoning seems circular, but, if it is not correct, the rest of the discussion on the evolution of the perching and climbing feet in birds breaks down.

Evolution of the Shift of a Toe

The shift of a toe from an anterior to a posterior position, or vice versa, is a relatively simple evolutionary change. However, the original shift of a toe, as, for example, the fourth toe to a posterior position in the evolution of the zygodactyl foot, is more difficult than the secondary shift of a toe, as, for example, the rotation of the fourth toe back to an anterior position in the evolution of the ectropodactyl foot from the zygodactyl arrangement of the toes. The difference between an original and a secondary shift will become clear if we examine the changes that took place during the reversals of the fourth toe in these examples. The first step in the evolution of the zygodactyl foot would be the accidental placing of the fourth toe behind the branch in an awkward position as shown by the Musophagidae or *Leptosomus*. The extensor and flexor muscles of this toe would still have the same function as when the toe was anterior to the tarsometatarsus, but their effectiveness would be reduced because of the absence of an efficient pulley system to reverse their pull and of the lack of a suitable trochlea for this toe. However, if there was an advantage for the bird to have its fourth toe reversed, then there would be a selective advantage favoring these and other structural modifications which would increase the effectiveness of the reversed position of the toe. The best discussion of these structural modifications in all groups of birds having a reversed toe is that of Steinbacher (1935) to which the interested reader is referred. Turning of the fourth toe back to an anterior position is an exceedingly simple change; all that need to be done is for the muscles attaching to this toe to pull it around to the front of the foot. The necessary placement of the tendons and trochlea is already present. Proof of the ease of the latter shift of the fourth toe lies in the fact that in most groups of birds in which a toe is secondarily anterior, that toe is reversible in life, such as the fourth toe in the woodpeckers and the mouse-birds. This is not to say that all birds with a reversible toe in life are of this type, for in the Leptosomatinae and the Musophagidae the turnable fourth toe is in the early stages of being reversed for the first time.

Loss of a Toe

The other change in the arrangement of the toes discussed here is the loss of a toe. In almost every group of birds possessing a certain foot type, there are genera that lack a toe. Upon examination of related genera which still possess this toe, it is usually found to be small and without an important function, or degenerate and clearly functionless. These cases are important, for they indicate which toes had a limited function in the ancestral forms and thus provide us with clues to the probable evolution of the different foot types. I do not discuss the rare variations in the number of phalanges of the digits. In almost all birds, the number of phalanges in a digit is uniform; there are two phalanges in the first toe, three in the second toe, four in the third, and five in the fourth. In the dendrogram (fig. 7), the number of a toe can be determined from the number of phalanges shown, the formula being that the number of the digit equals the number of phalanges shown minus one.

EVOLUTION OF THE PERCHING FOOT

The major functional requirement of a perching foot is a strong set of opposable toes by which the branch can be grasped. A foot in which several strong toes are opposed by one weak toe is a very unsatisfactory perching foot. It does not matter which toes oppose one another, nor must there be an equal number of opposing toes; one toe can oppose two or three toes. Hence if a toe is small and weak it can be lost without harm to the perching ability of the bird, if at least one strong toe remains to oppose the others. Very often the toes are bound together basally or along a greater part of their length, so that they are held parallel to one another and at right angles to the branch. If the toes are spread apart when grasping the branch, not all the force of flexion is directed against the branch and is lost. If the toes are held at right angles to the longitudinal axis of the branch, then all the force of flexion is directed against the branch. Lateral forces on the bird are compensated for by its holding its feet apart, not by spreading its toes. These characteristic features of the perching foot are best illustrated by the foot of the African chameleon (see above, p. 11).

Birds have solved the problem of evolving a suitable perching foot from the poorly developed ancestral perching foot in the four different possible ways available to them. The resulting foot structures are the four perching-foot types known in modern birds (anisodactyl, syndactyl, heterodactyl, and zygodactyl), and in each instance they evolved in response to the selection force for a strong set of opposable toes.

Anisodactyl

The simplest method of achieving a perching foot is by an elongation of the hallux until it can provide strong opposition to the anterior toes. Commonly, but not necessarily, the basal phalanges of two or more toes are bound together by a common sheath of skin. Because of the ease with which a perching foot is developed by this method, it is not surprising that the anisodactyl foot is the commonest type of perching foot and is found in the Passeres, the Caprimulgi except the Steatornithidae, the Columbae, the Gressores, the Falcones, the Galli, the Trochilidae, and the Hemiprocninae. The foot of the Coraciinae and the Brachypteraciinae is an anisodactyl foot, not a syndactyl foot as claimed for the entire order of the Coraciae. Of interest are those perching birds, the Striges, the Pandionidae, and the Musophagidae, that have a reversible fourth toe in life. These birds may employ the anisodactyl or zygodactyl arrangement of the toes when perching; the Musophagidae almost always use the zygodactyl arrangement. When perching, the mouse-birds, *Colius*, may have an anisodactyl or a zygodactyl foot.

Most Caprimulgi have an anisodactyl foot, but one that varies in its adaptation to perching. The Caprimulgidae nest on the ground, and, when they perch on branches, they sit along the branch. Their hallux is very short and provides only slight opposition to the fore toes; consequently their foot is a very poor perching foot. The Aegothelidae and the Podargidae nest in trees and sit crosswise on branches. Their hallux is long and opposes the fore toes, thus forming a very satisfactory perching foot. The Nyctibiidae are the most arboreal family in this order and have the most specialized perching foot. The hallux is long and very broad, while the anterior toes are bound together basally; the foot is thus similar to the syndactyl foot of the Bucerotidae.

The only loss of a toe among birds possessing an anisodactyl foot is that of the fourth toe in *Cholornis* (Chamaeini of the Timaliinae; see Forbes, 1882a, p. 388). Only the basal phalange of this toe remains in this genus, yet there is no indication of a functional basis for the degeneration of this toe. In all other birds possessing an anisodactyl foot, including the close relatives of *Cholornis*, the fourth toe is well developed and is clearly functional. The absence of this toe in *Cholornis* is of great interest, for it proves that not all of the three anterior toes of the anisodactyl foot are needed and that genetical factors for the loss of one of them may accumulate. In *Cholornis*, genetical factors for the degeneration of the fourth toe have increased until they permit the development of only the basal phalange of this toe. In this case, the genetical factors for the loss of the fourth toe are not favored because of any advantage in losing this toe, but were allowed to accumulate because of the lack of a selection force against them. This explanation is equally applicable to all cases of a loss of a toe in the several perching- and climbing-foot types.

Syndactyl

A second way for a perching foot to evolve without a shift in the position of the toes is for the fore toes to be bound together in a common sheath of skin in addition to a lengthening of the hallux. It is possible that the syndactyl foot evolved from an anisodactyl perching foot rather than from the ancestral, poorly developed perching foot, but such a possibility is a minor detail and does not affect the general conclusions of this paper. However, it should be pointed out that the degree of syndactylness varies greatly between the different families of the Coraciae, from the extreme syndactyl condition in the Bucerotidae to a very slight degree of fusion in the Upupidae to the true anisodactyl foot of the Coraciinae. Thus the anisodactyl foot and syndactyl foot grade into each other.

Loss of the second toe in *Alcedo* and *Ceyx* (see Delacour, 1951) is similar in all respects to the loss of the fourth toe in *Cholornis* and need not be discussed further.

Heterodactyl

The weak hallux in the ancestral foot can be compensated for by a reversal of one of the anterior toes. In the trogons, the second digit has become reversed and opposes the remaining anterior toes—the heterodactyl foot. No loss of toes or other structural changes have occurred in the heterodactyl foot.

Zygodactyl

The last way to compensate for a weak hallux is for the fourth toe to be reversed, as has happened in the Pici, the Psittaci, and the Cuculidae which have a permanent zygodactyl foot. The Striges, the Pandionidae, the Musophagidae, and the Coliidae have a temporary zygodactyl foot; the fourth toe can be held either anterior or posterior when the bird is perching. Although most texts list the syndactyl foot as one of the characteristic features of the Coraciae, the cuckoo-rollers (Leptocomatinae) have a functional zygodactyl foot (Milne-Edwards and Grandidier, 1876; Forbes, 1880; Steinbacher, 1935, p. 230). The fourth toe of these birds is reversible in life and is very similar to the musophagid condition. Perhaps the cuckoo-rollers had evolved from the ground rollers (Brachypteraciinae) which are ground-dwelling birds and have a short hallux. If so, there would be a selective advantage for the Leptosomatiinae to have a reversible toe. The cuckoo-rollers have a short hallux similar to that of the ground-rollers, which is unlike the rest of the order.

Many birds possessing a permanent zygodactyl foot have a reduced hallux, or, in the case of *Sasia* of the Picidae or *Jacamaralycon* of the Galbulidae, the hallux is completely lacking. These facts agree with the assumption that the ancestral foot had a weak hallux.

EVOLUTION OF THE CLIMBING FOOT

The toes of the climbing foot must be so arranged that they oppose the pull of gravity. Because most birds climb or cling head up, the anterior toes are the functionally important ones. Posterior toes are of no functional value unless the bird descends the tree head first as does the nuthatch. For some climbing birds, a laterally directed outer toe is of great value in bracing the bird against lateral forces or, as in the ectropodactyl foot, by permitting the two feet to grasp the trunk in the manner of a pincer. The claws of the functionally important toes are strongly curved, so that they can be hooked into the bark; the claws of the toes that point down the tree are usually unmodified and often are relatively straight. In many cases, the climbing foot is associated with stiffened tail feathers; the tail is used as a prop to help support the bird. The major exceptions are the nuthatch (*Sitta*), the wall-creeper (*Tichodroma*), and the black and white warbler (*Mniotilta*), which have short tails but are excellent climbers.

One important aspect of climbing birds is that they can cling to the under side of a branch as well as ascend a vertical tree trunk. The arrangement of the toes used in climbing on vertical surfaces is no longer suitable and in fact is quite useless when the bird is clinging to the under side of a branch. When a bird is in this position, gravity pulls it away from the branch; hence in order to hold the bird to the branch, the toes must act as pincers. Presumably when the feet function as pincers, the toes must oppose one another, which is the exact opposite of the arrangement used when the bird is climbing on a vertical surface. This is, however, only conjecture and must be proved or rejected by direct observation. The functional requirement for clinging to the under side of a branch can be easily met by all the climbing passerines, the woodpeckers, and *Micropsitta*, which can arrange their toes into opposable sets. Birds with a permanent pamprodactyl foot never cling to the under side of a branch. A strongly curved claw on the hallux of birds that climb only head up may have developed in connection with clinging to the under side of a branch.

In contrast to the evolution of the perching-foot types, which all began with the same ancestral foot type, the climbing-foot types (anisodactyl, syndactyl, pamprodactyl, and ectropodactyl) evolved from several different perching-foot types. The adaptive modifications of the different climbing feet depend greatly on the specific perching foot from which they evolved. The differences as well as the similarities of these climbing feet compared to their starting points can be understood most readily by an examination of figure 7. In each case, however, the selection force guiding the evolution of the climbing-foot types was for the toes that oppose the pull of gravity, with the development of strongly curved claws on the functionally important toes.

ANISODACTYL

The anisodactyl foot is not only a highly efficient perching foot but a perfectly suitable climbing foot; the three anterior toes are apparently sufficient to fulfill the functional requirements of the climbing foot. Within the Passeres there have been a number of independent lines that have acquired climbing habits. The three major ones are the Sittidae, the Certhiidae, and the Dendrocolaptinae, and the minor ones are *Mniotilta* of the Parulidae, *Loxops* and *Hemignathus* of the Drepanididae (Amadon, 1950), *Camarhynchus pallidus* of the Geospizinae (Lack, 1943, pp. 58–59), *Phormoplectes* (all species), *Malimbus rubicollis* and slightly so in *Anaplectes rubriceps* of the Ploceidae (Stresemann, 1927–1934, p. 550; Chapin, 1939, pp. 383, 390–394, and 397), and no doubt several more. The relationships of a number of genera [*Salpornis, Rhabdornis, Climacteris, Tichodroma, Neositta, Daphoenositta* (for habits, see Rand, 1936), and *Hypositta*] that are usually placed in the Sittidae or the Certhiidae are much disputed (see Mayr and Amadon, 1951, pp. 23–24). These genera may represent a number of independent acquisitions of climbing modifications and may be completely unrelated. However, for descriptive purposes, *Tichodroma* and *Salpornis* are similar to *Certhia,* while the other genera are similar to *Sitta.* The most interesting feature of the scansorial passerines is the variation in the claws which reflects their climbing habits. *Camarhynchus, Phormoplectes,* and *Malimbus* appear to be the least specialized for climbing; their claws are the same as those of their perching relatives. In all other genera, the claws of the anterior toes are more strongly curved than those of their close relatives. The claw on the hallux of the Dendrocolaptinae and the Certhiidae, which climb only upward on vertical surfaces, is relatively straight and apparently cannot be hooked into the bark. It is pointed out above that a toe pointing down the tree is of no value to a climbing bird, so that there is no selection force for a strongly curved claw on the hallux. Richardson apparently missed this point, for he stated that the hallux of the creeper is strongly curved and is hooked into the bark when the bird is climbing. To be sure, the claw on the hallux of the creeper is not straight, but somewhat curved. This may well be a modification for clinging to the under side of a branch when the foot probably functions as a pincer. On the other hand, the nuthatches (*Sitta*), the black and white warbler (*Mniotilta*), *Hemignathus*, and *Loxops*, which descend the tree head first as well as climb up the trunk, have a large, strongly curved claw on the hallux. This claw hooks into the bark when the bird is climbing down the tree and opposes the pull of gravity. It must be large, because it is the only functional claw when the bird is descending the tree. Most of the climbing passerine birds perch at least occasionally which has prevented the loss of the hallux.

Syndactyl

The tree hoopoes (Phoeniculinae) apparently climb on tree trunks in the manner of a creeper (Stresemann, 1927–1934, p. 550; Bates, 1930, pp. 333–335). They have retained the typical syndactyl foot, but the claws on all four toes have become strongly curved, which indicates that they descend the tree head first as well as climb up the trunk. Most works state that the tree-hoopoes climb about branches or on trunks but do not definitely say whether or not they climb down the trunk. The nearest relatives of the tree-hoopoes, the true hoopoes (Upupinae), spend most of their time on the ground and have relatively long, straight claws on all digits.

Pamprodactyl

The most specialized climbing foot is marked by the anterior position of all four toes—the pamprodactyl foot. Because the pamprodactyl foot has evolved in several quite different groups of birds, each case is discussed separately.

Only one genus of parrots, *Micropsitta*, has acquired climbing habits. In this genus the zygodactyl foot of the parrots has evolved into a pamprodactyl foot by a forward rotation of both the hallux and the fourth toe. Further details on the structure of the foot in *Micropsitta* can be found above (p. 25).

The mouse-birds, which employ either a zygodactyl or an anisodactyl foot when perching, move both the hallux and the fourth toe to the front of the foot when clinging to a vertical surface or to the top of a stump. These birds are the outstanding example of a group of birds that can alter the arrangement of their toes to suit the functional demands of the particular mode of locomotion employed at any time.

The foot structure of the swifts (Apodidae) varies greatly and may be (from Lack, 1956) as follows:

Anisodactyl: *Hemiprocne, Cypseloides, Chaetura,* and *Collocalia*
Zygodactyl: *Cypsiurus* and *Tachornis*
Pamprodactyl: *Apus, Aëronautes,* and *Panyptila*

Hemiprocne, the only swift that perches on branches, has a typical anisodactyl perching foot; the hallux is long and opposes the fore toes. In the "primitive" clinging genera, *Cypseloides, Chaetura,* and *Collocalia,* the hind toe is short; hence this anisodactyl foot serves as a clinging foot. At least some of these forms employ their tails as a prop and have modified (stiffened) tail feathers. The pamprodactyl foot is also an adaptation for clinging to a vertical rock wall or tree trunk. In those genera with a pamprodactyl foot, the tail is not used as a prop, which may be the reason why a more highly developed clinging foot has evolved in these genera. A zygodactyl foot is present only in those genera that nest and probably roost during the non-breeding season in palm leaves. A zygodactyl foot would enable the bird to anchor itself firmly to the palm leaf by piercing the leaf with the claws of its foot in the manner of a pincer (as has been suggested previously by Bates, 1930, p. 227). Palm leaves sway in the wind so that the swifts must anchor themselves securely to the leaf; they cannot just cling to it. The other swifts nest and roost on a solid substrate so they must support themselves only against the pull of gravity, which can be accomplished by an anisodactyl or a pamprodactyl foot.

The zygodactyl foot of the nestling *Apus apus* reported by Ingram (1955) and probably of other swifts may be an adaptation for moving about in the nest. There is no reason to suggest, as does Lack (1956, p. 14), that the zygodactyl condition is more specialized than the pamprodactyl foot and that the zygodactyl foot of the palm swifts is neotenic. Additional study of the foot structure and of the evolution of the swifts is needed before we can speculate further on the evolution of the foot types within this family.

Most Caprimulgi have an anisodactyl foot, but the foot of *Steatornis* is pamprodactyl in both the nestling and the adult (Ingram, 1958, p. 115). The hallux has rotated about to the inner side of the foot and extends at right angles to the anterior toes or lies next to the second toe and extends forward. Ingram states that these birds cannot perch in trees and, in contrast to the other goatsuckers, nest and roost on the rocky ledges inside the caves they inhabit. The pamprodactyl foot of the oilbird is thus an adaptation to clinging to these ledges.[1] (It is important to know the angle at which these ledges slope which is unknown at present.) The tail of the oilbird is long and somewhat stiffened and probably serves as an additional brace. Similarly, the Nyctibiidae quite often perch upright on the end of a stump and partly support their body with their long and somewhat stiffened tail.

Zygodactyl

The barbets (Capitonidae) and the most generalized picine woodpeckers (*Colaptes*) can climb on vertical surfaces but possess a zygodactyl foot. I discuss the scansorial ability of the zygodactyl foot above and show that, while the zygodactyl foot is suitable for short periods of climbing, it is a very poor scansorial foot and becomes modified if the bird becomes a specialized climber. For this reason, the zygodactyl foot cannot be considered a true climbing foot and is included in this section for completeness only.

Ectropodactyl

The evolution of the ectropodactyl foot of the woodpeckers from the zygodactyl foot is discussed above in this paper. The loss of the hallux in the three-toed woodpeckers is another case of the loss of a functionless toe.

CONCLUSION

The dilemma facing us is, Can the evolution of the different perching-foot types and the different climbing-foot types be explained exclusively on a functional basis, if their morphological differences cannot be explained on functional grounds? In the above discussion, I

[1] While this paper was in press, Dr. D. W. Snow, who is studying the oilbird in Trinidad, kindly sent me the following observations on the position of the toes in this species. The observations were made from photographs which show all of the points very clearly. When the oilbird is perching on flat surfaces (e.g., the nest, which is placed on a horizontal ledge), the three anterior toes point forward, while the hallux is held inward at right angles to the fore toes. When the bird is clinging on a sloping ledge (which may slope at an angle of 45 degrees or even steeper), the second and third toes point forward as usual, the hallux still points inward or in some cases points backward, and the fourth toe may be held more to the outside of the foot than usual. Thus the toes are spread out considerably which may be a more efficient method of clinging for the oilbird than if all four toes point forward. The tail is pressed hard against the rock which provides additional support.

show that the evolution of each type of foot has definitely been the result of functional demands of the bird, usually when it has taken on some mode of life for which its original foot structure was not adequate. Yet the second part of the dilemma is also true in part. If we consider only the different types of perching feet, then the morphological differences between them cannot be explained on functional grounds[1]; they are all equally suitable for perching. The several arrangements of the toes in these perching feet are simply the result of different ways of achieving the same functional goal—multiple pathways of adaptation (for a further discussion of this topic, see Bock, MS). Whichever choice was made by a particular group of birds depends on the genetic and phenotypic characteristics of that group and the genetically controlled modifications that happened to appear. The same is true for the several types of climbing or clinging feet. Thus it is incorrect to attempt to explain the morphological differences between the perching-foot types or those between the climbing-foot types on functional grounds. In this respect, I agree with Steinbacher; the differences between the foot types are not functional but phylogenetic. Therefore both parts of the dilemma are correct, but it should be stated slightly differently, namely,

> The several perching- or climbing-foot types evolved because of functional demands, but the morphological differences between the types of perching feet or between those of climbing feet are the result of the different ways that birds happened to adapt to these functional demands (multiple pathways) and cannot be explained on functional grounds.

Simpson reached the same conclusion when he compared the cephalopod eye and the vertebrate eye by stating simply that (1953, p. 181) "The differences between the two adaptive characters is simply irrelevant as regards adaptation." Simpson also points out that it is fallacious to conclude that a set of characters or their evolution is non-adaptive just because their morphological differences are non-adaptive

1 In this discussion, only one function (and hence only one selection force) is considered at a time. Thus all references to function in discussions of the perching foot are to the function of perching. The same is true for the climbing foot. Similarly, the statement that the morphological differences between the several types of perching feet are non-adaptive is in terms of perching only. It must be emphasized that the morphological differences between the several adaptive answers for perching may be adaptive in terms of other functions and that one adaptive answer can evolve to another (i.e., the zygodactyl foot to the heterodactyl foot) under the action of other selection forces. This point is discussed at greater length in my other paper (Bock, in press).

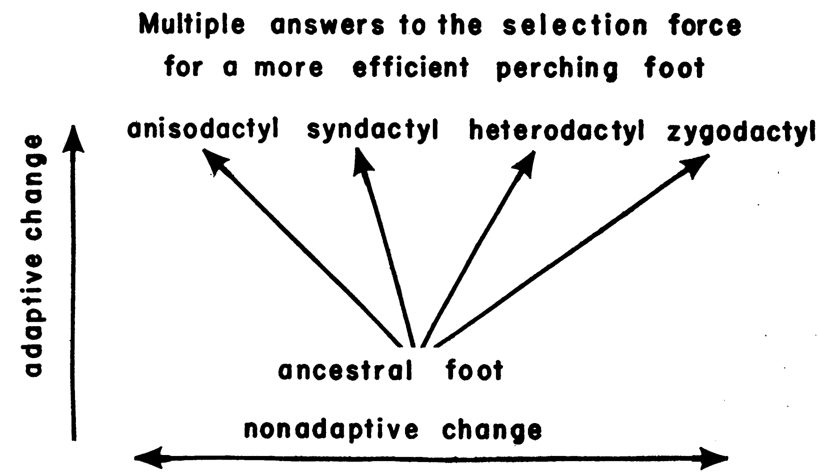

FIG. 8. Evolution of the perching-foot types to illustrate the principle of multiple pathways of adaptation. See text for further explanation.

(1953, p. 179). This conclusion has been illustrated by the use of the evolution of the perching-foot types (fig. 8).

The second part of Steinbacher's general conclusion is that the foot types possess great taxonomic value because their differences "appear to be the result of phylogenetic divergence." This is not correct, for the taxonomic value of a structure is dependent upon the ease with which it can shift from one type to another. I have not made a systematic study of the foot in birds, but there is much evidence to indicate that the foot can be easily changed to meet the functional needs of the bird and that birds with the same foot type, i.e., the pamprodactyl foot, are not necessarily related. Thus I would conclude that, although the morphological differences between the foot types serving one particular function (i.e., perching or climbing) cannot be explained on functional grounds and although the divergence between these birds may have occurred at the time the orders of birds evolved, the foot types are too rigidly tied to their function to provide reliable taxonomic characters.

SUMMARY

1. The scansorial foot of the woodpeckers is not a zygodactyl foot, as commonly believed, but a quite different structure—the ectropodactyl foot. With the exception of the most generalized members of the Picinae, which retain the ancestral zygodactyl foot as the climbing foot, the toes of a climbing woodpecker are arranged as follows; toes

two and three point forward, the fourth toe is thrust out to the lateral side at right angles to the fore toes, and the hallux usually lies beneath the distal end of the tarsometatarsus in a cramped position and is functionless. In the ivory-billed woodpecker, the hallux is long and functional and is directed laterally next to the fourth toe. The fourth toe is either directed forward or thrust out to the side. In all the climbing woodpeckers, the fore toes, together with the stiffened tail feathers which are propped against the tree trunk, serve to support the bird against the downward and inward component of gravity. The laterally directed fourth toes, and to a slight extent the fore toes, prevent the bird from being pulled away from the trunk by the outward component of gravity. Any toe pointing down the tree trunk would be functionless. Lastly, the evolution of the ectropodactyl foot from the zygodactyl foot is outlined.

2. The evolution of the perching- and climbing-foot types in birds is described. It is shown that the main requirement of a perching foot is a set of strong opposable toes. The anisodactyl, syndactyl, heterodactyl, and zygodactyl arrangements of the toes fill the requirements of a perching foot. On the other hand, the toes of a climbing foot must be arranged to oppose the pull of gravity and should bear strongly curved claws. The anisodactyl, syndactyl, pamprodactyl, and ectropodactyl foot types comply with the functional demands of a climbing foot. A dendrogram showing the foot types and their evolution is given. It is shown that each arrangement of the toes evolved in response to a particular function (i.e., anisodactyl foot evolved for perching), but once evolved it was also suitable for other functions (i.e., running or climbing).

3. A brief discussion of the principle of multiple pathways of adaptation or evolution is presented. It is shown that there may be several morphologically different answers to the same selection force and that the morphological differences between these adaptive answers are not the result of differences in function but are a result of phylogenetically different starting points. Furthermore, it is shown that one cannot conclude that different structures (i.e., arrangements of the toes) are non-adaptive just because their morphological differences are non-adaptive. Examples from the evolution of the perching- and climbing-foot types were chosen to illustrate these conclusions.

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