FOOT-SCUTE DIFFERENCES AMONG CERTAIN NORTH AMERICAN OSCINES

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Although avian species often differ in arrangement of the scutes and papillae of the feet (Blaszyk, 1935; Staaland, 1964; Morlion, 1968; Clark, 1972, 1973a), the extent of differences remains undescribed for most birds. I here report selected examples of such differences among North American oscine species and suggest some initial interpretations. The species discussed were chosen in view of their potential interest for functional or systematic interpretation.

MATERIALS AND METHODS

I have examined more than 6000 study skins of 250 North American oscine species, using a binocular dissecting microscope or hand lens to study foot scutellation. Specimens were at the University of Arizona, Harvard Museum of Comparative Zoology, Yale Peabody Museum of Natural History, U.S. National Museum of Natural History, and the University of Connecticut. Throughout the text, a statistically significant difference refers to a probability of less than 0.01 in a Chi-square test. As I have found no evidence for a statistically significant bias between right and left feet within a species, I inspected only the right foot for most species.

OBSERVATIONS AND PRELIMINARY INTERPRETATIONS

Verdin (*Auriparus flaviceps*).—Although usually placed among the Paridae, the Verdin differs sufficiently from typical parids to suggest to Taylor (1970) the possibility of a coerebid affinity. Among Verdins that I have examined ($n = 25$), 64 percent have an intact scute in a position equivalent to that found at the base of the two outer toes in thrashers (*Toxostoma*; Clark, 1972: Fig. 2). In contrast, parids (*Psaltriparus, Parus* spp.) and coerebids (*Coereba, Cyanerpes, Conirostrum*) that I examined typically have a divided scute in this position. In addition, coerebids as a rule have nine scutes in the row along toe II, whereas small parids commonly have fewer (seven in *Auriparus*). Thus in this regard the Verdin is like Paridae rather than Coerebidae, but it differs from both in the high incidence of an undivided basal scute.

Wrentit (*Chamaea fasciata*).—The affinities of the Wrentit have been a controversial subject, but many authorities believe it to be related to the Timaliidae (Mayr and Short, 1970). Species of North American Cinclidae, Troglodytidae, Mimidae, and Turdidae, to which *Chamaea* might be related, have two narrow scutes adjacent to one another at the proximal end of toe IV near its confluence with toe III (Fig. 1). These two narrow scutes are absent in the Wrentit, which is thus like many genera of Old World Timaliidae.

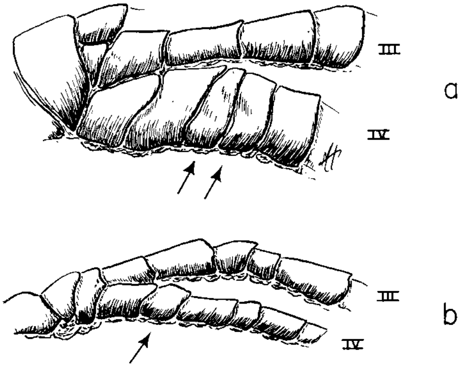

FIG. 1. a) Two narrow scutes near the base of toe IV in a typical thrush (Eastern Bluebird, *Sialia sialis*); b) only one such scute in a typical parulid (Ovenbird, *Seiurus aurocapillus*).

Wrens (*Thryothorus*).—In this genus, two Mexican species for which Grant (1966a) found no notable difference in habitat utilization differ significantly in scutellation. The Happy Wren (*T. felix*; n = 10) has an intact scute at the proximal end of rows extending along the dorsal surface of toes III and IV, in contrast to a divided scute in the corresponding position in the Bar-vented Wren (*T. sinaloa*; n = 20). All ten species of wrens occurring in the United States are like the Bar-vented Wren. I have no explanation for the departure from "normal" in *T. felix*, but the case does illustrate the divergence that can occur in closely related species.

Kinglets (*Regulus*).—Golden-crowned Kinglets (*R. satrapa*; n = 16) differ from Ruby-crowned Kinglets (*R. calendula*; n = 26; Fig. 2) in having one more scute near the distal end of toe IV. Grant (1966b) observed more hanging during feeding by Golden-crowns than by Ruby-crowns; conceivably the extra scute on the outer toe of the Golden-crowns might aid in this behavior by allowing greater bending. In the past, *R. calendula* has been placed in a separate genus, *Corthylio*.

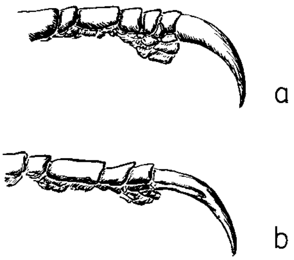

FIG. 2. Distal end of toe IV: a) Golden-crowned Kinglet with three scutes adjacent to claw; b) Ruby-crowned Kinglet with two scutes adjacent to claw.

Olive Warbler (*Peucedramus taeniatus*).—Although the Olive Warbler has generally been considered a parulid, George (1962, 1968) has emphasized its aberrant features and removed it from that family. In scutellation I find that *Peucedramus* differs from parulids (e.g., *Vermivora, Parula, Dendroica,* and *Wilsonia*) in having an extra scute at the proximal end of the rows of scutes extending along both toes III and IV. I have failed to find a *Peucedramus*-like condition in other families thus far examined, including the Muscicapidae (sensu lato) to which George (1962) thought it related.

Yellow-breasted Chat (*Icteria virens*).—This species, ordinarily placed among the Parulidae, is aberrant in numerous ways (Eisenmann, 1962a; Ficken and Ficken, 1962). *Icteria* also differs from all other examined parulids (including *Granatellus*) in scutellation, in possessing an intact scute at the confluence of toes III and IV and in having an extra scute on the second phalanx of toe III. In scutellation *Icteria* is unlike any other oscine examined.

Meadowlarks (*Sturnella*).—The Icteridae are a large and diverse group, and meadowlarks are seemingly bona fide members of the family. However, both Eastern (*S. magna*) and Western (*S. neglecta*) Meadowlarks typically have only two small scutes near the distal end of toe IV, in contrast to three such scutes in representatives of other North American icterid genera.

Rose-breasted Thrush-tanager (*Rhodinocichla rosea*).—This species is now generally placed among the New World nine-primaried oscine assemblage (Eisenmann, 1962b), but it forages like a mimid or thrush. I find that, unlike North American mimids or turdids (Fig. 1), *Rhodinocichla* lacks the two narrow scutes adjacent to one another at the base of toe IV. In this it agrees with the Thraupidae and allies.

Cardinal grosbeaks (*Cardinalis*).—Cardinals (*C. cardinalis*) and Pyrrhuloxias (*Pyrrhuloxia sinuata*) are frequently treated as congeneric (Gould, 1961; Bock, 1964), but they differ in scutellation patterns to a degree. Pyrrhuloxias ($n = 24$) have a divided scute at the base of toes III and IV, a condition typical of cardinaline finches, including the Cardinal (Clark, 1972; this study). However, 39 percent of sampled Cardinals ($n = 138$) had an intact scute at the base of toes III and IV; the difference is statistically significant. The variation in scutellation in Cardinals shows no simple age, sexual, or geographic association in my sample. While the two conditions of scutellation in Cardinals might be associated with an undetected behavioral dimorphism, perhaps more likely the variation is functionally unimportant with respect to use of the feet.

Towhees (*Pipilo*).—Brown (*P. fuscus*) and Abert's (*P. aberti*) Towhees are closely related emberizines that coexist in a limited area of southern Arizona; there their habitat utilization appears to be similar (Marshall, 1960). Among Brown Towhees ($n = 58$) I found that 21 percent had an

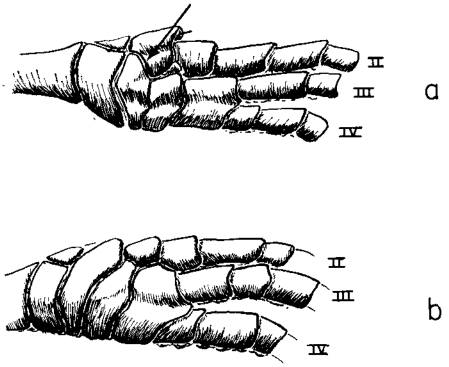

FIG. 3. Dorsal view of the base of the toes showing a) the divided transverse scute of a Fox Sparrow and b) the intact one of a Song Sparrow.

extra (third) scute near the distal end of toe IV. In contrast, 96 percent of Abert's Towhees (n = 30) possessed this scute. This statistically significant difference is structurally analogous to that between the kinglets. Green-tailed (*Chlorura chlorura*) and Rufous-sided Towhees (*P. erythrophthalmus*) resemble Brown Towhees in scutellation.

Sparrows (*Passerella* and *Melospiza*).—The Fox (*P. iliaca*) and Song (*M. melodia*) Sparrows are often considered congeneric (Mayr and Short, 1970). However, I find that the two differ in the condition of an elongate scute that lies transversely across the foot at the base of the toes (Fig. 3). In 98 percent of Song Sparrows (n = 133) the elongate scute was intact, but it was divided in 88 percent of Fox Sparrows (n = 50). The difference is statistically significant. Large Song Sparrows (*M. m. sanaka*) from the Aleutians, comparable to Fox Sparrows in body size, have the intact elongate scute typical for Song Sparrows of smaller body size. The Fox Sparrow is unique among examined emberizines in its divided scute; this is presumably a derived rather than primitive character among emberizines.

DISCUSSION

Only conjectural interpretations, if any, have been offered concerning the functional significance of the species differences found in this study. Similarly, Blaszyk (1935) was generally unable to provide a functional explanation for variations in passerine tarsal scutellation. However, he, Staaland (1964), and Lennerstedt (1972) did find partial association between the structure of toe pads and the size and nature of commonly used perches in European passerine species. Moreover, Clark (1973a) found notches in the toe pads of a number of only distantly related taxa of oscines that climb on trees or rocks. Detailed functional and behavioral studies seem necessary to develop more precise ideas on the adaptive aspects of scutellation. Existing analyses of scutellation in reptiles (e.g., Horton, 1972; Kerfoot, 1970; Marx and Rabb, 1970) indicate that functional interpretation can be difficult due to complex interactions of genetic, developmental, physiological, and environmental factors.

The findings of this study and those of Clark (1972) indicate that significant differences in number of foot-scutes occur between species that are reasonably assigned to the Sittidae, Troglodytidae, Mimidae, Regulidae, Icteridae, Cardinalinae, and Emberizinae. However, unusual features of scutellation also occur in a number of genera aberrant in their respective families, e.g., *Auriparus* ("Paridae") and *Peucedramus* and *Icteria* (both "Parulidae"). Arrangement of foot-scutes might suggest new ideas on evolutionary affinities, but studies of scutellation of oscines from outside North America are needed to enable extended analysis. Caution must be used in interpreting the evidence of scutellation, for convergence and parallelism have probably occurred frequently (Clark, 1973b). As one example from the present study, the number of scutes near the distal end of the outer toe shows convergence between kinglets, icterids, and towhees.

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SUMMARY

This study provides new examples of taxonomic variation in foot-scutes. Coexisting, closely related, species sometimes differ significantly in the arrangement of foot-scutes; examples are *Thryothorus sinaloa—T. felix, Regulus satrapa—R. calendula, Cardinalis cardinalis—Pyrrhuloxia sinuata, Pipilo fuscus—P. aberti*, and *Passerella iliaca—Melospiza melodia.* Variations in scutellation in some cases possibly correlate with behavioral differences, but marked variation within *Cardinalis cardinalis* might be functionally unimportant with respect to use of the feet.

Auriparus, Peucedramus, and *Icteria* are distinct in scutellation with respect to the families to which they are currently assigned, at least in North America. *Sturnella,* on the other hand, seems well-placed in the Icteridae, although it differs in scutellation from other North American members of the family. *Chamaea* is like many Old World Timaliidae in lacking two narrow scutes at the proximal end of the outer toe, as found in North American representatives of the Cinclidae, Troglodytidae, Mimidae, and Turdidae to which Wrentits have sometimes been linked taxonomically. The scutellation of *Rhodinocichla* resembles that of the New World nine-primaried oscine assemblage more than that of mimids or turdids, to which relationship has also been suggested. Certain taxonomic interpretations of scutellation are tempting, but without more study

of function and of a wider array of species, this must be done with caution, particularly in view of variation between more clearly related taxa.

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