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Systematic interpretations of foot-scute patterns in Neotropical finches.—Past investigations of foot-scutes emphasizing North American taxa have documented taxonomic differences (Clark 1972, 1974, 1977). My more recent studies have emphasized several cases of taxonomic differences among those Neotropical finches traditionally placed in the Emberizinae. Here I summarize those differences and discuss their systematic interpretations, including consideration of the question of the affinities of the Galapagos finches with those of the mainland.

Materials and methods.—I examined more than 15,000 study skins of oscines, including representatives of more than 2400 species worldwide and samples of all genera of the Emberizinae, Cardinalinae, and Thraupinae. I also inspected 64 species representing all suboscine families except Oxyruncidae. All specimens were viewed either with a binocular dissecting microscope or a hand lens. The collections used are in the National Museum of Natural History (Washington, D.C.), the American Museum of Natural History (New York), the British Museum (Natural History) at Tring, the Yale University Peabody Museum of Natural History (New Haven), and the Museum of Natural History at the University of Connecticut (Storrs). My classification follows that of Morony et al. (1975).

Sporophilines.—Many Neotropical finches such as *Tiaris, Melanospiza, Lophospingus,* all the species of Galapagos and Cocos Island finches (geospizines), and all mainland genera of tanagers (Thraupinae) have a divided scute at the base of the two outer toes (scute E of Clark 1977) (Fig. 1A). Only in 5 genera, *Volatinia, Sporophila* (except *S. obscura,* discussed below), *Oryzoborus, Dolospingus,* and *Charitospiza,* is the lateral part of scute E most commonly fused with the most proximal scute on the outer toe (Fig. 1B). Such a fusion is not known to characterize any other passerine taxon. Morony et al. (1975) list 36 species in the 5 genera; I have examined representatives for all these except *Sporophila frontalis, S. ardesiaca, S. melanops, S. nigrorufa, S. insulata, S. palustris,* and *S. cinnamomea.* Some variant individuals within at least *Volatinia* and *Sporophila* show a *Tiaris*-like condition (Fig. 1A). For example, in a series of 58 specimens of *Volatinia,* 5 showed this *Tiaris*-like condition. In contrast, a *Sporophila*-like condition is apparently very rare as an individual variant in passerine species that typically have a *Tiaris*-like condition; I have seen one exceptional specimen of the tanager *Cnemoscopus rubrirostris* showing a *Sporophila*-like condition. The occurrence of such individual variations does not negate the potential taxonomic usefulness of species differences (Clark 1972).

The unique pattern of foot-scutes in the 5 genera might indicate their monophyletic origin. Olson (1981) summarized other evidence, including intergeneric hybridization (Sick 1963),

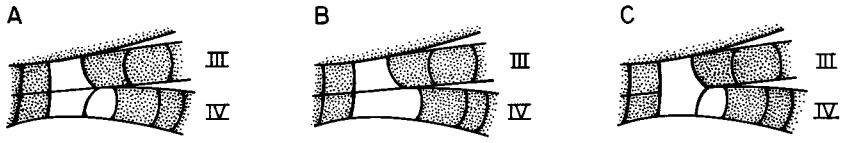

FIG. 1. Schematic dorsal view of the scutes at the base of the two outer toes in (A) *Tiaris,* (B) *Volatinia,* and (C) *Zonotrichia.* The region of differences is unshaded; see text for discussion.

indicating the close affinity of 2 of the 5 genera, *Sporophila* and *Oryzoborus.* Paynter and Storer (1970) placed the genera *Volatinia, Sporophila, Oryzoborus, Dolospingus,* and *Tiaris* within a group of 11 genera of thick-billed ground finches, but they considered this assemblage to be probably polyphyletic in origin. *Dolospingus* is a rare and little known monotypic genus from Venezuela and Brazil. Tordoff (1954) considered *Dolospingus* to be emberizine rather than cardueline on the basis of skull structure. *Charitospiza* is a poorly known monotypic genus from Brazil and northeastern Argentina. Miller (1928) believed that *Charitospiza* and *Lophospingus* were relatively closely related, but he noted a number of differences between them, to which may now be added the difference in foot-scutes. Paynter and Storer (1970) placed *Charitospiza* among their group of emberizines of uncertain affinities.

Historically, no structural characters have been found that would separate all emberizines from all tanagers (Thraupinae), but studies of DNA hybridization by Bledsoe (1985) indicate that 5 genera of finches traditionally considered to be emberizines, *Haplospiza, Diuca, Sicalis, Volatinia,* and *Oryzoborus,* are closer to traditional tanagers than they are to emberizines. Numerous Neotropical taxa including the geospizines have not been studied with respect to their DNA, but the DNA evidence does suggest that *Volatinia, Sporophila,* and *Oryzoborus* are evolutionarily well separated from many other traditional emberizines. The possibility that the similarity of foot-scutes in *Volatinia, Sporophila, Oryzoborus, Dolospingus,* and *Charitospiza* results from some convergence cannot be ruled out, but an hypothesis of homology is more parsimonious in the absence of contrary evidence.

Sporophila obscura.—This species differs from the other 23 examined species of *Sporophila* in having a *Tiaris*-like condition (Fig. 1A) at the base of the two outer toes.

The difference in scutellation between *S. obscura* and the other species of *Sporophila* matches their difference in nest structure and natal pterylosis. *S. obscura* builds a domed nest, unlike other *Sporophila* but like *Tiaris,* and hence Schwartz (in Paynter and Storer 1970) suggested that *S. obscura* should be placed in *Tiaris.* Collins and Kemp (1976) found that the young of *S. obscura* lack natal downs, like *Tiaris* but unlike other *Sporophila.* Nest structure and natal pterylosis might not be independent taxonomic characters in view of the tendency among avian taxa in general for sparse natal feathering to accompany enclosed nest sites. Foot-scutellation, however, also supports the hypothesis that *S. obscura* is misplaced in *Sporophila* and is better assigned to *Tiaris.*

Affinity of geospizines with mainland finches.—Steadman (1982) has summarized the comments of a number of earlier investigators who suggested, without citing many specific details, that the Galapagos finches arose from emberizines of the same stock that produced *Tiaris,* a widespread genus on the mainland, and the West Indian *Melanospiza.* One character shared by *Tiaris, Melanospiza,* and the geospizines is the building of a domed nest placed off the ground; *Tiaris* is the sole mainland genus of the traditional emberizines showing this behavior. The similarity, however, is rather simple and might be convergent (Steadman 1982).

In an extensive comparison, Steadman (1982) found that certain of the geospizines are more similar in osteology and plumage to *Volatinia* than to other traditional emberizines of the mainland. Steadman (1982) therefore reasonably proposed that the geospizines have evolved from *Volatinia*-like ancestors. Bledsoe's (1985) finding that *Volatinia* is a tanager raises the possibility that the geospizines are also tanagers. Barrowclough (1983), however, noted that the resemblances between *Volatinia* and the geospizines might be shared primitive features and hence perhaps misleading as to affinities. Thus there remains controversy concerning the relationships of the geospizines.

The difference in foot-scutes between *Volatinia* and the geospizines would not be expected under the hypothesis that *Volatinia* is the closest mainland relative of the geospizines. However, the difference in foot-scutes might have evolved after their divergence from a common ancestry. Further studies of DNA and other characters are needed to clarify the evolutionary radiation of these taxa.

The Myospiza *sparrows.*—As previously reported (Clark 1972), sparrows, juncos, towhees, and brush-finches placed in 23 New World emberizine genera (including *Zonotrichia, Ammodramus, Pipilo,* and *Atlapetes*) are characterized by an intact scute E at the base of the two outer toes (Fig. 1C). Species differences in presence or absence of an intact scute E in numerous other oscine families (Clark 1972, unpubl. data) indicate that this feature has been subject to considerable evolutionary convergence among oscines as a whole. Nevertheless, this feature in the emberizines is most parsimoniously interpreted as a shared, derived feature indicating a monophyletic origin of these 23 genera (Clark 1972). Further support for this interpretation is found in the close match between this group of genera characterized by an intact scute E and the group Ridgway (1901:27) characterized as having relatively small bills and plain coloration.

Among North American emberizine species with an intact scute E, only the Grasshopper Sparrow (*Ammodramus savannarum*) typically has 9 scutes on the middle toe (III), in contrast to the other species with 10 scutes (Clark 1974). In the present study I found this 9-scute condition in only 2 additional emberizines, the Grassland Sparrow (*A. humeralis*) and the Yellow-browed Sparrow (*A. aurifrons*), both Neotropical and together constituting a formerly recognized genus *Myospiza.*

Meyer de Schauensee (1966) considered the Grassland and Yellow-browed sparrows to be closely related. Mayr and Short (1970) commented that further study was needed of the relationship between the *Myospiza* sparrows and the Grasshopper Sparrow, and, in a phenetic osteological study, Robins and Schnell (1971) concluded that both the Grassland and Yellow-browed sparrows were appropriately placed in the genus *Ammodramus.* The evidence of foot-scutellation leads to the hypothesis that Grasshopper, Grassland, and Yellow-browed sparrows constitute a monophyletic group within a broader genus *Ammodramus.*

General conclusions.—Like other taxonomic characters, features of scutellation can constitute a shared and evolutionarily derived (synapomorphic) attribute in one case and yet be uninformative in another. This study, as well as previous studies (Clark 1977), indicates that foot-scutes, where useful in oscine systematics, are more likely to aid in recognizing affinities of closely related species and genera rather than at interfamilial levels.

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Northern Harrier predation on Willow Ptarmigan.—There are few reports of Northern Harriers (*Circus cyaneus*) killing ptarmigan, although Braun and Rogers (1971) observed a harrier stooping on 2 White-tailed Ptarmigan (*Lagopus leucurus*). In North America, small mammals and birds comprise most of the diet of harriers (Watson 1977). In Scotland, however, Jenkins et al. (1964) found that harriers killed a substantial number of Red Grouse.

Here we document Northern Harrier predation on Willow Ptarmigan (*L. l. albus*) and detail the responses of the prey to presence of harriers during the breeding season in northern Canada. We suggest that harriers may be more important predators on ptarmigan, especially hens with nests, than has been reported previously.

Interactions between Northern Harriers and Willow Ptarmigan were observed in 3 populations in northern Canada between 1978 and 1985. A population of Willow Ptarmigan was investigated at La Perouse Bay near Churchill, Manitoba (58°24′N, 94°24′W), from 1981 to 1985 (Martin 1985). SJH studied populations of *L. l. albus* during 1978 at the