ON THE ORIGIN OF DARWIN'S FINCHES

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ABSTRACT.—We critically reviewed recent attempts to identify the ancestor of Darwin's finches (Emberizidae, "Geospizinae"), and summarized new information on taxa that have been suggested as sister groups of the geospizines, specifically the emberizines *Tiaris*, *Melanospiza*, and *Volatinia*. Reproductive behaviors and displays are conservative among Darwin's finches, and have been neglected in discussions of the ancestry of the group. We concentrate on these characters. We found that *Tiaris* and *Melanospiza* share a large number of apparently derived epigamic behaviors with the geospizines, none of which are exhibited by *Volatinia*.

Received 5 February 1988, accepted 10 May 1988.

DARWIN'S finches include 13 species that inhabit the Galápagos archipelago, 1,000 km west of Ecuador, and one species endemic to Cocos Island, 500 km southwest of Costa Rica (Swarth 1931, Lack 1945, Grant 1986). They have been variously assigned their own family, the Geospizidae (Swarth 1929, Beecher 1953); their own subfamily (Geospizinae) of the Fringillidae (*sensu lato*, Ridgway 1901, Lowe 1936, Lack 1947, Bowman 1963); or included in the subfamily Emberizinae of the Emberizidae (Tordoff 1954, Paynter 1970, Steadman 1982).

Darwin's finches can be divided into 4 groups based on characters of the bill, plumage, and foraging behavior. These are the ground-finches (*Geospiza*), the tree-finches (*Camarhynchus*, *Platyspiza*, and *Cactospiza*), the Warbler Finch (*Certhidea*), and the Cocos Finch (*Pinaroloxias*). The ground-finches and tree-finches possess finchlike beaks of varying sizes, whereas *Certhidea* and *Pinaroloxias* have thin, warblerlike beaks. The affinity of the Cocos Finch to the Galápagos finches was recognized early, on the basis of the similar black plumage possessed by males of *Pinaroloxias* and *Geospiza* (Ridgway 1901). The brownish Warbler Finch, however, was placed originally in Parulidae (equals Mniotiltidae, Ridgway 1902). Snodgrass (1903) noted anatomical characters linking *Certhidea* with other geospizines, and subsequent workers have agreed that *Certhidea* is part of this group (Sushkin 1925, 1929; Lowe 1936; Beecher 1953; Tordoff 1954).

Lack's classic work on adaptive radiation among Darwin's finches (1945, 1947) led to acceptance of the monophyletic nature of the geospizines. This hypothesis is supported by the anatomical studies cited above, as well as by behavioral (Bowman 1983), karyotypic (Jo 1983), and biochemical (Yang and Patton 1981, Polans 1983) characters. However, McKitrick (McKitrick and Fink 1987; pers. comm.) has pointed out that the evidence for monophyly is not strong. Darwin's finches possess a large number of characters in common, but no unambiguous synapomorphies have been identified. McKitrick's analysis of cranial characters in Darwin's finches and other New World nine-primaried oscines failed to detect any such uniquely shared derived characters (McKitrick and Fink 1987). We recognize the need for additional evidence supporting geospizine monophyly, and discuss below several characters that may uniquely define the geospizines.

Many researchers have considered the affinities of Darwin's finches an unresolved problem. Swarth (1929: 41) wrote "I think that we must realize that we are contemplating a group of birds that has been isolated on its island home since a remote period of time, and that has developed such distinctive group characters of its own as to have made it well nigh impossible now to recognize the nearest collateral mainland stock." Lack (1947) and Bowman (1963) agreed that either the mainland ancestor had become extinct, or that the geospizines had diverged so far from it that determination of relationship was no longer possible. Other investigators have maintained a more optimistic view and pointed to the emberizine genera *Tiaris* and *Melanospiza* as the closest relatives of Darwin's finches (Sushkin 1925, Lowe 1936, Bond 1948, Beecher 1953, Bowman 1983). These suggestions were based on general similarities to Darwin's finches, not on explicit analyses of characters. *Tiaris* is a group of small finches widespread in the Caribbean and South America. The little-known, monotypic *Melanospiza richardsoni* is endemic to St. Lucia, Lesser Antilles.

Two workers have singled out particular extant species as the ancestor of Darwin's finches. Harris (1972) argued that the evidence for a finchlike ancestor of Darwin's finches was weak. He proposed that the least derived member of the group is the Cocos Finch, *Pinaroloxias inornata*, a species whose thin, slightly curved bill resembles that of the Bananaquit, *Coereba flaveola* (Emberizidae, Coerebinae). The monotypic *Coereba* is a widespread Neotropical "honeycreeper" of uncertain affinities. Harris (1972) suggested that *Coereba* could be ancestral to Darwin's finches, based primarily on the appearance of the bill and on the occurrence of a black morph in some populations of *Coereba* that resembles male *Pinaroloxias*. In addition, *Coereba* builds a domed nest as do Darwin's finches. *Coereba*, however, is not an emberizine (Tordoff 1954, Paynter 1970, Raikow 1978) and Harris did not support his suggestion with any morphological analysis. Our review of behavioral characters did not reveal any traits of song or courtship display shared between *Coereba* and the geospizines. The resemblance of *Coereba* to *Pinaroloxias* appears to be a case of convergence (Steadman 1982, Grant 1986).

In a much more ambitious attempt to determine the ancestry of the geospizines, Steadman (1982) compared the cranial osteology of Darwin's finches with 19 genera of emberizine finches, *Coereba*, and 9 other nonemberizine genera. He proposed the monotypic genus *Volatinia*, an emberizine finch widespread throughout Central and South America, as the ancestor of Darwin's finches, concluding: "the Neotropical Blue-black Grassquit, *Volatinia jacarina*, appears to be so closely related to Darwin's finches that I propose it to be the species that singly gave rise to the entire radiation . . . I regard *Volatinia* and all species of Darwin's finches, both on the Galápagos and Cocos Island, to be members of a single, expanded genus *Geospiza*" (Steadman 1982: 294). This arrangement has been accepted by some authors (Wetmore et al. 1984), but was questioned by others (Barrowclough 1983, Ratcliffe and Boag 1983, Grant 1986). Potential problems with Steadman's work include his failure to find any characters that are uniquely shared by *Volatinia* and the geospizines, and the inadequate consideration of behavioral and plumage characters which do not support a close relationship between these taxa.

Given these problems with the analyses of Harris (1972) and Steadman (1982), we believe that the phylogeny of Darwin's finches remains an unresolved question. Recent ornithological research has produced information bearing on this problem, much of it concerning behavioral characters. We summarize these data, which indicate that *Tiaris* and *Melanospiza* share more characters with the geospizines than does *Volatinia*. Moreover, some of the characters common to Darwin's finches, *Tiaris*, and *Melanospiza* appear to be uniquely shared among these taxa. We were unable to find evidence for such synapomorphies between *Volatinia* and the geospizines.

METHODS

Data on the behavior of geospizines are based on published sources (Lack 1945, 1947; Orr 1945; Bowman 1961, 1963, 1983; Grant 1986), on our study of film footage taken by George Bartholomew, and on discussions with Robert I. Bowman. Information on *Melanospiza* was gathered during our field study of this species on St. Lucia in May 1987 (Trail and Baptista in press). We also made extensive field observations of *Coereba flaveola* (Puerto Rico, St. Lucia, Trinidad, Tobago, Panama, and Suriname); *Volatinia jacarina* (Trinidad, Tobago, Panama, and Suriname); *Tiaris bicolor* (Puerto Rico, St. Lucia, and Tobago); and *T. olivacea* (Puerto Rico). Captive *T. olivacea* and *Volatinia* enabled us to observe details associated with nest-building and precopulatory behavior which would be most difficult to obtain in the wild . Observations on captive *T. bicolor* continue. The other species of *Tiaris* are not included in the present discussion, either because they are little known (*T. fuliginosa* and *T. obscura*) or because their affinity to other members of the genus is questionable (*T. canora;* Goodwin 1959, Baptista in prep.). We did not attempt a general comparison of geospizines with other Neotropical emberizines, most of which are poorly known. We note below the few characters for which information on a wider sample of genera is available.

RESULTS

MORPHOLOGICAL CHARACTERS

Plumage.—Most scholars have sought a black-plumaged ancestor (or sister group) of the geospizines. In line with this assumption, Steadman (1982: 282) stated that ". . . the plumage pattern in primitive Darwin's Finches is more

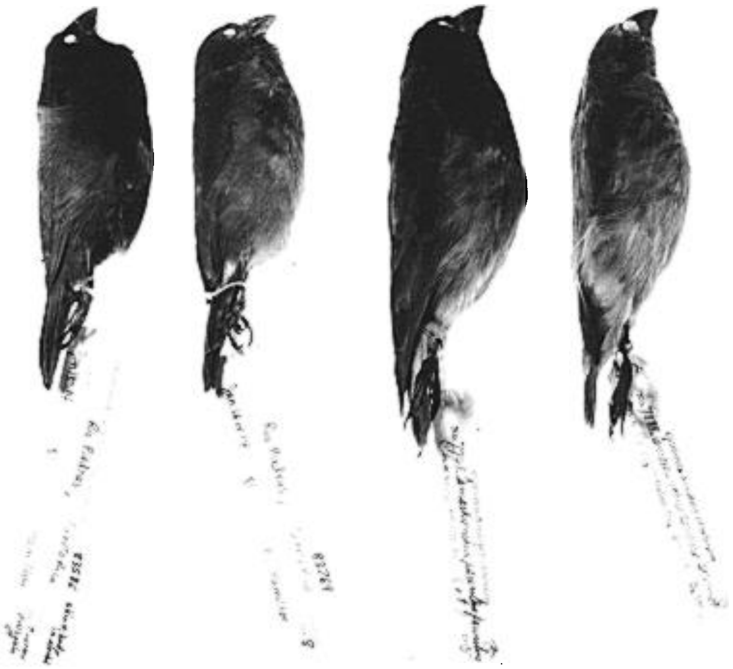

Fig. 1. From left to right: Skins of male *Tiaris bicolor*, female *T. bicolor*, male *Camarhynchus parvulus*, and female *C. parvulus*. In both species, males exhibit black plumage only on the head and breast; females are unstreaked.

closely matched by that in *Volatinia* than by that in any species of *Tiaris* . . . ." He noted (1982: 289) that *Geospiza* males are black and that females are streaked (characters shared with *Volatinia*). There are two difficulties with this argument. First, the principal reason for assuming that black plumage is primitive among geospizines appears to be that males of the best-known species of Darwin's finches, those in the genus *Geospiza*, are black. However, based on a study of plumage sequences, Snodgrass (1903) proposed that Darwin's finches descended from a yellow-olivaceous ancestor. Recently, Yang and Patton (1981) and Polans (1983) presented electrophoretic evidence that *Certhidea olivacea* was the earliest species of Darwin's finches to diverge from the ancestral stock. Plumages may thus have evolved from olive-colored to black-and-olive, to the black typical of the ground-finches (*Geospiza* spp.).

The second problem with assigning a polarity to plumage color is that current selective pressures may determine the amount of black in geospizine plumage. Arboreal species are primarily olive or brown, and increasingly terrestrial species exhibit increasing amounts of black, perhaps to enhance their crypticity against the dark lava which predominates in their arid habitat (Bowman 1963).

Steadman (1982) failed to mention several plumage characters of *Volatinia* that are not shared with any species of Darwin's finch, and did not discuss striking plumage similarities between geospizine species and other possible relatives. The plumage of male *Volatinia* is a shiny blue-black; that of the geospizines, *Melanospiza*, and *Tiaris* is a dull black (Grant 1986). Male *Volatinia* possess a white axillary patch that is absent in all the geospizines, *Tiaris*, and *Melanospiza*, and also molt into an eclipse plumage, a character absent in *Geospiza* (Grant 1986), *Tiaris*, and *Melanospiza*. The strong resemblance of the black male plumage of *Melanospiza* to the ground-finches (*Geospiza*) has been noted by several authors (Ridgway 1901, Bond 1929, Bowman 1983), whereas the black-and-olive coloration of the male *Tiaris bicolor* bears a strong resemblance to *Camarhynchus parvulus* (Fig. 1).

The interpretation of female geospizine plumage is equally problematic, despite Stead-

TABLE 1. Wing to tail ratios of Darwin's finches and other Neotropical emberizines (names in parentheses are of islands sampled).[a]

	n	Wing (mm)	Tail (mm)	Ratio
Sporophila aurita	10	51.9	43.2	1.2
Volatinia jacarina	29	47.2	40.1	1.2
Tiaris olivacea	31	51.8	39.6	1.3
T. bicolor	62	51.1	38.9	1.3
Melanospiza richardsoni	2	70.4	48.5	1.5
Geospiza difficilis (Culpepper)	10	71.9	47.9	1.5
G. conirostris (Gardner)	10	73.9	44.8	1.7
Camarhynchus psittacula (James)	10	73.0	44.9	1.6
C. pauper (Charles)	10	69.6	41.6	1.7
Cactospiza pallida (Albermarle)	10	69.9	43.3	1.6
C. heliobates (Albermarle)	10	71.5	43.3	1.7
Pinaroloxias inornata (Cocos)	10	65.9	41.8	1.6
Certhidea bifasciata (Barrington)	10	51.4	43.0	1.2

[a] Sources: data for all geospizines (Swarth 1931); data on remaining taxa (Ridgway 1901).

man's assumption that streaked female plumage is a primitive character. Based on the extensive series of skins at the California Academy of Sciences, Lack (1947) pointed out that females of *Cactospiza pallida* are almost unstreaked, and that streaking is absent altogether in females of the tree-finches (*Camarhynchus* spp.) (Fig. 1). There is considerable individual variation in the amount of streaking; some female tree-finches are as heavily streaked as typical female *Geospiza*, while some female ground-finches are only faintly streaked. Additional variation is shown among Warbler Finches (*Certhidea olivacea*). Both adults and juveniles are typically unstreaked, but juveniles from Floreana (Charles) Island are streaked. Females of the St. Lucia Black Finch (*Melanospiza richardsoni*) exhibit faint streaking, thus resembling some *Camarhynchus* (Trail and Baptista in press). Females of *Tiaris* spp. are unstreaked.

In summary, the plumage characters that Steadman (1982) cited as evidence linking *Volatinia* with Darwin's finches (black males, streaked females) are typical only of the ground-finches among the geospizines. In the absence of evidence that *Geospiza* is the least derived genus of Darwin's finches, the phylogenetic significance of these plumage similarities remains uncertain.

Tail length.—The relatively short tails of many geospizines has been mentioned as a group character (Swarth 1931, Bond 1947), and Bowman (1983) pointed out that this condition was also exhibited by *Melanospiza*. We computed an index of relative tail length (wing length/tail length) in several taxa of Neotropical emberizines (Table 1). *Melanospiza* had an index of 1.5, equal to that of *Geospiza difficilis* from Culpepper Island. *Certhidea*, however, has a relatively long tail, similar to *Sporophila*, *Volatinia*, and *Tiaris*. The variability in relative tail length among the geospizines makes this character of little use for reconstructing the group's phylogeny.

Scutellation.—Clark (1986) recently reported a unique pattern of foot scutes in the genera *Volatinia*, *Sporophila*, *Oryzyborus*, *Dolospingus*, and *Charitospiza*. This condition, which involves a partial fusion of scutes at the base of the outer 2 toes, was not seen in any other passerine taxon. Clark suggested that it may indicate that these 5 genera are monophyletic. In contrast, a divided scute characterizes other Neotropical finches, including *Tiaris*, *Melanospiza*, and all the geospizines, as well as all mainland genera of tanagers (Thraupinae). Although Clark appears to accept *Volatinia* as the ancestor of the geospizines, he pointed out that this would require the scute character to have differentiated after the geospizine lineage diverged.

Syrinx.—All the geospizines possess a distinctly structured syrinx, and exhibit a lower trachea completely enclosed in a heavy sleeve of muscle (Cutler 1970, cited *in* Grant 1986). Cutler surveyed the external aspect of the syringes of all the species in the Ames collection (Ames 1971), and several hundred specimens of her own. Her total sample was more than 600 species, including 46 genera in the Fringillidae and Emberizidae. The only taxa which shared the distinctive external sleeve of muscle with the geospizines were *Tiaris* and *Melanospiza*. Syringeal anatomy in *Tiaris bicolor* was almost identical to the geospizines; *T. olivacea* differed in some ways, but exhibited the enclosing sleeve of muscle. *Melanospiza* syringes closely resembled those of the geospizines, but were less massive. Syringes in *Volatinia* lacked this heavy muscular sleeve (Cutler pers. comm.).

BEHAVIORAL CHARACTERS

Darwin's finches share a number of distinctive behavioral characteristics, particularly relating to reproduction. These reproductive characters show less interspecific variation within the geospizines than virtually any morphological characters (Grant 1986). Behavioral traits may thus be useful for reconstructing the phylogeny of the group, or minimally confirming its monophyly. Following the classical work of Delacour and Mayr (1945) on Anseriformes, courtship displays have been used to understand the relationships of other avian taxa (e.g. Güttinger 1970, 1976; Baptista 1973). Immelmann (1976) called attention to the conservative nature of courtship displays and discussed their utility as taxonomic characters.

Holding behavior.—Holding behavior has been used as a taxonomic character in a number of avian taxa (Clark 1973). All the geospizines, including the completely arboreal Warbler Finch, are capable of manipulating (holding) food items or nest material with their feet (Bowman 1961, pers. comm.). This behavior is also present in *Tiaris* species (Baptista 1976) and *Melanospiza* (Trail and Baptista in press), but is absent in *Volatinia* (Lill 1977; pers. obs.).

Domed nest.—All species of Darwin's finches build very similar domed nests, a behavior shared with *Tiaris* and *Melanospiza* (Grant 1986), and the little-known Caribbean finches in the genera *Loxigilla, Loxipasser,* and *Melopyrrha* (Bond 1961). The domed nest of *Tiaris* is so characteristic that it has been used to define the genus (Collins and Kemp 1976). In contrast, *Volatinia* builds a cup nest, as do most Neotropical emberizines including *Sporophila, Oryzyborus,* and *Atlapetes.*

Role of the sexes in nest building.—Males of geospizine species build the outside domed shell of the nest and the female provides the interior lining (Lack 1945). Males may build several nests and display near the nest entrances when females approach. The pair eventually settles on one nest.

In *Melanospiza,* the male constructs the entire outer shell of the nest. Once this is completed, the female takes an increasingly larger role in shaping the nest and lining the interior. By the final day of construction, only she participates in nest building (Trail and Baptista in press). The pattern in *Tiaris* is similar. Skutch (1954) reported that the male of *T. olivacea* selects the nest site and begins construction. Only if the female approves of the nest site does she begin to visit him. Her efforts increase as the nest nears completion, and it is usually only the female that completes the nest by lining its interior. Not all nests begun by a male are accepted by the female. Field and aviary observations of *T. bicolor* reveal similar behavior (Baptista and Horblit in prep.).

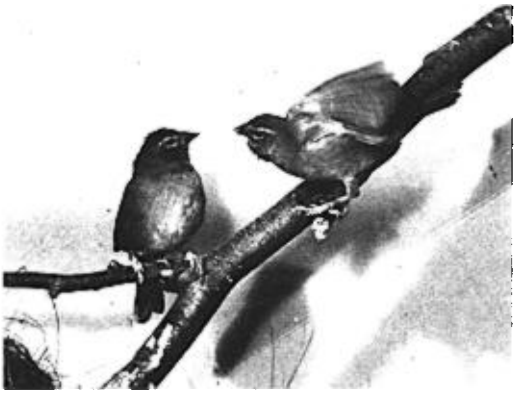
Fig. 2. High intensity courtship display of *Tiaris o. olivacea.* Note that the wings of the male are held over the back and quivered, a posture typical of geospizines.

The limited information available on the nest-building behavior of *Volatinia* is contradictory. Alderton (1963) observed wild birds and reported that both sexes build the shallow cup nest, and that "the male takes the initiative." In a captive pair observed by Baptista and Horblit, almost all nest building was done by the female, whereas only the males performed nest building in the captive birds observed by Stahl (1984). *Volatinia* appears to lack the consistent roles of the sexes in nest building that characterize the geospizines, *Tiaris,* and *Melanospiza.*

Displays at the nest.—Nest-building and courtship displays are closely linked in geospizines (Lack 1945). Nest building is accompanied by frequent song. The presence of a female stimulates much singing and posturing at the nest entrance. Orr (1945) and Downhower (1978) noted that songs and displays increased as the nest neared completion; and ceased abruptly once incubation commenced. Nest building is

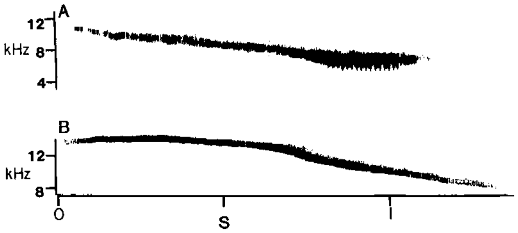

Fig. 3. Whistle songs of (A) *Melanospiza richardsoni*, St. Lucia, West Indies, and (B) *Geospiza fortis*, Isla Santa Cruz, Galápagos.

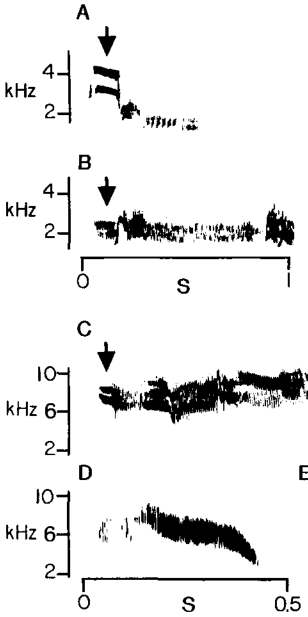

Fig. 4. Spectrogram of songs of (A) *Geospiza magnirostris*, (B) *Platyspiza crassirostris*, (C) *Tiaris bicolor* from Puerto Rico. Arrows point to introductory note with an overtone characteristic of songs of most species of geospizines and *T. bicolor*. (D) and (E) Spectrograms of two songs of *Volatinia jacarina* from Trinidad and Tobago, respectively. In "D," the song begins with a vibrato. In "E," the song begins with a soft vibrato followed by a note and then a second vibrato.

also accompanied by singing in *Melanospiza*, and the amount of singing increases significantly just prior to laying. The one male on which we made detailed observations often sang to the female from inside the nest while he was arranging nest material within (Trail and Baptista in press). Male geospizines have been observed to sing inside the nest in captivity (Bowman 1983), and similar observations have been made on *Tiaris bicolor* both in field and aviary (Baptista and Horblit in prep.).

The presence of a female inside the nest stimulates singing in the male *Tiaris olivacea*. He usually perches a few inches outside the nest and sings to her with his bill facing the nest entrance, the songs often accompanied by vigorous wing-flicking (pers. obs.). In contrast, nest building and displays are not coupled in *Volatinia* (pers. obs.) nor have we observed this species singing while on the nest.

Courtship display.—Geospizine courtship displays are uniform within the group (Lack 1945, Orr 1945, Grant 1986). This is true of the genera *Camarhynchus* and *Certhidea* as well as the better-known members of the genus *Geospiza* (Bowman pers. comm.). The male geospizine approaches the female and faces her with body held horizontally and with wings spread, drooped and quivering. At higher intensity the wings may be raised over the back and quivered. This is accompanied by swaying movements of the body. Copulation is followed by a postcopulatory display accompanied by extended and quivering wings (Orr 1945).

The display of *T. olivacea* is identical with that of the geospizines in all aspects including wing-raising (Fig. 2), body swaying, and a postcopulatory display. Raised wings or lowered and quivered wings were often seen in *T. bicolor* courtship displays in the field and in the laboratory; and body swaying has been observed in captives. Complete copulation has not yet been observed. In *Melanospiza*, the male sang to the female with both wings held up over the back during the only courtship display we observed (Trail and Baptista in press). This is a typical geospizine posture.

The precopulatory display of the *Volatinia* male bears no resemblance to that of the geospizines. Stimulated by the female's soliciting display, the male raises the feathers of the forehead to form a crest, a feature found at the bottom of its jump display (illustrated *in* Weathers 1986). The body is erect and the carpals of the wing held out to display the white axillary patch. He sings to her in this posture, mounts, and leaves with no postcopulatory display (Baptista and Horblit in prep.). In a second display, the male raises its crest, then faces the female with tail held straight up like a *Troglodytes* wren (Stahl 1984, Baptista unpubl.). Wing-raising is also absent in the widespread Neotropical finch genus *Sporophila* (Godfrey Bourne pers. comm.).

Song flight displays.—*Volatinia* is known for a jump-display which has earned it the local name

TABLE 2. Character states of Darwin's finches and proposed sister groups.

	Geospizines	*Tiaris olivacea*	*T. bicolor*	*Melanospiza*	*Volatinia*
Courtship display components					
Wing up	+	+	+	+	−
Wing down and quivered	+	+	+	?	−
Lateral body sway	+	+	+	?	−
Postcopulatory display w/wing quiver	+	+	?	?	−
Display w/nest material	+	+	+	+	−
Display associated w/nest building	+	+	+	+	−
Male builds dome, female lines nest	+	+	+	+	−
Horizontal song flight	+	+	+	+	−
Whistle song	+	−	?	+	−
Other character states					
Syrinx in sleeve of muscle	+	+	+	+	−
Black male plumage[1]	+	−	−	+	+
Holds items w/feet	+	+	+	+	−
Domed nest	+	+	+	+	−
Total characters shared w/Darwin's finches	13	11	10	10	1

[1] Among geospizines, *Cactospiza* and *Certhidea* lack black male plumage; *Tiaris* species are black and olive-brown, as in the geospizine *Camarhynchus.*

"Johnny-Jump-Up" (ffrench 1973). In this display, the male flaps its wings vigorously, sometimes producing a snapping sound (Webber 1985; pers. obs.), ascends 20–50 cm above its perch, and then drops on the spot where the display commenced. Song is produced at the apex of the ascent phase. Steadman (1982) suggested that the jump display is a homolog of the song-flight display common to all geospizines. Grant (1986) pointed out, however, that the display of *Volatinia* is on a vertical plane (illustrations *in* Weathers 1986) whereas that in the geospizines is on a horizontal plane. A horizontal song-flight display is highly developed in *Tiaris bicolor* (ffrench 1973; pers. obs.), and is also present in *T. olivacea* and *Melanospiza* although in less elaborate form (Trail and Baptista in press).

Song.—All geospizine songs can be classified as one of 3 distinct song types (Bowman 1983). *Whistle song* is a long continuous whistle starting at a high frequency and descending either gradually or precipitously, depending on the species, to a lower frequency. In the genus *Camarhynchus,* this song is a long series of short whistles. In *Certhidea,* the whistle is attached to the "basic song." *Basic song* consists of several dissimilar buzzy phrases. There are a number of versions of this song type. *Derived song* is the final type, and differs from basic song in that it consists of trills made up of identical syllables repeated in series. All geospizines produce variants of the whistle song and basic song, but derived song is characteristic only of *Geospiza, Cactospiza,* and *Camarhynchus.*

Bowman (1983) described in detail the similarities between the songs of *Melanospiza* and the 5-part basic song of *Certhidea.* The *Melanospiza* song available to him consisted of a whistle attached to the basic song proper, as in *Certhidea.* We found that *Melanospiza* also delivers a long descending whistle song similar to that found in *Geospiza* species (Fig. 3). The whistle in *Melanospiza* terminates in a vibrato as in *Pinaroloxias.* The derived song is absent in *Melanospiza, Platyspiza, Pinaroloxias,* and *Certhidea.*

The basic song of many geospizines consists of a note with an overtone followed by a series of buzzy phrases. Songs of *Tiaris bicolor* are similar (Fig. 4), including the introductory note and buzzy phrases. In contrast, the song of *Volatinia* lacks this introductory note and phrase structure (Fig. 4). The highly variable song of *Volatinia* has been described as "szee yew" (Slud 1964), "bzee-eep" (Wetmore et al. 1984), and "weezit" (Peterson and Chalif 1973). *Volatinia* does not produce the whistle song, based on published accounts (Webber 1985) and our own extensive field and aviary observations.

For 13 characters exhibited by Darwin's finches, *Melanospiza* and *Tiaris* spp. share 10–11 character states with the geospizines, in contrast to *Volatinia,* which shares only one character state (Table 2). We suggest that the suite of epigamic displays shared by the geospizines and *Tiaris*/*Melanospiza* (namely the horizontal-flight song, whistle song, unique basic song, display at the nest, display with nest material, and wing-up posture) are derived displays present in their common ancestor. We conclude that the bulk of the available evidence does not support Steadman's (1982) identification of *Volatinia* as congener and direct ancestor of the geospizines. Resolution of the affinities of Darwin's finches will require further work on morphological characters, and the use of biochemical techniques to examine the relationships between the geospizines and their proposed sister groups. We are currently engaged in such studies.

ACKNOWLEDGMENTS

We acknowledge with thanks the birds, space, and many happy hours discussing this project with Klaus Immelman (University of Braunschweig). For all the kindness and assistance shown Baptista at Braunschweig, we thank Hans Klingel, Ekke Pröve, Roland Sossinka, and Otto von Frisch. Dr. R. Piechocki, Sektion Biowissenschaften der Martin-Luther Universitat Halle-Wittensberg, and Dr. R. Grummt, Tierpark Berlin, provided the original wild-caught *Tiaris* from Cuba.

We thank Paul Butler and Christopher Cox for their assistance and hospitality on St. Lucia, and Julio Cardona Alonso, Betsy Anderson, Kelly Brock, Paul Gertler, Jean Lodge, Frank Milan, Rolf Olson, Jose Vivaldi, and Joseph Wunderle Jr. for their help during our work on Puerto Rico.

Discussions with Robert Bowman were most helpful. He kindly provided the spectrograms of geospizine songs. Betsey Cutler generously discussed her studies of geospizine syringeal anatomy. George Barrowclough, Walter Bock, Betsey Cutler, Sylvia Hope, and Mary McKitrick read earlier versions of the manuscript and provided valuable comments. We thank Ann Giordano for the photograph (Fig. 1).

Research funds were provided by the Max Planck Gesellschaft, the Forschungsmittel des Landes Niedersachsen, N.A.T.O., and the California Academy of Sciences to Baptista, and by the National Geographic Society to Trail and Baptista.

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