

GENERIC LIMITS AND RELATIONSHIPS OF AIMOPHILA  
(AVES: FRINGILLIDAE)

By

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## ABSTRACT

The genus Aimophila is a highly variable assemblage of grassland and thornscrub sparrows whose phylogenetic relationships have long been in doubt. In the present paper I re-examine the relationships both within the genus and between it and other emberizine genera. My study is based almost entirely upon internal and external morphology.

Several cranial characters help to delineate relationships within Aimophila and also suggest possible relationship to other emberizines. These are the intraorbital cristae and the auditory bullae, which occur in several forms within the genus Aimophila. These characters, in addition to plumage characters, suggest that Aimophila may be treated as four subgenera, which are Haemophila, Aimophila, Peucaea and Torreornis. They also indicate a strong link between Aimophila and Spizella, and a possible link between Aimophila and Ammodramus. In addition, they suggest that the monotypic genus Oriturus should actually be included in Aimophila. I conclude that the genus Aimophila is in fact a monophyletic group. This natural group does not include the species quinquestriata, which is here transferred to the genus Amphispiza.

Preliminary dissections show that cranial differences within Aimophila are associated with differences in jaw musculature, and extensive survey dissections seem a promising avenue for further research on relationships within the Emberizinae.



## INTRODUCTION

The genus Aimophila, a group of sparrows of grassland, desert scrub, savanna and rocky hillsides, has intrigued ornithologists for over a century. While appearing to be more closely related to each other than to any other emberizines, these sparrows nevertheless constitute an unusually diverse assemblage. Apparently because of this diversity, no satisfactory diagnosis has ever been written for the genus Aimophila, though a partial attempt may be found in Ridgway (1901). Storer (1955) outlined the possible relationships within the genus based on a survey of anatomical material. He concluded that the genus was an unnatural group and probably divisible into two separate genera. One genus would consist of "Aimophila" mystacalis, humeralis, ruficauda, sumichrasti and strigiceps, while A. aestivalis, botterii, petenica (currently recognized as a subspecies of botterii) and cassinii would form the second genus. Storer considered the affinities of quinquestriata, carpalis, ruficeps, notosticta and rufescens to be uncertain. In a recent monograph, Wolf (1977) used morphological and ecological information to determine specific relationships in Aimophila. His conclusions were somewhat different from those of Storer (1955) in that he placed carpalis next to sumichrasti and grouped ruficeps, rufescens and notosticta as a distinct unit. Wolf could not assign "Aimophila" quinquestriata to any of these groups, and considered the species separately.

The work of previous authors on the genus Aimophila has left certain questions unanswered and certain other questions unasked. A thorough study of the genus and its phylogenetic history requires investigation of other emberizine genera, and I have undertaken the present study to readdress the problem of whether Aimophila (sensu Paynter, 1970) constitutes a natural group. Further, an attempt is made here to determine the closest relatives of the genus. In addition to the species treated by Wolf (1977), I consider the two remaining species, A. strigiceps and A. stolzmanni, and the Cuban endemic Torreornis inexpectata.

Following the conclusions of Storer (1955) and Wolf (1977), the genus Aimophila may be subdivided into the following three species groups (excluding A. quinquestriata):

<u>Haemophila</u>	<u>Aimophila</u>	<u>Peucaea</u>
<u>A. mystacalis</u>	<u>A. rufescens</u>	<u>A. aestivalis</u>
<u>humeralis</u>	<u>notosticta</u>	<u>botterii</u>
<u>ruficauda</u>	<u>ruficeps</u>	<u>cassinii</u>
<u>carpalis</u>		
<u>sumichrasti</u>		
<u>strigiceps</u>		
<u>stolzmanni</u>		

The inclusion of A. stolzmanni in the first group, referred to as the Haemophila group by Wolf (1977), requires discussion, as there has been some debate over the taxonomic status of this form. Very little is known of the habits of the species. Ridgway (1898) removed the

species from its original position in Haemophila (=Aimophila) and placed it in the monotypic genus Rhynchospiza on the basis of its much shorter tail relative to wing length and its very small and circular nares. The species was subsequently returned to Aimophila by Paynter (1967, p. 3), who rejected Ridgway's characters as being "of dubious value." In plumage pattern, stolzmanni fits well with the Haemophila group on the basis of its brown and grey crown pattern, the pattern and coloration of the streaks on the back, the rusty wrist-patch, the rufous edgings on the dark secondaries and the grey breast, white belly and buffy flanks. A. stolzmanni also possesses the dark maxilla and two-toned mandible typical of the Haemophila group (except sumichrasti, which has a pink-orange bill). In spite of its short tail and large bill, the retention of the species in a monotypic genus probably does not properly reflect its evolutionary history. I do not favor the elimination of monotypic taxa if the affinities of such are truly uncertain, but I do agree with Paynter (1967) that stolzmanni is closer to Aimophila than to other emberizines and should be placed in that genus. I also believe, however, that A. stolzmanni may constitute a form intermediate between Aimophila and Ammodramus, a position I will explore in a later section.

Storer (1955) remarked that the resemblance between Aimophila carpalis and A. sumichrasti is probably "fortuitous" (p. 198) and that A. carpalis "does not appear to have any close relatives" (p. 199). Ridgway (1901), on the other hand, considered the two species to be very closely related, while Hellmayr (1938) went so far as to suggest that they are

conspecific. Although Paynter (1967) included A. carpalis among the species that "lack eye stripes, shoulder patches and conspicuously colored wrist feathers" (p. 4), the species does in fact possess the bright rust-colored wrist patches of the Haemophila group. Few emberizines other than the members of this group possess this rusty patch. The inclusion of carpalis in Haemophila by Wolf (1977) and others is justified, but certain plumage, osteological and behavioral characters strongly suggest an intermediate position for carpalis between Aimophila and Spizella. These characters will be discussed below.

The close relationships within each of the three groups of Aimophila mentioned above have been, I believe, adequately defended by previous authors, and it is not my purpose to restate the justification for such groupings. My intention is to outline the evidence for considering the three groups to be sufficiently closely related to warrant their retention in a single and discrete genus. This evidence comes primarily from plumage patterns and secondarily from osteological characters.

## MATERIALS AND METHODS

Abbreviations: AMNH: American Museum of Natural History; AMR: Amadeo M. Rea; GMS: George M. Sutton; KU: University of Kansas Museum of Natural History; LSU: Louisiana State University Museum of Zoology; MCZ: Museum of Comparative Zoology, Harvard University; MVZ: Museum of Vertebrate Zoology, University of California (Berkeley); UA: University of Arizona; UMMZ: University of Michigan Museum of Zoology; USNM: United States Museum of Natural History.

I examined all skeletons of Emberizinae available at the United States National Museum. In addition I used the following skeletal specimens: Vireo huttoni UA 13427, 13874; Dendroica graciae UA 6111, 6281; Cardellina rubrifrons UA 12370, 13877; Piranga flava UA 6124, 6284; P. erythrocephala UA 10297; Cardinalis sinuatus UA 6128, 6201; Calcarius lapponicus UA 12306; C. ornatus UA 6242, 10111, 13410-13414; Plectrophenax nivalis UA 11895; Calamospiza melanocorys UA 6214, 8680, 8681, 13665; Zonotrichia melodia UA 6081; Z. lincolni UA 6136, 10044, 11725; Z. albicollis UA 13211; Junco phaeonotus UA 6284, 11720, 13207; Ammodramus sandwichensis UA 10306, 13408, 13409; A. bairdii UA 9985; A. savannarum UA 9984, 10308, 11728, 13406; A. aurifrons AMNH 10230; Spizella arborea UA 11694, 11695; S. passerina UA 6227, 6228, 11696, 11697, 11699, 12246; S. breweri: all 21 UA specimens; Poocetes gramineus UA 6219-6223, 12495; Chondestes grammacus UA 11690, 11691, 12327, 13769; Amphispiza bilineata UA 9999, 1000, 11718, 11821, 12374,

12462, 13250, 13715; A. belli UA 13083, uncat.; Aimophila humeralis AMR 3872, GMS 10845, MVZ 15312, 154045, 154293, UA 11913, UMMZ 139394; A. ruficauda KU 36611, MVZ 153156, 153158, 153168, 153135, 153136, 153137, 153143, 153144, 156657; A. stolzmanni LSU 81357, 86439; A. botterii MVZ 153255, 153256, 154088, 154089, 154090, UA 11709-11711, 11713, 12516; A. cassinii UA 11701, 11703, 13863, 13253-13255, 13486 13666; A. quinquestriata MVZ 153081-153083, UA 9986; A. carpalis UA 8610, 8695, 9988, 9990-9992, 9994, 10309; A. ruficeps MVZ 153251, 153252, 153254, 154074, 154075, 154076, UA 6224, 11704, 11706, 11709, 13203; A. notosticta MVZ 153234, UMMZ 209397; A. rufescens LSU 22696, 32021, 49037, KU 31005, 34792, 34793, MVZ 150919, 153237, 153237, 153242, 154069, 154070, 154072; Oriturus superciliosus AMR 3865, 3873, KU 35927, 36608, 36609, MVZ 153062, 153063, 154032, 153060, 153061, 154033, UA 6050; Pipilo fuscus UA 6036, 6134, 6211, 6234, 8685, 8689, 12137, 13886, uncat. A & B; Carduelis notatus UA 8253; Loxia curvirostra UA 8743; Vestiaria coccinea UA 11756, 11758; Icterus cucullatus UA 12436; Xanthocephalus xanthocephalus UA 6293; Molothrus aeneus UA 6188, 6193.

I examined skins of all species of Calcarius, Plectrophenax, Calamospiza, Zonotrichia, Junco, Ammodramus, Chondestes, Poocetes, Spizella, Amphispiza, Aimophila, Torreornis, Phrygilus, Pipilo, Melospiza, Atlapetes, Arremon, Arremonops, Incaspiza and Saltatricula from the collections at AMNH, MCZ, UA, UMMZ, and USNM.

I measured the rostral angle of many emberizine species with the aid of a "photogram" and protractor. Skulls were aligned with clay

on a sheet of clear glass, and a piece of photographic paper laid underneath the glass was exposed to light for six seconds at  $f/16$ .

The resulting "reversed silhouettes" were then used to measure the angle.

## MORPHOLOGY

### External Morphology

The group comprising Aimophila aestivalis, botterii and cassinii forms the most homogeneous of the current three subdivisions, for which Ridgway (1873) used the generic name Peucaea (type Fringilla bachmanni Audubon). Certain intermediate plumage characters in A. notosticta and ruficeps, however, seem to ally the Aimophila with the Peucaea group. For example, A. notosticta, essentially a small version of rufescens, has a black bill like that of rufescens but the bill is much closer to that of aestivalis in shape and size, as is that of ruficeps. The bold crown pattern of rufescens becomes paler in notosticta and more closely resembles the pattern in aestivalis and botterii. Similarly, the rufous coloration in the wing is reduced in extent in notosticta, becoming more nearly like that of aestivalis and botterii. The coloration of the back in A. ruficeps closely resembles that found in the peucaeas. All three of the peucaeas have dark malar streaks as do the members of the Aimophila group, although the streaks are markedly reduced in the former. The presence of bright rufous secondary feathers in A. aestivalis and botterii are reminiscent of A. rufescens and notosticta, which also have bright rufous secondary feathers. These characters considered together indicate relationship of the Peucaea and Aimophila groups.



The Aimophila and Haemophila groups appear to be linked also, by a form not recently included with Aimophila, viz., the monotypic genus Oriturus (see range map, Figure 1). Oriturus superciliosus exhibits a number of external morphological characters that ally it with both Aimophila rufescens and A. ruficauda (Figure 2). In Oriturus the bill is heavy with maxilla black, mandible yellow and "horn" colored. All three species possess a striped crown; the stripes are black and white in A. ruficauda, rufous-brown and grey streaked with black in Oriturus and rufous-brown and grey in A. rufescens. A. ruficauda has a black cheek patch that extends to the neck; in Oriturus this area is black giving way to grey posteriorly while the same area in A. rufescens is grey. All three forms have a conspicuous superciliary streak; this is white in ruficauda, dull white or buffy in Oriturus and grey becoming white anteriorly in A. rufescens.

The central rectrices of Oriturus have the Sturnella-like pattern of a dark, serrated bar running the length of the feather. This pattern, while not so striking in Aimophila ruficauda, ruficeps and rufescens, is nevertheless perceptible in these species. K. C. Parkes (personal communication, 1980) noted the remarkable similarity of the tail pattern in Oriturus and Aimophila botterii arizonae; further inspection proved the tail of A. cassinii to bear an equally pronounced similarity to that of Oriturus (Figure 3), lending further support to the proposed connection between the "two" genera.

Oriturus was originally described as Aimophila superciliosa by Swainson (1838) and subsequently described as a new form, Oriturus



Figure 1. Distribution of *Aimophila superciliosa*.



Figure 2. Aimophila ruficauda, A. superciliosa,  
A. rufescens, lateral view. -- Top to  
bottom.



Figure 3. Aimophila cassinii, A. superciliosa. --  
Left to right.

mexicanus, by Bonaparte (1851, in Paynter, 1970). Bonaparte (1856) later realized his error and recognized his "new" form as an Aimophila, but Ridgway (1898, p. 224) erected a new genus, Plagiospiza (later changed to Oriturus by rules of priority), for the species. The characters given for Oriturus are the following: "Similar to Aimophila Swainson, but tail shorter than wing instead of longer, and wing much less rounded, the first primary longer than eighth instead of shorter than tenth, and second to sixth primaries longest and nearly equal." These characters are of doubtful value. The inclusion of "Rhynchospiza" stolzmanni in Aimophila renders the tail character useless, and there are no osteological characters that distinguish Oriturus from Aimophila. I believe the similarities outlined above between A. rufescens, A. ruficauda and Oriturus superciliosus warrant the return of the latter to Aimophila.

#### Aimophila quinquestriata

In his treatment of the genus Aimophila, Wolf (1977) considered A. quinquestriata separately from the rest of the genus and suggested that it was probably "no more closely related to Aimophila sparrows than to certain other emberizines" (p. 203). Wolf suggested a possible relationship between A. quinquestriata and species of the genus Melozone. The main similarity to Melozone seems to be the black central spot on the breast, a character which is present in other sparrows as well, e.g., Spizella arborea, Chondestes grammacus and Amphispiza belli. Wolf (1977) also mentions the clear yellow wash on the underside of Melozone and A. quinquestriata. I believe the affinities of A. quinquestriata to lie rather with Amphispiza as was once suggested by Ridgway (1883) and by

Salvin and Godman (1886). Ridgway (1901, p. 232) later revised his opinion and stated that A. quinquestriata was "wholly out of place" in Amphispiza but offered no explanation for this change of conviction. It should be noted that the genus Amphispiza Coues (Coues, 1874; type Emberiza bilineata Cassin) was erected with no mention whatever of generic characters; further, Ridgway's (1901) description of Amphispiza fails to distinguish that genus adequately from Aimophila quinquestriata.

Storer (1955) mentioned the much stouter tarsi of quinquestriata relative to those of Amphispiza; he also stated that the central rectrices of quinquestriata are tapered as in nearly all other species of Aimophila while they are truncated in Amphispiza. The specimens I have examined do not support the latter contention. Although the tarsometatarsus is stouter in A. quinquestriata than in Amphispiza, the difference is no greater than between Aimophila notosticta and A. rufescens; the tarsometatarsus of the former is stouter while being of the same absolute length as the latter, and yet the relationship between the two species is undeniable.

In addition to possessing characters which appear to deny a relationship to Aimophila, A. quinquestriata has certain characters that appear to ally it with Amphispiza. In overall plumage color, black, greys and taupes are predominant as in Amphispiza. A. quinquestriata lacks the streaking characteristic of all other Aimophila, while possessing a central black chest spot like that of Amphispiza belli and a facial pattern strongly suggestive of A. bilineata (Figures 4 and 5). The outer rectrices of the species of Amphispiza have white



Figure 4. Amphisiza bilineata, A. quinquestriata, ventral view. -- Left to right.



Figure 5. Amphispiza bilineata, A. quinquestriata, lateral view. -- Left to right.



tips and this character is present, in reduced form, in A. quinquestriata as well. In general body form A. quinquestriata resembles Amphispiza much more than it does Melospiza. The slender bill of A. quinquestriata is more similar to those of Amphispiza than to those of most species of Aimophila, although this is probably not of great importance. G. S. Mills and K. Groschupf (1980, personal communication) report that even after two years of studying songs of A. quinquestriata they still have difficulty distinguishing some of its songs from those of Amphispiza bilineata. Phillips, Marshall and Monson (1964) noted such similarities also, although Borror (1971) and Wolf (1977) dismissed the resemblance as non-existent. Geographic variation in songs of both species may be responsible for the dispute.

There are certain differences between "Aimophila" quinquestriata and members of Amphispiza, such as the yellow wash on juveniles of the former; this appears in juveniles of only one species of Aimophila, viz. A. rufescens, and in the latter species the yellow is darker than in quinquestriata and covers the entire underside of the bird. In A. quinquestriata the yellow is limited to the belly region. There are also cranial differences between quinquestriata and members of Amphispiza, but there are also cranial differences between A. bilineata and A. belli to which I have found no published reference. These differences will be discussed in the following sections. I maintain that the species quinquestriata is out of place in Aimophila and that it is closer to members of Amphispiza than to any other living emberizines and should be returned to that genus.

### Osteology

I compared skeletons of each species of Aimophila with those of other genera of emberizines (Group I of Morony, Bock and Farrand, 1975). Post-cranial elements were of little value in defining generic limits of Aimophila as I noted no consistent differences either among other emberizine genera or between these and Aimophila. I examined the following cranial characters: auditory bulla, transpalatine process, maxillopalatine, palatine process of the premaxilla (palato-maxillary of Tordoff, 1954), intraorbital cristae, postorbital process, zygomatic process, ectethmoid plate, mandible and rostral angle. In most of these characters I found no pattern in the variation among genera. Wolf (1977) noted some consistency in the shape of the transpalatine process within the Aimophila; I did not find this to be the case but rather noted a tendency for this paired structure to vary within species and occasionally within individuals! Storer (1955) stated that the transpalatine process is pointed in Spizella; this was usually true in the specimens I examined, though I found that 7 out of 21 specimens of Spizella breweri had the transpalatine process divided rather than pointed.

The intraorbital cristae (Figure 6) occur in pairs, one pair in each orbit. They may occur either as two stubs or with the interior crista elongated and the exterior one stubby. The interior crista, if elongated, may be divided at the tip but this is variable. I found that the intraorbital cristae occurred as stubs in the following: all



Figure 6. Aimophila cassinii, A. ruficeps, intraorbital cristae. -- Top to bottom.

members of the Haemophila group including stolzmanni; all members of the Peucaea group; all members of Spizella except arborea; Ammodramus humeralis, A. aurifrons and A. savannarum; "Aimophila" quinquestriata; all members of Calcarius. Dissection of the jaw muscles in Aimophila cassinii, a species with stubby cristae, and ruficeps, a species with an elongated crista, showed that M. pseudotemporalis superficialis is larger in A. ruficeps. This muscle attaches to the intraorbital cristae and is involved in raising the lower jaw.

Another cranial character that appears to vary in a "non-random" fashion was the auditory bulla, which is either uninflated, moderately inflated or strongly inflated. I found the uninflated condition in Calcarius, Plectrophenax, and the members of the Haemophila group except humeralis and mystacalis, which showed moderate inflation. In all other emberizines I examined I found moderate to strong inflation of the auditory bulla.

In the case of the rostral angle, small sample sizes preclude definite conclusions, but the following information was suggestive: the highest figures (= sharpest angles) found were for Ammodramus bairdii (54, n = 1), Aimophila stolzmanni ( $\bar{x}$  = 49.5, n = 2), A. rufescens ( $\bar{x}$  = 47.0, n = 7), A. superciliosa ( $\bar{x}$  = 43.9, n = 7), A. botterii ( $\bar{x}$  = 43.2, n = 5), Ammodramus savannarum ( $\bar{x}$  = 42.5, n = 3), Aimophila notosticta (39.8, n = 1), A. cassinii ( $\bar{x}$  = 39.3, n = 8) and A. ruficauda ( $\bar{x}$  = 36.4, n = 5). Other species ranged from  $\bar{x}$  = 19 to  $\bar{x}$  = 35.3 (see Appendix A).

In the section on External Morphology I attempted to show that Aimophila is a natural group, with the exception of the species quinquestriata. Although the evidence is scanty, it appears that certain members of the genus have retained some primitive cranial characters that suggest an early origin for these species. I believe the ancestral condition of the auditory bullae and intraorbital cristae to be uninflated and stubby, respectively. These conditions were found in Calcarius and, in the case of the auditory bullae, in Plectrophenax, two genera currently considered to be primitive within the Emberizinae (Paynter, 1970). I also found these character states in all other families (or subfamilies; see Raikow, 1978) of nine-primaried oscines. Although none of the cranial characters I examined appears to be of value in defining the genus Aimophila, the intraorbital cristae are suggestive of relationships with other genera, as will be explored in the next section.

## EVOLUTIONARY HISTORY

### Affinities of Aimophila

#### Spizella

The first published suggestion that the generic affinities of Aimophila carpalis might lie with Spizella rather than with Aimophila comes from van Rossem (1936, in Pitelka, 1951, p. 47), who noted that this species was "a typical Spizella in every respect." Van Rossem (1945) later changed his opinion without explanation. The question was re-opened by Pitelka (1951), who described the behavioral similarity of Aimophila carpalis and the typical spizellas, particularly Spizella breweri and S. pallida, with which A. carpalis is often found associated in flocks. Pitelka (1951) remarked that the nest structure, perching behavior, song and sociability of carpalis all suggest Spizella rather than Aimophila.

The possibility of a link between the two genera first struck me in examining skins (see Figure 7). A. carpalis is closer to Spizella than to Aimophila in size and bodily form, and in plumage pattern the resemblance is quite apparent, particularly in the pale olive-brown coloration of the back with its delicate, dark streaking. The bill is pink-orange in A. carpalis as it is in several of the spizellas and in A. sumichrasti. A. carpalis differs from Spizella in bill shape and in its lack of a forked tail, two characteristics in which the genus Spizella



Figure 7. Spizella breweri, S. pallida, Aimophila  
carpalis, Spizella pusilla, S. passerina,  
S. arborea, S. atrogularis, dorsal view. --  
 Left to right.

is quite homogeneous. Spizella is also distinct from A. carpalis in possessing the inflated condition of the auditory bullae and in its slender, acuminate transpalatine process (with the exception that S. breweri may sometimes have a divided transpalatine). One cranial character that does suggest unity between the two genera, however, is the stubby condition of the intraorbital cristae, a relatively uncommon character state in the Emberizinae. This condition occurs in all members of Spizella except arborea, and in all members of the Haemophila group, which includes A. carpalis. The differences between Aimophila and Spizella seem to warrant the maintenance of the two as distinct genera; however the similarities between A. carpalis and the species of Spizella are sufficient to suggest that the two may be very closely related. The question of which gave rise to which may be one for debate; the relative uniformity of the genus Spizella both in plumage pattern and cranial characters suggests a recent origin for that group as does the inflated condition of the auditory bullae, which seems to be the derived state for that character.

#### Ammodramus

A possible link between Aimophila and Ammodramus was suggested to me by S. L. Olson (personal communication, 1980), who pointed out the similarities between Aimophila stolzmanni and some species of Ammodramus. These are most apparent in the South American forms of Ammodramus, A. humeralis and A. aurifrons, formerly placed in the genus Myospiza. The distribution of these two species and of Aimophila is



shown in Figures 8, 9 and 10. The characteristics shared by these three forms are the bright yellow wrist feathers, which are considerably brighter than those found in the northern species of Ammodramus and most other emberizines in which such yellow feathers occur (this area may be just as bright in Aimophila botterii mexicana, however); the short tail relative to wing length; the rufous edgings on the secondary feathers, particularly evident in Ammodramus humeralis; and to a certain extent the pattern and coloration of the back. Ammodramus humeralis, A. aurifrons and A. savannarum all possess the stubby condition of the intraorbital cristae as do all members of the Haemophila group including stolzmanni, although the genus Ammodramus as a whole displays the moderately inflated condition of the auditory bullae while Aimophila stolzmanni has the uninflated condition. In addition, A. stolzmanni and some species of Ammodramus have rostral angles which are among the sharpest I measured (see Appendix A).

These similarities are, of course, only suggestive and one should not attempt to draw conclusions from them, especially considering the paucity of information on habits of A. stolzmanni which come from only a few brief accounts (Paynter, 1967; Taczanowski, 1886). Life history information on Ammodramus humeralis and A. aurifrons is also scarce and consists of scattered observations made during the course of other studies (e.g., Wetmore, 1926:427 ff.). When more complete information becomes available it may be possible to suggest more firmly a link between the two genera, perhaps an origin for Ammodramus from Aimophila via A. stolzmanni.



Figure 8. Distribution of *Ammodramus humeralis*.



Figure 9. Distribution of *Ammodramus aurifrons*.



Figure 10. Distribution of *Aimophila stoltzmanni*.

## Torreornis

Torreornis inexpectata is confined to the area of the Zapata Swamp near Santo Tomás and to the coast near Baitiquirí, Cuba (Barbour, 1943; Bond, 1971). My examination of skins of Torreornis i. inexpectata and T. i. sigmani at the United States National Museum leads me to conclude that Torreornis is most closely related to Aimophila rufescens and is probably derived from a population of the latter species (e.g., from Honduras). The shared plumage characters that unite the two species are the following: white or light-colored throat contrasting with buffy or grey breast; pronounced malar streaks, rufous crown (light in Torreornis, dark in A. rufescens) with grey medial stripe (stripe may be faint in either species) becoming buffy in rufescens; white lores, grey superciliary streak; black bill. The back is faintly streaked in Torreornis. Streaking on the back in A. rufescens is not as bold as that, for example, of A. ruficauda, but the plumage of rufescens is darker than that of Torreornis, rendering the streaking on the back obsolete. Torreornis lacks the bright rufous coloration of A. rufescens.<sup>1</sup> Paynter (1970:102) notes that "except for the yellow underparts, Torreornis much more closely resembles some species of Aimophila" than it does Pipilo or Melozone as suggested by Hellmayr (1938). The yellow underparts of Torreornis do provide a link with Aimophila rufescens, however, as the latter has yellow underparts in

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1. S. L. Olson (1980, personal communication) informs me of an undescribed subspecies of Torreornis inexpectata from Cayo Coco, Cuba, in which the rufous crown is brighter than in the other two subspecies. I have not yet had the opportunity to examine specimens of this newly discovered form.

the juvenal plumage. Further evidence for the relationship is the remarkable similarity in the songs of Aimophila rufescens and Torreornis (Morton, personal communication, 1980).

The generic characters for Torreornis were given by Barbour and Peters (1927, p. 96) as "a medium-sized fringillid with short, rounded wings; rounded, almost graduated tail; plumage long and lax." In a study of size trends in island birds, Grant (1965b) found that while insular forms tend to have larger tarsi and bill than their mainland counterparts, wings and tails are equally likely to be smaller or larger on islands than on the mainland. Other authors reporting small wings in insular species are Hesse, Allee and Schmidt (1937) and Bourne (1955). Such trends are commonly attributed to the absence of ecologically similar species on islands (ecological release; Pianka, 1978:318). Hence it would not be surprising to find an insular species of Aimophila with smaller wings than its mainland congeners.

The plumage of Torreornis inexpectata is indeed "long and lax" but in this respect it cannot be considered appreciably different from that of Aimophila rufescens, which it most closely resembles. Further, the pale coloration of the plumage of Torreornis is another example of a common trend in avian species on islands (Grant, 1965a; Murphy, 1938; Murphy and Chapin, 1929).

The similarities in Aimophila rufescens and Torreornis inexpectata are considerable, although the differentiation that has occurred in the latter cannot be ignored. I suggest that the genus Torreornis be merged with Aimophila and that the former be maintained as a subgenus

characterized by the original generic features of Barbour and Peters (1927). To these characters should be added "yellow underside in adult plumage" and from them deleted "plumage long and lax" (see Diagnosis).

### Pipilo

The observation has been made that the genus Pipilo may be closely related to Aimophila (Wolf, 1977). This was not supported by morphology. The only behavioral observation that suggests a possible relationship is the occurrence in Pipilo fuscus, P. aberti and P. albicollis of a squeal duet, which occurs in Aimophila ruficeps (Marshall, 1964) and in A. rufescens as well (Wolf, 1977). This is also reported for Arremonops conirostris, a possible relative of Pipilo, by Skutch (1954) and Moynihan (1963). Marshall (1964) states quite firmly and correctly that the brown towhees form a distinct unit that "has no close relatives." The morphological differences between Pipilo and Aimophila are detailed in the Diagnosis.

## DIAGNOSIS

Being an exceptionally diverse group of taxa, the genus Aimophila is difficult to diagnose in the usual manner, and is perhaps best characterized, in part, in terms of features it does not possess.

### Aimophila

Small or medium-sized fringillids; underparts of adults unstreaked; flanks buffy to rich buff except in A. carpalis, A. cassinii, A. superciliosa and A. stolzmanni. Malar streaks present, either obscure (cassinii) or pronounced (rufescens). Tail long and rounded, not forked as in Spizella or short as in Ammodramus (except stolzmanni). Lack white in rectrices. Differ from the Zonotrichia with unstreaked underparts in lacking solid black on the pileum except for some members of Haemophila, which are in turn distinguished by their stouter bills and their stubby intraorbital cristae. The members of Aimophila differ from Pipilo in their considerably smaller size and lack of rufous crissum; dorsum and pileum streaked (only P. erythrophthalmus has dorsal streaks, and these are boldly white with black); underparts generally unmarked, or if marked then not streaked in adults; rectrices without white or tan edges. The genus Aimophila as a whole may also be distinguished from other emberizine genera by the predominance of rufous on the dorsum.



Only five of the 15 species of Aimophila have an elongated intraorbital crista. The remaining 10 species have the stubby condition which they share only with Calcarius, Spizella (except arborea), some species of Ammodramus and Amphispiza quinquestriata. The five species with an elongated crista are inexpectata, ruficeps, notosticta, rufescens and superciliosa.

#### Subgenus Haemophila

Small to medium sized. Seven species: ruficauda, humeralis, mystacalis, stolzmanni, strigiceps, sumichrasti and carpalis. Flanks buffy (except in carpalis); belly white, breast grey, or black (humeralis). Bill moderately large to stout. Auditory bullae uninflated except in humeralis in which they are moderately inflated; intraorbital cristae stubby.

#### Subgenus Aimophila

Medium sized. Four species: superciliosa, rufescens, notosticta and ruficeps. These species have the pileum rufous with a grey central stripe. In ruficeps this central stripe may be indefinite; in superciliosa it is bold and streaked with black. Malar streaks pronounced except in superciliosa, which instead has a black cheek patch. Bill black except in ruficeps. Auditory bullae inflated; interior intraorbital crista elongated.

#### Subgenus Peucaea

Small to medium sized. Three species: aestivalis, botterii and cassinii. The dorsum is streaked with rufous and grey, palest in

cassinii; feathers at wrist yellow; bill slender; malar streaks present but obscure; buffy pectoral band present except in cassinii. Central rectrices with dark serrated central bar in cassinii and A. botterii arizonae. Secondaries rufous except in cassinii. Auditory bullae inflated, intraorbital cristae stubby.

#### Subgenus Torreornis

Medium sized. One species: inexpectata. Underparts yellow, pileum rufous with grey central stripe. Dorsum pale with faint streaking, bill black and moderately slender. Auditory bullae inflated, interior intraorbital crista elongated.

#### Amphispiza

The genus Amphispiza must be defined here as well, as the original description (Coues, 1874) did not include generic characters. Its three members are not uniform either in plumage or in cranial osteology, neither do they form a diverse a group as the genus Aimophila.

Medium sized fringillid. Three species: bilineata, belli and quinquestriata. Dorsum olive brown in bilineata and belli, with delicate streaking in belli. Dorsum darker and unstreaked in quinquestriata. Pileum of same color as dorsum and unstreaked in all species. Superciliary streak white, malar streak white. Chin black in bilineata and quinquestriata, with wide, white central streak in quinquestriata. Breast with central spot except in bilineata, which has a black bib. Outer rectrices tipped or edged with white. Bill

moderately slender. Auditory bullae inflated (belli) or moderately inflated (bilineata and quinquestriata). Interior intraorbital crista elongated (bilineata and belli) or stubby (quinquestriata).

## DISCUSSION

The members of the emberizine Group I of Morony et al. (1975) are extremely closely related. As anyone attempting to sort out these relationships can attest, unifying characteristics are difficult to identify, with the result that the subfamily Emberizinae is particularly plagued with monotypic genera or genera with only a few species.

The characters that have proved most useful thus far in suggesting relationships within the Emberizinae are plumage characters (see Diagnosis) and a few features of the skull. The latter are the auditory bullae, intraorbital cristae and, to a lesser extent, the rostral angle. The pattern that emerges from these characters is not extremely clear, and in fact it provokes several perplexing questions. What, for example, is the functional significance of an inflated versus an uninflated bulla? Elongated versus stubby cristae? Why do these differ in such closely related forms? The most obvious questions, perhaps, are whether these various conditions truly reflect relationships at the generic level, or whether they have arisen several times within the subfamily? The inflated bullae and elongated crista are conditions not found outside the Fringillidae, and clearly represent the derived states for these characters. The haemophilas possess uninflated bullae (except humeralis and mystacalis) and stubby cristae; the peucaeas have inflated bullae and stubby cristae, while the Aimophila and Torreornis groups have inflated bullae and an elongated crista. The

Haemophila group seems to be linked with Spizella (inflated bullae and stubby cristae), the latter presumably being the more derived group. They may also be related to Ammodramus, in which some species have stubby cristae and some an elongated one; the bullae in Ammodramus are moderately inflated. Clearly, the genus Aimophila is an assemblage of diverse forms possessing both ancestral and derived character states among its various members. Morphological evidence indicates that it is indeed a monophyletic group (except quinquestriata), probably a fairly primitive one, and one which gave rise to several other more "advanced" genera.

The genus Amphispiza, to which I have relegated Aimophila quinquestriata, presents a similar problem. Although it is, relative to Aimophila, a fairly homogeneous group in plumage, it is variable osteologically. A. belli has strongly inflated auditory bullae while bilineata has only moderately inflated ones. Both species have an elongated intraorbital crista. A. quinquestriata has moderately inflated bullae and stubby cristae. Such variation indicates that the members of Amphispiza sensu lato may not be as closely related inter se as the members of other, more homogeneous groups such as Spizella, in which only one member, S. arborea, deviates from the rest in possessing an elongated interior crista.

Examination of jaw muscles reveals differences associated with differences in intraorbital cristae in Aimophila cassinii (stubby cristae) and A. ruficeps (elongated interior crista). The extent of this kind of variation requires investigation by survey dissections

involving, preferably, every emberizine species. This is not presently feasible due to lack of specimens, but such a study, necessarily long-term, may prove to be essential in unravelling relationships among the sparrows and particularly Aimophila. Life history information can also prove useful in some systematic studies, as is shown admirably by Olson and Feduccia (1980a, 1980b); this information is lacking for many emberizine species.

## TAXONOMIC CONCLUSIONS

The scanty evidence available from osteological and plumage characters indicates that the genus Aimophila, excluding the species quinquestriata, is a natural group, though not as homogeneous a group as some other genera. The gap between the Haemophila and the Aimophila groups is bridged by "Oriturus" superciliosus which should henceforth be considered Aimophila superciliosa. The gap between the Aimophila and the Peucaea groups is bridged by A. ruficeps and A. notosticta. Aimophila carpalis partially bridges the gap between Aimophila and Spizella, although not to the extent that the two should be merged; I recommend that they be placed next to each other in the classification of Emberizinae. In addition I suggest tentatively that Ammodramus may be related to Aimophila via Aimophila stolzmanni but that behavioral studies and dissection of jaw muscles may offer the only hope of confirming this possibility. Finally, a direct link between Aimophila rufescens and Torreornis of Cuba is clearly evident, and I recommend that Torreornis be synonymized with Aimophila. I divide the genus Aimophila into four subgenera: Haemophila, Aimophila, Peucaea and Torreornis.

Aimophila quinquestriata seems to be closest to Amphispiza and I recommend that it be returned to that genus. I am uncertain of the placement of Amphispiza relative to Aimophila, but the two do not

appear to be any more closely related to each other than any other two genera.

These ideas are summarized in the Proposed Classification (Appendix B).



APPENDIX A

ROSTRAL ANGLE (IN DEGREES)

## ROSTRAL ANGLE (IN DEGREES)

Species	n	$\bar{x}$	SD
<u>Calcarius lapponicus</u>	1	31.0	--
<u>C. ornatus</u>	7	27.0	2.71
<u>Plectrophenax nivalis</u>	--	--	--
<u>Calamospiza melanocorys</u>	4	29.5	3.42
<u>Zonotrichia melodia</u>	1	37.0	--
<u>Z. lincolni</u>	3	33.7	4.04
<u>Z. capensis</u>	2	32.5	4.95
<u>Z. querula</u>	--	--	--
<u>Z. albicollis</u>	1	29.0	--
<u>Z. leucophrys</u>	6	28.7	6.12
<u>Junco phaeonotus</u>	3	31.3	4.73
<u>Ammodramus sandwichensis</u>	2	32.0	5.66
<u>A. bairdii</u>	1	54.0	--
<u>A. savannarum</u>	2	42.5	3.54
<u>A. humeralis</u>	1	32.0	--
<u>A. aurifrons</u>	--	--	--
<u>Spizella arborea</u>	2	29.0	4.24
<u>S. passerina</u>	5	26.2	5.76
<u>S. breweri</u>	4	29.8	3.30
<u>Poocetes gramineus</u>	6	26.7	1.86

Species	n	$\bar{x}$	SD
<u>Chondestes grammacus</u>	4	31.3	2.36
<u>Amphispiza bilineata</u>	8	29.4	2.62
A. <u>belli</u>	2	24.5	3.54
A. <u>quinqestriata</u>	4	34.0	3.83
<u>Aimophila carpalis</u>	8	37.3	3.99
A. <u>sumichrasti</u>	5	32.0	7.84
A. <u>strigiceps</u>	1	39.0	--
A. <u>stolzmanni</u>	2	49.5	3.54
A. <u>ruficauda</u>	5	36.4	5.32
A. <u>mystacalis</u>	6	33.3	2.66
A. <u>humeralis</u>	7	33.6	3.21
A. <u>superciliosa</u>	7	43.9	2.12
A. <u>rufescens</u>	7	47.0	4.93
A. <u>notosticta</u>	2	39.8	1.06
A. <u>ruficeps</u>	4	35.3	2.22
A. <u>aestivalis</u>	2	31.5	2.12
A. <u>botterii</u>	5	43.2	4.44
A. <u>cassinii</u>	8	39.3	3.33
A. <u>inexpectata</u>	1	31.0	--
<u>Pipilo fuscus</u>	11	32.9	3.33
<u>Saltatricula multicolor</u>	1	19.0	--

APPENDIX B

PROPOSED CLASSIFICATION

## PROPOSED CLASSIFICATION

Genus AimophilaSubgenus Haemophila

Aimophila carpalis  
sumichrasti  
strigiceps  
stolzmanni  
ruficauda  
mystacalis  
humeralis

Subgenus Aimophila

Aimophila superciliosa  
rufescens  
notosticta  
ruficeps

Subgenus Peucaea

Aimophila aestivalis  
botterii  
cassini

Subgenus Torreornis

Aimophila inexpectata

Genus Spizella

The genera Ammodramus and Amphispiza should be left in their current taxonomic position (Paynter, 1970) until further evidence is available.

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