

## SYSTEMATIC RELATIONSHIPS AMONG THE EMBERIZID SPARROWS

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**ABSTRACT.**—We developed a phylogeny for 34 taxa (species, species groups, or genera) in the Emberizidae, including all of those placed in the “first group” of the Emberizidae by Paynter and Storer (1970). Structural, plumage-related, behavioral, oological, and allozymic characters were employed. The lateroventral process of the laterosphenoid, a skeletal feature not previously used in comparative anatomy among passerines, also was included. Majority-rule, strict-consensus, and bootstrapped maximum-parsimony trees were constructed. Phylogenies uncovered were in fairly close agreement with previously published work that used molecular data, although the Old World bunting clade (*Emberiza*, *Melophus*, *Plectrophenax*, *Calcarius*, etc.) was basal to all other emberizid sparrows examined. The majority-rule and strict-consensus phylogenies supported the monophyly of all currently accepted genera (e.g. *Aimophila*, *Ammodramus*, *Spizella*, and *Zonotrichia*), provided that “*Amphispizza*” *quinquestriata* is placed in the genus *Aimophila*. In some cases, however, the monophyly was weak (e.g. *Melospiza*, especially *M. melodia* vs. *Passerella*), and for others (e.g. *Ammodramus*) more work is needed to establish fully the intrageneric relationships. Received 11 March 1997, accepted 3 November 1997.

RELATIONSHIPS AMONG THE NEW WORLD NINE-PRIMARIED OSCINES (Parulidae, Thraupidae, Emberizidae, Icteridae, and Fringillidae) have long been contentious (Ridgway 1901, Paynter and Storer 1970, AOU 1983, Bledsoe 1988). A particularly muddled group has been the emberizid sparrows, with various classifications merging them with cardueline finches (Fringillidae), retaining them as a separate family (Emberizidae), or treating them as a subfamily (Emberizinae) of an expanded Emberizidae that includes wood-warblers, tanagers, icterines, and others (e.g. AOU 1983).

Within the family Emberizidae, relationships are even less clear, and few systematic studies beyond “intuitive” ones (e.g. Paynter 1964) have been published. A study by Avise et al. (1980) is a notable exception, although their allozyme data were limited to only 12 members of the family, some of which were closely allied species (e.g. *Spizella pusilla* and *S. passerina*) that provided little insight into relationships among the other taxa. Additional studies using only a subset of genera (e.g. Zink 1982, Zink and Blackwell 1996) or a single genus (e.g. Wolf 1977, Zink 1986) have been produced. Although these studies helped resolve relationships within the groups studied, they did not offer a broader perspective about relationships

among the 32 genera (Sibley and Monroe 1990) in this subfamily.

Our study concentrated on the 18 genera within the Emberizinae from *Aimophila* to *Plectrophenax*, following the linear sequence of the 7th edition of the American Ornithologists’ Union Check-list (AOU 1998). These genera form the whole of the “first group” of the Emberizidae, the “typical” emberizids, in Paynter and Storer (1970). A phylogenetic hypothesis, based on types of characters and number of characters, was generated to delineate relationships within and among these genera.

### MATERIALS AND METHODS

**Operational taxonomic units.**—The 18 genera we examined were: *Aimophila*, *Oriturus*, *Torreornis*, *Spizella*, *Pooecetes*, *Chondestes*, *Amphispizza*, *Calamospiza*, *Passerculus*, *Ammodramus*, *Xenospiza*, *Passerella*, *Melospiza*, *Zonotrichia*, *Junco*, *Calcarius*, *Emberiza*, and *Plectrophenax*. Of these genera, *Oriturus*, *Torreornis*, *Pooecetes*, *Chondestes*, *Calamospiza*, *Passerculus*, *Xenospiza*, and *Passerella* currently are treated as monotypic, although future species-level splits are possible within *Passerculus* and *Passerella* (see Zink et al. 1991a, Zink 1994). To reduce the number of taxa being tracked, our operational taxonomic units within *Aimophila*, *Ammodramus*, and *Spizella* included species groups that were chosen in a way that minimized the number of polymorphisms in the characters we examined. We treated *Aimophila* as three groups, following exactly the three species groups outlined by Wolf (1977). Our treatment of *Ammodramus* followed tra-

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TABLE 1. Discrete characters and states used in parsimony analysis. Unless stated otherwise, characters and states refer to those of adults (of both sexes).

1. Palato-maxillary fusion (ordered; 0, palato-maxillaries free or adjacent to prepalatine bars for most of length; 1, palato-maxillaries fused for most/all of length; suture present; 2, palato-maxillaries completely fused; no suture evident)
2. Inflation of squamosal region (ordered; 0, squamosal region not inflated; 1, squamosal region slightly inflated; 2, squamosal region much inflated)
3. Length/shape of lateroventral process of the laterosphenoid (ordered; 0, short; 1, moderate; 2, long with thin, pointed tip; 3, long with wide, flat tip)
4. Shape of nostril (0, rounded; 1, pointed)
5. Nostrils exposed (ordered; 0, nostrils exposed; 1, nostrils partially exposed; 2, nostrils concealed)
6. Ratio of hallux to inner toe (0, hallux shorter; 1, inner toe shorter)
7. Lengthened hind claw (0, hallux $\gg$ hindclaw; 1, hallux $\leq$ hindclaw)
8. Ratio of primary extension (longest primary-longest secondary) to tarsus (0, primary extension $<$ tarsus; 1, primary extension $\geq$ tarsus)
9. Ratio of primary 9 to primary 6 (0, primary 9 $\leq$ primary 6; 1, primary 9 $>$ primary 6)
10. Ratio of primary 9 to primary 2 (0, primary 9 $\leq$ primary 2; 1, primary 9 $>$ primary 2)
11. Ratio of inner secondaries to outermost primary (0, primaries $\gg$ than all secondaries; 1, longest secondaries $>$ outermost primaries)
12. Lengthened interscapulars (0, interscapulars not lengthened; 1, interscapulars lengthened)
13. Shape of tail (unordered; 0, rounded/double-rounded, i.e. rectrices 1 and 2 $<$ rectrices 3 and 4 $>$ rectrices 5 and 6; 1, emarginated tail, i.e. rectrix 1 $<$ rectrices 2 and 3 $<$ rectrices 4, 5, and 6; 2, graduated tail, i.e. rectrices 1 and 2 $>$ rectrix 3 $>$ rectrix 4 $>$ rectrix 5 $>$ rectrix 6)
14. Tail-to-wing ratio (ordered; 0, tail $<$ wing; 1, tail $\approx$ wing (within 2 mm); 2, tail $>$ wing)
15. Rectrices pointed (0, rectrices squared/rounded; 1, rectrices pointed)
16. Double scratching feeding behavior (0, absent; 1, present)
17. Sexually dimorphic (0, sexually dimorphic; 1, not sexually dimorphic)
18. Seasonally dimorphic (0, seasonally dimorphic; 1, not seasonally dimorphic)
19. Central breast streaking on adult female (ordered; 0, streaking present; 1, central breast spot present; 2, breast unmarked)
20. Breast streaking as juvenile (0, present; 1, absent)
21. Back streaking on adult female (0, present; 1, absent)
22. Yellow/orange supraloral region (0, absent; 1, yellow present)
23. Dusky/blackish lores; i.e. concolorous or not postocular area (0, absent; 1, present)
24. Yellow on bend of wing (0, absent; 1, present)

TABLE 1. Continued.

25. White wingbars (0, absent; 1, present)
26. Rusty shoulder; i.e. lesser/median wing coverts (0, absent; 1, present)
27. Buffy flanks (0, absent; 1, present)
28. Bold black-and-white head pattern (0, absent; 1, present)
29. Distinct eye ring (0, absent; 1, present)
30. Rufous/rusty crown (ordered; 0, absent; 1, rusty confined to lateral stripes; 2, rusty crown solid)
31. Streaked crown on adult female (0, present; 1, absent)
32. White on outer web of outer rectrix (0, absent; 1, present)
33. Color of leg (0, gray/blackish; 1, pink/pinkish)
34. Color/pattern of bill (0, dark maxilla, pale mandible; 1, concolorous)
35. Markings on eggs (0, present; 1, absent)
36. Ground color of eggs (unordered; 0, brownish to whitish; 1, white/whitish; 2, whitish to bluish; 3, blue/bluish; 4, blue to green; 5, green; 6, greenish to whitish)
37. Allele A of LDH-1 (0, absent; 1, present)
38. Allele C of LDH-1 (0, absent; 1, present)
39. Allele A of $\alpha$ GPD-1 (0, absent; 1, present)
40. Allele B of $\alpha$ GPD-1 (0, absent; 1, present)
41. Allele C of $\alpha$ GPD-2 (0, absent; 1, present)
42. Allele E of $\alpha$ GPD-2 (0, absent; 1, present)
43. Allele C of PEP (0, absent; 1, present)
44. Allele D of PEP (0, absent; 1, present)
45. Allele F of PEP (0, absent; 1, present)
46. Allele B of TO (0, absent; 1, present)

ditional groupings (Robins and Schnell 1971) of the marshland sparrows (*A. henslowii*, *A. leconteii*, *A. caudatus*, *A. nelsoni*, and *A. maritimus*) and the grassland sparrows (*A. aurifrons*, *A. humeralis*, and *A. savannarum*), although we treated *A. bairdii* separately. We split *Spizella* into five operational taxonomic units: *S. arborea*, *S. atrogularis*, *S. passerina*, the *pallida* group (*S. breweri* and *S. pallida*), and the *pusilla* group (*S. pusilla* and *S. wortheni*). The five species of *Zonotrichia*, three species of *Melospiza*, and three species of *Amphispiza* (sensu AOU 1983) were treated separately, whereas *Junco*, *Emberiza*, *Plectrophenax*, and *Calcarius* were included only at the generic level.

*Data characterization.*—Morphological, behavioral, and oological characters and selected protein data were used in the phylogenetic analysis (Table 1). Morphological characters for separating genera were gleaned primarily from Ridgway (1901), supplemented by information in Coues (1903), Chapman (1939), Mayr and Short (1970), Oberholser (1974), and Rising (1996). Additional information for *Aimophila* was gathered from Wolf (1977); for "*Amphispiza*" [= *Aimophila*] *quinquestrata* from Mills et al. (1980) and Phillips and Phillips (1993); for *Junco*, *Melospiza*, *Passerella*, and *Zonotrichia* from Paynter (1964); for *Torreornis* from Barbour and Peters (1927) and Bond (1980); and for *Xenospiza* from Bangs (1931)

and Dickerman et al. (1967). Data for the lateroventral process of the laterosphenoid are presented here (Appendix 1).

A single behavioral character was used, the "double-scratching" feeding habit (see Greenlaw 1977). Oological data were taken mainly from Harrison (1979), with some additional information from Wolf (1977) and Bond (1980). Protein data were adapted from Avise et al. (1980), Zink (1982), Zink and Avise (1990), and Johnson and Marten (1992). Allelic frequencies were not employed; instead, each locus was used as a character and its different alleles were employed as unordered character states (Buth 1984).

*Phylogenetic analysis.*—Characters were polarized using primitive states inferred from reference to sister taxa to the emberizids we examined. Specifically, we determined ancestral states (Appendix 2) by examining characters in three genera in the closely related family Cardinalidae (*Cardinalis*, *Pheucticus*, and *Passerina*) and in genera from the other groups of Emberizidae in Paynter and Storer (1970), namely *Phrygilus* (group 2); *Sicalis* (group 3); *Tiaris* (group 4); and *Pipilo*, *Arremon*, and *Arremonops* (group 6). After initial analysis, it became clear that the *Emberiza* clade lay outside of the remainder of the taxa we considered; it was used as the outgroup in all subsequent analyses. The presumed ancestral character was assigned a value of 0, but Wagner parsimony was used because often it was difficult to determine whether a trait was ancestral or derived. Thus, for two-state characters, changes from 0 → 1 or 1 → 0 were treated as equally likely given constraints of the data. Operational taxonomic units that were polymorphic for a given character were coded as such, and missing data were entered into the matrix.

Phylogenetic analyses were performed with PAUP version 4.0d61 (Swofford 1997). Input order of taxa was randomly varied for each iteration, with 10 replicates performed. Parsimony analyses were performed using a heuristic search on unweighted data until a set of most-parsimonious trees was uncovered. We used total length of the tree, consistency index (CI), and retention index (RI) to describe the inferred trees. We used both a strict-consensus tree and a majority-rule tree (Margush and McMorris 1981) to summarize regions supported in the resultant equally parsimonious trees.

A standard bootstrap analysis could not be conducted to assess branch support because the character data we employed violated assumptions of statistical independence required for bootstrapping (Felsenstein 1985, Sanderson 1989, Livezey 1996) and because the number of taxa we traced versus the number of characters we used was too large. Thus, we assessed stability of the nodes in the minimum-length trees using a fast heuristic bootstrap with 5,000 replications. As with standard bootstrapping, this method likely yields biased percent bootstrap support (see Li and Zharkikh 1995), so the resultant

bootstrap tree was used only as a heuristic tool (i.e. as an index to empirical support; see Livezey 1996).

We compared our results against existing phylogenies largely in a heuristic fashion. However, because data were available for a more robust analysis of the genus *Spizella*, we conducted a partition-homogeneity test with a heuristic search to test congruence between that region of the phylogeny we developed against a phylogeny for this genus based on a sequence of mitochondrial DNA (mtDNA; Dodge et al. 1995).

## RESULTS

A total of 99 most-parsimonious trees was found (length = 280 steps, CI = 0.629, RI = 0.652). Topologies of the majority-rule (Fig. 1), strict-consensus, and bootstrapped trees (Fig. 2) were reasonably similar, and the topology of the majority-rule tree was identical to that of one of the most-parsimonious trees. Traditionally recognized genera virtually always formed monophyletic clusters. The majority-rule tree (Fig. 1) and strict-consensus tree (which is found by collapsing to polytomies those branches not shared by all equally parsimonious trees; i.e. all those in the majority-rule tree without "100" at the node) showed that five nodes could not be resolved with the characters we used: (1) the Old World buntings (*Emberiza*, *Plectrophenax*, and *Calcarius*); (2) the placement of *Spizella arborea*, a species that often clustered with *Zonotrichia*; (3) relationships within *Spizella*; (4) relationships within *Ammodramus*; and (5) placement of *Melospiza* + *Passerella* with regard to other taxa. Our data never resolved the position of *Zonotrichia atricapilla*, so it always appeared as part of a polytomy.

Using a linear classification procedure like that described by Mayr and Ashlock (1991:154), a sequence of genera derived from the majority-rule tree (Fig. 1) would be: *Emberiza* and other Old World buntings, *Calcarius*, *Plectrophenax*, *Calamospiza*, *Amphispiza*, *Melospiza*, *Passerella*, *Chondestes*, *Poocetes*, *Xenospiza*, *Passerculus*, *Ammodramus*, *Oriturus*, *Aimophila*, *Torreornis*, *Junco*, *Zonotrichia*, and *Spizella*. With species, species groups, and subgenera included, our majority-rule sequence would be: *Emberiza* and other Old World buntings, *Calcarius*, *Plectrophenax*, *Calamospiza melanocorys*, *Amphispiza belli*, *A. bilineata*, *Melospiza melodia*, *M. lincolni*, *M. georgiana*, *Passerella iliaca*, *Chondestes grammacus*, *Poocetes gramineus*, *Xenospiza baileyi*, *Passerculus*

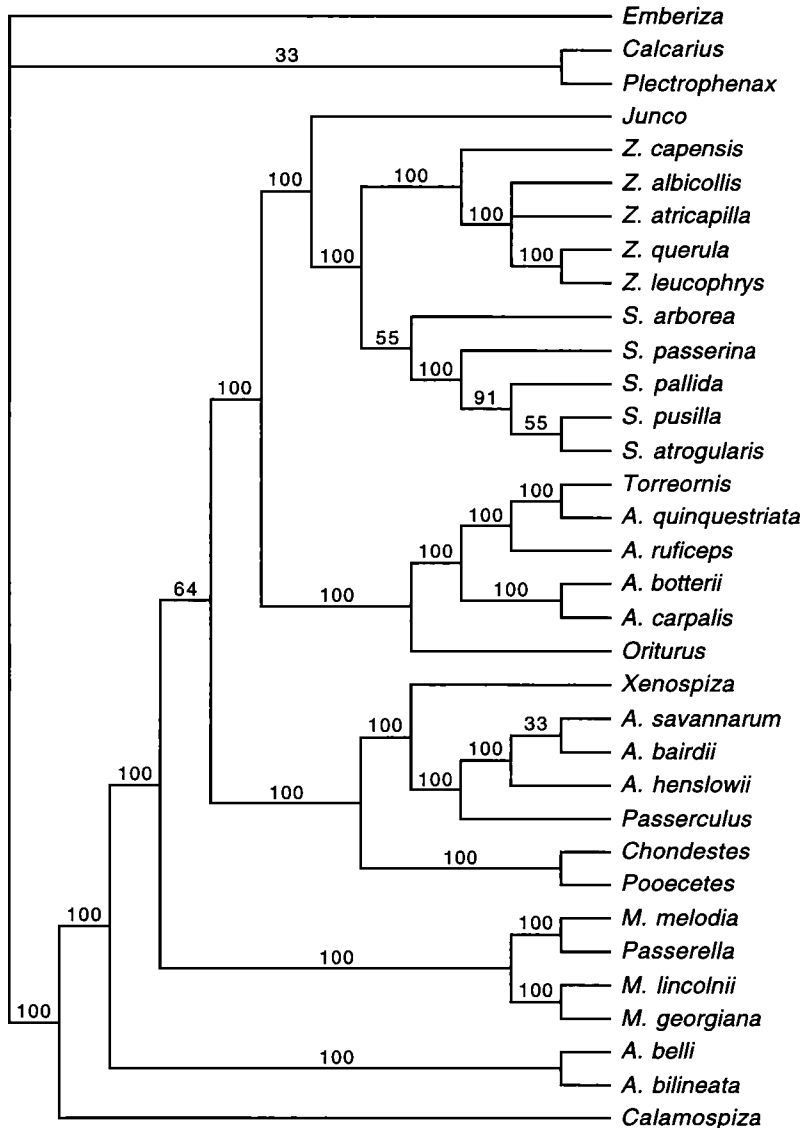


FIG. 1. Majority-rule tree of 99 shortest trees (length = 280,  $CI = 0.629$ ,  $RI = 0.652$ ) based on a parsimony analysis of discrete character data (numbers at the nodes indicate the percentage that the given arrangement appeared in the set of 99 equally-parsimonious trees). All characters were weighted equally and the outgroup was the *Emberiza* / *Calcarius* / *Plectrophenax* clade.

*sandwichensis*, *Ammodramus bairdii*, *A. savannarum/humeralis/aurifrons*, *A. henslowii/leconteii/caudacutus/nelsoni/maritimus*, *Oriturus superciliosus*, *A. aestivalis/botterii/cassinii*, *A. mystacalis/humeralis/etc.* (the "Haemophila" group; Wolf 1977), *A. ruficeps/notosticta/rufescens*, *Aimophila quinquestriata*, *Torreornis inexpectata*, *Junco hyemalis/pheonotus/vulcani*, *Zonotrichia capensis*, *Z. albicollis*, *Z. atricapilla*, *Z. leucophrys*,

*Z. querula*, *Spizella arborea*, *S. passerina*, *S. pallida/breweri*, *S. atrogularis*, and *S. pusilla/wortheni*. These sequences differ markedly from the one presented by the AOU (1983, 1997). Although data presented by Sibley and Ahlquist (1990) do not strongly support the linear sequence presented by Sibley and Monroe (1990), their arrangement is closer to the one we developed here.

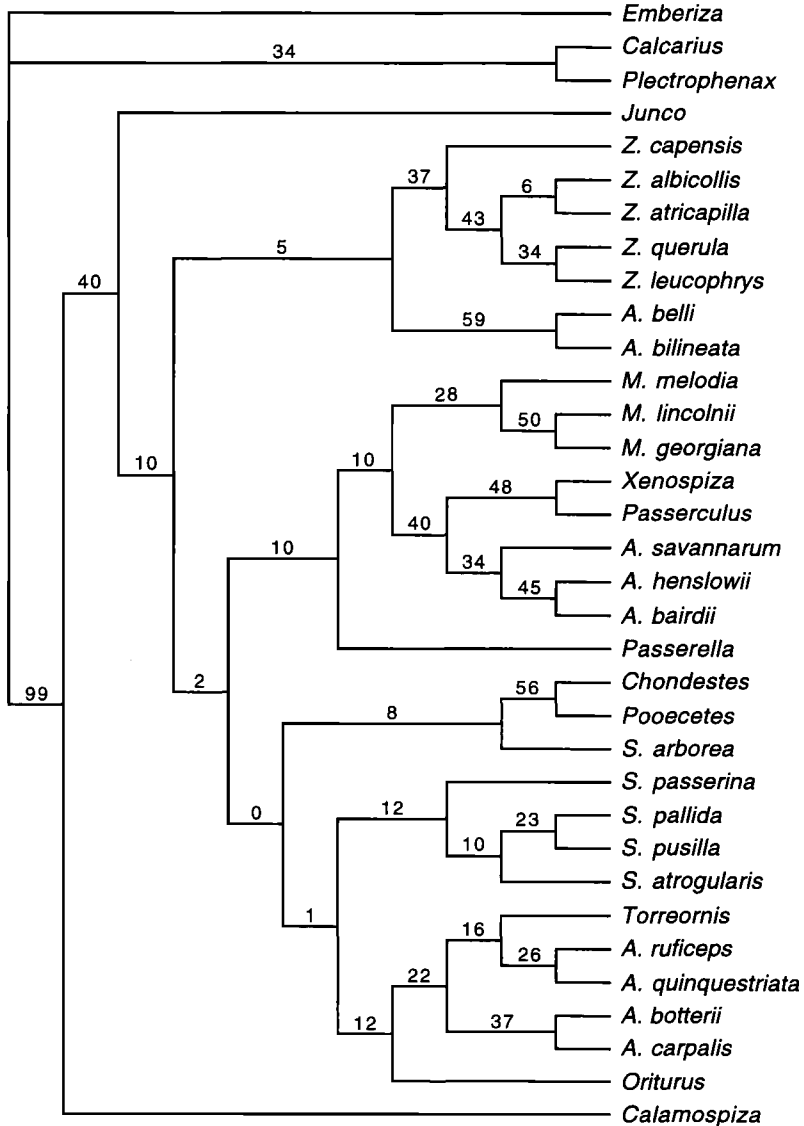


FIG. 2. Unrooted bootstrap tree based on discrete character data, with all characters weighted equally. Numbers at the nodes indicate branch support from a 5,000-replication fast-heuristic bootstrap.

#### DISCUSSION

Previous phylogenetic studies using morphometrics, protein electrophoresis, and mtDNA included a subset of the genera considered in our study (e.g. Robins and Schnell 1971, Avise et al. 1980, Zink 1982, Zink and Avise 1990, Zink et al. 1991b, Zink and Dittmann 1993, Zink and Blackwell 1996). Whereas we adapted and used some data from these studies, their resulting phylogenies were not em-

ployed. The phylogeny we developed is, nevertheless, in general agreement. For example: (1) allozyme data indicate that *Calcarius* is an outgroup to the other emberizid sparrows (Avise et al. 1980); (2) our data suggest that *Junco* lies outside the main *Zonotrichia*/*Melospiza*/*Passerella* clade, a notion previously supported by molecular data (Zink 1982), although a different result, with *Junco* and *Zonotrichia* being sister genera, recently has been presented (Zink and Blackwell 1996); and (3) the system-

atic relationships within the genus *Spizella* were consistent with those reported by Dodge et al. (1995) using mtDNA sequence data, including the finding that *S. arborea* is the most distantly related member of that genus. Indeed, in terms of the lateroventral process of the laterosphenoid and the presence of double-scratching behavior, *S. arborea* is more like *Zonotrichia* or *Melospiza* than any other *Spizella*. Particular points of interest and problem areas are discussed separately below.

*The Emberiza/Calcarius/Plectrophenax clade.*—The *Emberiza* clade (*Emberiza*, *Calcarius*, and *Plectrophenax*) is strongly supported by our analysis. Note that this clade also comprises the monotypic Old World genera *Melophus*, *Latoucheornis*, *Miliaria*, and *Urocynchramus*, which we did not examine. *Miliaria* frequently is merged into *Emberiza* (e.g. Clements 1991, Howard and Moore 1991), Mayr and Short (1970) suggested that *Plectrophenax* is separated only doubtfully from *Emberiza*, and the other genera are closely related to *Emberiza* (except *Urocynchramus*, which often is placed in the Fringillidae; e.g. Meyer de Schauensee 1984, Howard and Moore 1991:504, cf. Sibley and Monroe 1990:715).

The strongly resolved *Emberiza* clade definitely is more basal than the linear sequence presented by the AOU suggests. Analysis of the extent and nature of palato-maxillary fusion supports this relationship, with the "palato-maxillaries free from prepalatine bars for one-half or more of their length" being ancestral to completely fused palato-maxillaries lacking a suture and states in between (Tordoff 1954, cf. Bock 1960). Both *Calcarius* and *Plectrophenax* show the primitive character state, whereas virtually all of the sparrows examined have the more-derived state. The only behavioral trait examined, the double-scratching feeding technique, is best considered a derived trait almost exclusively confined to emberizid sparrows (Greenlaw 1977). Of the genera we considered, only *Emberiza*, *Calcarius*, *Plectrophenax*, and certain *Spizella* (*passerina*, *pallida*, *breweri*, and perhaps *atrogularis*) do not exhibit this behavior.

Additional information not incorporated into our study supports the notion that the *Emberiza* clade is basal to other emberizid sparrows. From studies of myology and osteology of oscines, *Calcarius*, *Emberiza*, and *Plectrophenax* are somewhat advanced (compared with the prim-

itive parulines) in myology, and the *Emberiza* clade is "likewise primitive in having the exoccipital uninflated or but slightly inflated, and none scratch for food" (Beecher 1953). In contrast, at least some *Emberiza* lack a ligamentous vestige (a derived state) to their left radix aorta, although its presence is to be expected and is shown in the other emberizid sparrows (Glenny 1942).

In many characters (e.g. palato-maxillary fusion, lateroventral process of the laterosphenoid, tail/wing ratios, behavior), the *Emberiza* clade is more similar to cardinalids than to other emberizids. Other osteological and myological evidence, however, supports the Emberizidae being a monophyletic group and suggests that *Emberiza* forms a natural group within this clade; that is, they do not suggest that *Emberiza*, *Calcarius*, and *Plectrophenax* differ from others in the Emberizidae group. With regard to the pneumatic fossa of the humerus, the Emberizidae and the Icteridae are uniform in having a well-developed double fossa (the more-derived state), although in some *Ammodramus* the second fossa is so small that the humerus approaches the single-fossa condition (Bock 1962). Furthermore, emberizid finches show great uniformity in appendicular musculature and tend to consistently show a combination of ancestral and derived states compared with other nine-primaried oscines (Rai-kow 1978). These similarities support the current classification of the *Emberiza* clade in the family Emberizidae. Data presented herein and by Avise et al. (1980), however, strongly suggest that the current linear arrangement followed by the AOU is incorrect, and that the *Emberiza* clade is actually basal to the other genera examined. In contrast to the AOU, Sibley and Monroe (1990) treat the *Emberiza* clade as basal.

*The genus Aimophila.*—Since Ridgway (1901), the avian genus *Aimophila* has defied convenient classification. Whereas *Aimophila* (as currently recognized) does not appear to be a natural group, further subdivision has proved unsatisfactory because several taxa in this genus are problematic (Wolf 1977). Our phylogeny supports *Aimophila* as a monophyletic group, although the placements of *Torreornis inexpectata* and *Aimophila quinquestrata* were troublesome. Indeed, *A. quinquestrata* is the most problematic (and perhaps the most controversial) member of the genus *Aimophila* (Hubbard

1984, Phillips and Phillips 1993). The AOU (1983) placed this species in *Amphispiza*, as it was initially classified in this study. Given various character conflicts between it and other members of *Amphispiza*, however, we concluded that retaining this species in the genus *Aimophila* as originally designated (Ridgway 1901) was the most-parsimonious treatment (see Wolf 1977, Phillips and Phillips 1993). Based on the characters examined in this study, *quinquestriata* more naturally fits into *Aimophila* rather than *Amphispiza*. Although this species tended to pair with *Torreornis inexpectata* (Fig. 1), this pairing was perhaps an artifact of certain characters (unstreaked juvenal plumage, unmarked eggs) rather than a true relationship because Barbour and Peters (1927) suggested no obvious close relatives to *Torreornis*.

*The genus Ammodramus.*—A great deal of polymorphism exists within *Ammodramus* (Appendix 2), and in its current form, it may not be a natural group. Based on allozymes and restriction sites of mtDNA, Zink and Avise (1990) showed that *A. henslowii/bairdii*, *A. leconteii/caudacutus/maritimus*, and *A. savannarum/humeralis/aurifrons* form distinct clusters. Given their genetic distinctiveness, and problems with placement of *Passerculus sandwichensis*, Zink and Avise (1990) suggested that *Ammodramus*, as currently recognized (AOU 1997), is not monophyletic. Our results suggest that *Ammodramus* is monophyletic (Figs. 1 and 2), although we employed slightly different subgroups within the genus: we treated *A. bairdii* as its own operational taxonomic unit and grouped *A. henslowii* with *A. leconteii/caudacutus/maritimus* (Zink and Avise [1990] provided evidence that *A. bairdii* and *A. henslowii* are sister taxa). Nevertheless, *A. henslowii* and *A. leconteii* differ in structure of the skull and in other features from other *Ammodramus*, suggesting a close relationship between these species. In our study, species of *Ammodramus* that most often possessed characters lacking in other *Ammodramus* were in the *A. savannarum* group, a finding consistent with molecular evidence (Zink and Avise 1990).

*The genus Zonotrichia.*—*Zonotrichia capensis* formerly was placed in the monotypic genus *Brachyspiza* because it was believed to be intermediate to *Zonotrichia* and *Melospiza* (Ridgway 1901). A review of *Zonotrichia*, *Junco*, *Melospiza*, *Passerella*, and *Brachyspiza* refuted this notion

and suggested that all five of these genera be merged into *Junco* (Paynter 1964). This rather extreme view was followed by only a few taxonomists, but it serves to underscore some of the difficulties encountered in studying relationships among passerines (Mayr and Bock 1994). Molecular data could be interpreted in favor of either treatment, because *capensis* often lay outside the main cluster of the four northern *Zonotrichia* (Zink 1982, Zink and Blackwell 1996). Even with *Z. capensis* included, our data support current AOU (1983, 1997) treatment of *Zonotrichia* as monophyletic. Allozyme and mtDNA data strongly suggest that *Zonotrichia leucophrys* and *Z. atricapilla* are sister taxa (Zink 1982, Zink et al. 1991b, Zink and Blackwell 1996), which goes against conventional treatments based on morphology. Because we developed a character-based phylogeny, ours agrees with the more conventional treatments with regard to relationships among *albicollis*, *atricapilla*, and *leucophrys*.

## CONCLUSIONS

The most significant finding in our analysis is strong tendency for species within traditionally defined genera to form monophyletic clusters. At a finer scale, we echo the sentiments of Mayr and Bock (1994), who make an important distinction between provisional and standard classifications, stating that any changes to widely accepted standard classifications and sequences create difficulties for information retrieval. The sequence we developed differs markedly from the standard sequence of the AOU (1983), but in any case, these differences are only a matter of process. From the tree we developed, it is possible to rearrange our sequence in many ways, some of which more closely resemble the AOU sequence. Nevertheless, some of the differences between our sequence and that of the AOU are well-supported by our data and by other published sources: (1) *Emberiza* (and the related monotypic Palearctic genera *Latoucheornis*, *Melophus*, *Miliaria*, and perhaps *Urocynchramus*), *Calcarius*, and *Plectrophenax* should be moved to the front of standard sequences because a preponderance of evidence indicates that this clade is basal to the rest of the *Emberizidae*; and (2) based on data we examined, *Aimophila* is monophyletic, if *quinquestriata* is included as a member of that

genus, and clearly is paraphyletic if *quinquestriata* is placed in *Amphispiza*, the genus in which the AOU (1983) and Rising (1996) placed it (although the AOU [1997] recently moved this species back to *Aimophila*). Among the *Aimophila*, *quinquestriata* is most closely related to the *ruficeps/notosticta/rufescens* group. Placement of *quinquestriata* in *Aimophila* agrees with Ridgway (1901), Storer (1955), Phillips and Phillips (1993), Sibley and Monroe (1993: 78), and Howell and Webb (1995). Further studies should be conducted to resolve its relationship to other *Aimophila* and to determine whether a monotypic genus (the generic name *Amphispizopsis* is listed by Sibley and Monroe 1990:723) for this species is a more appropriate treatment. Other alterations to standard sequences are not warranted at this time, at least based upon our findings.

## ACKNOWLEDGMENTS

We thank S. L. Olson, M. S. Springer, J. D. Webster, R. M. Zink, and R. L. Zusi for kindly answering inquiries regarding avian osteology and/or systematics of emberizids. J. D. Webster also graciously provided extensive data on the lateroventral process of the laterosphenoid. P. Unitt provided access to the collection of avian skeletons at the San Diego Natural History Museum, D. L. Swofford permitted us to use output from a prerelease version of PAUP, M. S. Springer assisted with the phylogenetic analyses, and B. L. Monroe, Jr. provided a copy of the draft for the 7th edition of the *AOU Check-list*. J. D. Rising, J. T. Rotenberry, P. Unitt, R. M. Zink, and three anonymous referees provided excellent comments and suggestions on various drafts of this paper.

## LITERATURE CITED

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Associate Editor: R. M. Zink

APPENDIX 1. This appendix includes information gathered by J. Dan Webster, Michael A. Patten, and Philip Unitt regarding the lateroventral process of the laterosphenoid (this process does not appear in Baumel et al. 1979). Taxonomy and nomenclature follow AOU (1983), whereas the arrangement follows Paynter and Storer (1970).

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The type of process is encoded in a form like that used by Tordoff (1954), as follows:

Lateroventral process short (0.1 to 0.4 as long as zygomatic process)	L1
Lateroventral process moderate (0.5 to 0.7 as long as zygomatic process)	L2
Lateroventral process long (0.8 to 1.3 as long as zygomatic process)	L3
Lateroventral process long (as above), with wide, flat tip	L4

Numbers following this code refer to the number of specimens examined

#### Emberizidae

- Melophus lathami* L1 (4)  
*Emberiza* L1 (25 species, 78 specimens)  
*Calcarius* L1 (4 species, 15 specimens)  
*Plectrophenax nivalis* L1 (8)  
*Calamospiza melanocorys* L4 (8)  
*Zonotrichia* L3 or L4  
*Z. leucophrys* L3 (12 + 11 more between this and next two taxa)  
*Z. atricapilla* L3 (6)  
*Z. albicollis* L3 (4; some tendency toward L4)  
*Z. querula* L4 (1)  
*Melospiza* L3 or L4  
*M. melodia* L3 or L4 (7)  
*M. lincolni* L3 (6)  
*M. georgiana* L3 (1)  
*Passerella iliaca* L4 (5)  
*Junco* L3 (3 species, 21 specimens) or L4 (rarely in *J. hyemalis*)  
*Passerculus sandwichensis* L3 (9) or L4 (1)  
*Xenospiza baileyi* L3 (1)  
*Ammodramus* L1 or L3  
*A. maritimus* L3 (5)  
*A. caudacutus* L3 (5)  
*A. lecontei* L3 (3)  
*A. bairdii* L3 (3)  
*A. henslowii* L3 (2)  
*A. savannarum* L1 (2)  
*A. humeralis* L1 (7)  
*A. aurifrons* L1 (2)  
*Spizella* L1 or L4  
*S. arborea* L4 (4)  
*S. passerina* L1 (18)  
*S. pusilla* L1 (8)  
*S. atrogularis* L1 (4)  
*S. pallida* L1 (3)  
*S. breweri* L1 (8)  
*Poocetes gramineus* L3 or L4 (12)  
*Chondestes grammacus* L2 (2) or L3 (6)  
*Amphispiza* L1, L2, or L3  
*A. bilineata* L3 (5)  
*A. belli* L1 (2) or L3 (5)  
*A. quinquestriata* L2 (3)  
*Aimophila* L1 or L3  
*A. mystacalis* L1 (2)  
*A. humeralis* L1 (2)  
*A. ruficauda* L1 (5)  
*A. sumichrasti* L1 (2)  
*A. stolzmanni* L1 (1) or L3 (1)  
*A. aestivalis* L1 (2)  
*A. botterii* L1 (3)  
*A. cassinii* L1 (4)  
*A. carpalis* L1 (3)  
*A. ruficeps* L3 (6)
-

## APPENDIX 1. Continued.

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- A. notosticta* L3 (2)  
*A. rufescens* L3 (5)  
*Torreornis inexpectata* L3 (5)  
*Oriturus superciliosus* L3 (3)  
*Phrygilus* L1 or L4  
*P. atriceps* L1 (3)  
*P. gayi* L1 (2)  
*P. patagonicus* L4 (3)  
*P. fruticeti* L1 (4)  
*P. unicolor* L1 (5)  
*P. erythronotus* L1 (1)  
*P. plebejus* L1 (5)  
*P. alaudinus* L1 (3)  
*P. carbonarius* L1 (3)  
*Melanodera* L1 or L2  
*M. melanodera* L1 (5)  
*M. xanthogramma* L1 (1) or L2 (1)  
*Haplospiza* L1 (2 species, 11 specimens)  
*Acanthidops bairdii* L1 (2)  
*Lophospingus* L1 (2 species, 8 specimens)  
*Donacospiza albifrons* L1 (3)  
*Rowettia goughensis* L1 (2)  
*Nesospiza acunhae* L1 (1)  
*Diuca* L1 (2 species, 12 specimens)  
*Idiopsar brachyurus* L1 (2)  
*Piezorhina cinerea* L1 (5)  
*Xenospingus concolor* L1 (3)  
*Incaspiza* L1 (4 species, 7 specimens)  
*Poospiza* L1 (10 species, 30 specimens)  
*Sicalis* L1 (8 species, 25 specimens)  
*Emberizoides* L1 (2 species, 7 specimens)  
*Embernagra platensis* L1 (7)  
*Volatinia jacarina* L1 (5)  
*Sporophila* L1 (18 species, 48 specimens)  
*Oryzoborus* L1, L2, or L3  
*O. angolensis* L2 (3) or L3 (3)  
*O. crassirostris* L1 (2) or L2 (1)  
*Amaurospiza moesta* L1 (6)  
*Melopyrrha nigra* L1 (5)  
*Dolospingus fringilloides* ?  
*Catamenia* L1 (3 species, 10 specimens)  
*Tiaris* L1 (4 species, 22 specimens)  
*Loxipasser anotanthus* L1 (4)  
*Loxigilla* L1, L2 or L3  
*L. portoricensis* L2 (2)  
*L. violacea* L2 or L3 (10)  
*L. noctis* L1 (3)  
*Melanospiza richardsoni* L1 (2)  
*Geospiza* L1 or L2  
*G. magnirostris* L2 (2)  
*G. fortis* L1 (2)  
*G. fuliginosa* L1 (2)  
*G. difficilis* L1 (3)  
*G. scandens* ?  
*G. conirostris* L1 (2)  
*Camarhynchus* L1 or L2  
*C. crassirostris* L2 (2)  
*C. psittaculus* L1 (2)  
*C. pauper* L1 (1)  
*C. parvulus* L1 (1)  
*Certhidea olivaceus* L1 (5)
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## APPENDIX 1. Continued.

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- Pinaroloxias inornata* L1 (6)  
*Pipilo* L3 or L4 (7 species, 29 specimens + figures listed below)  
   *P. chlorurus* L3 (3)  
   *P. erythrophthalmus* L3 (4)  
   *P. fuscus* L4 (3)  
   *P. crissalis* L4 (4)  
   *P. aberti* L3 or L4 (3)  
*Melospiza* L3 (3 species, 8 specimens)  
*Arremon* L2 or L3  
   *A. rufivirgatus* L3 (10 between this and next two taxa)  
   *A. chloronotus* L3  
   *A. conirostris* L3  
   *A. abeillei* L2 (1) or L3 (2)  
   *A. aurantiostris* L2 or L4 (4)  
*Arremonops* L1 (3 species, 13 specimens)  
*Atlapetes* L3 (16 species, 41 specimens)  
*Pezopetes capitalis* L3 (7)  
*Pselliophorus tibialis* L3 (1)  
*Lysurus castaneiceps* L1 (1)  
*Coryphaspiza melanotis* L1 (1)  
*Saltatricula multicolor* L1 (6)  
*Gubernatrix cristata* L1 (2) or L2 (1)  
*Coryphospingus* L1 (2 species, 10 specimens)  
*Rhodospingus cruentus* L1 (3)  
*Paroaria* L1 (4 species, 17 specimens)

**Cardinalidae**

- Cardinalis* L1 or L2  
   *C. cardinalis* L2 (5)  
   *C. sinuatus* L1 (1) or L2 (1)  
*Pheucticus* L2  
   *P. ludovicianus* (7)  
   *P. melanocephalus* (9)  
*Guiraca caerulea* L1 or L2  
*Passerina* L1 or L2  
   *P. cyanea* L1 (5)  
   *P. amoena* L1 (5) or L2 (1)  
   *P. ciris* L1 (4)  
   *P. versicolor* L1 (2)
-

APPENDIX 2. Character-state matrix (see Table 1) for selected genera of sparrows (family Emberizidae).

Taxon	Character state																																																																																																		
	0								1								2								3								4																																																																		
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99
<i>Emberiza</i> , etc. (genus)	0	0-2	0	0	0-2	0P	111	0	0	2	0	0	0	11	0-2	0	0	P	0	0P	P	PP	0-2	0	1	0P	0	0	???????????																																																																						
<i>Calcarius</i> (genus)	1	0	0	0	0-2	01	111	0	0	2	0	0	0	11	0	0	0	0	0	0P	P	P	0	0	1	PP	0	0	0000000001																																																																						
<i>Plectrophenax</i> (genus)	1	0	0	0	2	01	111	0	0	2	0	0	0	11	2	0	0	0	0	010	P	00	0	0	1	0P	0	0	???????????																																																																						
<i>Junco</i> (genus)	2	2	2-3	0	1	10	001	0	0	3	0	0	1	10	2	0	P	0	P	0P	0	P	00	0	1	P	1P	0	2	0001111111																																																																					
<i>Zonotrichia capensis</i>	1	2	2	0	1	10	001	0	0	3	1	0	1	00	2	0	0	0	1	010	0	10	0	1	0	10	0	4	1000101011																																																																						
<i>Zonotrichia albicollis</i>	1	0	2-3	0	1	10	000	0	0	3	1	0	1	00	2	0	0	1	1	110	0	10	0	1	0	10	0	4	1010111011																																																																						
<i>Zonotrichia atricapilla</i>	1	0	2	0	1	10	000	0	0	3	1	0	1	00	2	0	0	0	0	010	0	10	0	1	0	10	0	4	1010101011																																																																						
<i>Zonotrichia querula</i>	1	0	3	0	1	10	000	0	0	3	1	0	1	00	2	0	0	0	P	010	0	00	0	1	0	11	0	0	1011101011																																																																						
<i>Zonotrichia leucophrys</i>	1	0	2	0	1	10	000	0	0	3	1	0	1	00	2	0	0	0	1	010	0	10	0	1	0	11	0	4	1010111011																																																																						
<i>Melospiza melodia</i>	2	2	3	0	1	10	001	0	0	3	1	0	1	00	0	0	0	0	1	000	P	00	0-1	0	0	10	0	5	0110101001																																																																						
<i>Melospiza lincolni</i>	2	2	2	0	1	10	001	0	0	3	1	1	1	00	0	0	0	0	1	000	1	00	1	0	0	10	0	5	01101?1001																																																																						
<i>Melospiza georgiana</i>	2	2	2	0	1	10	001	0	0	3	1	1	1	00	0	0	0	0	1	000	1	00	2	0	0	10	0	5	0111111001																																																																						
<i>Passerella iliaca</i>	2	2	3	1	1	11	001	0	0	3	1	0	1	00	0	0	P	0	0	000	P	00	0	P	0	10	0	6	010001????																																																																						
<i>Xenospiza baileyi</i>	?	?	2	?	?	10	001	1	1	3	0	1	1	00	0	0	0	0	1	100	0	00	1	0	0	10	0	5	???????????																																																																						
<i>Ammodramus savanarum</i> group	2	0	0	1	0	10	001	1	1	2-3	1	1	1	00	2	0	0	1	0	100	1	00	0	0	0	10	0	1	0000111101																																																																						
<i>Ammodramus henslowii</i> group	2	2	2	1	1	10	001	1	1	2-3	1	1	1	00	0	0	0	1	P	100	1	00	0	0	0	1P	0	3	0100101111																																																																						
<i>Ammodramus bairdii</i>	2	2	2	1	1	10	001	0	1	2-3	1	1	1	00	0	0	0	1	0	100	1	00	0	0	0	10	0	3	00?1?????																																																																						
<i>Passerculus sandwichensis</i>	2	2	2-3	1	0	10	001	1	1	3	0	1	1	00	0	0	0	1	1	100	0	00	0	0	0	10	0	5	1010111111																																																																						
<i>Calamospiza melanocorys</i>	2	2	3	0	0	10	001	1	0	3	0	0	1	11	0	0	0	0	0	010	0	00	0	0	1	01	1	4	???????????																																																																						
<i>Amphispiza belli</i>	2	0	0-2	0	1	10	001	0	0	3	0	0	1	00	1	0	1	0	1	100	0	10	0	1	1	0P	1	5	1???1?????																																																																						
<i>Amphispiza bilineata</i>	2	0	2	0	1	10	001	0	0	3	0	0	1	00	0	0	1	0	1	000	0	10	0	1	0	01	0	1	0000100100																																																																						
<i>Chondestes grammacus</i>	2	2	1-2	1	1	10	101	1	0	3	0	0	1	00	1	0	0	0	1	000	0	11	1	1	1	10	0	1	???????????																																																																						
<i>Poocetes gramineus</i>	2	2	2-3	1	1	10	101	1	0	2	0	0	1	00	0	0	0	0	1	001	0	01	0	0	1	10	0	1	???????????																																																																						
<i>Spizella arborea</i>	1	2	3	1	1	10	101	0	0	2-3	0	0	1	00	1	0	0	0	1	010	1	00	1	1	0	10	0	4	???????????																																																																						
<i>Spizella passerina</i>	1	2	0	1	1	10	001	0	0	2-3	0	0	0	00	2	0	0	0	1	010	0	00	2	1	0	10	0	4	0000101010																																																																						
<i>Spizella pallida/breweri</i>	1	2	0	1	1	10	001	0	0	2-3	1	0	0	00	2	0	0	0	0	000	1	01	0	0	0	10	0	4	0000101000																																																																						
<i>Spizella pusilla/wortheni</i>	1	2	0	1	1	10	101	0	0	2-3	1	0	1	00	2	0	0	0	0	010	1	01	1-2	1	0	11	0	4	???????????																																																																						
<i>Spizella atrogularis</i>	1	2	0	1	1	10	101	0	0	2-3	2	0	?	00	2	0	0	0	0	000	0	00	0	1	0	11	P	4	???????????																																																																						
<i>Torreornis inexpectata</i>	?	?	2	?	?	10	000	0	0	1	2	0	1	01	2	1	0	0	0	000	0	10	1	1	0	10	0	2	???????????																																																																						
<i>Orinurus superciliosus</i>	1	2	2	1	1	10	000	0	0	1	0	0	1	00	2	0	0	0	1	000	0	10	1	0	0	10	0	1	???????????																																																																						
" <i>Peucaea</i> "	2	2	0	1	1	10	001	0	0	1	2	0	1	00	2	0	0	0	0	100	1	00	1	0	0	10	1	2	???????????																																																																						
<i>Aimophila ruficeps</i> group	2	2	2	1	1	10	000	0	0	1	2	0	1	00	2	0	0	0	1	000	0	01	1-2	1	0	10	1	2	???????????																																																																						
" <i>Haemophila</i> "	2	2	0	1	1	10	000	0	0	1	2	0	1	00	2	0	0	0	1	0P1	1	P0	0	P	0	1P	1	2	???????????																																																																						
<i>Aimophila quinquestriata</i>	2	2	1	1	1	10	000	0	0	1	2	0	1	00	1	1	1	0	1	000	0	11	0	1	0	01	1	2	???????????																																																																						