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A Molecular Phylogeny of Warbling-Finches (*Poospiza*): Paraphyly in a Neotropical Emberizid Genus

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We investigated the phylogenetic relationships of 12 species within a single genus of neotropical passerine (*Poospiza*) using 849 bp (283 codons) of the cytochrome *b* mitochondrial gene. We further explored evolutionary affinities of these taxa using sequence from an additional 47 thraupine (tanagers) and 7 emberizine (sparrows and buntings) genera, members of the predominantly New World family Emberizidae. *Poospiza* have traditionally been considered part of the emberizine radiation. However, our analyses suggest that members of this genus are more closely related to some thraupine lineages than they are to the other neotropical emberizine genera included in our study (*Atlapetes, Embernagra, Melopyrrha, Phrygilus, Saltatricula, Tiaris*). Although member taxa are closely related, the genus *Poospiza* appears to be paraphyletic with representatives of 6 thraupine genera (*Cnemoscopus, Cypsnagra, Hemispingus, Nephelornis, Pyrrhocoma, Thylpopsis*) interspersed among four well-supported *Poospiza* clades. The majority of species within this *Poospiza*–thraupine clade have geographic ranges that are exclusive to, or partially overlap with, the Andes Mountains. It is probable that these mountains have played an important role in driving cladogenesis within this group. Sequence divergence (transversions only; mean 4.7 ± 1.3%) within the clade suggests that much of this diversification occurred within the late Miocene and Pliocene, a period coincident with major orogenic activity in central-western South America.

INTRODUCTION

The neotropical avifauna includes a large and complex radiation of sparrow-like forms whose phylogenetic affinities are far from understood. These taxa are traditionally placed within the Emberizinae, or "true sparrows," but this subfamily is acknowledged to have imprecise limits and is difficult to discriminate from a similarly indistinct group, the Thraupinae, or tanagers (Storer, 1969; Isler and Isler, 1987; Sibley and Ahlquist, 1990; Burns, 1997). The problematic taxonomy of this assemblage has been attributed by Sibley and Ahlquist (1990), among others, to repeated convergence on the "seed-eater" morphology from numerous lineages within the tanager group (see Appendix 1 for a guide to this enormous taxonomic problem). These "tanager-finches" include some of the most speciose genera of neotropical finch-like birds, such as *Phrygilus* (11 spp.), *Sicalis* (12 spp.), *Poospiza* (17 spp.), and *Sporophila* (31 spp.), and study of any of these genera will contribute significantly to our understanding of this difficult group.

Warbling-finches and mountain-finches (*Poospiza*) are particularly recommended for study. Regarded as part of the subfamily Emberizinae in current classifications, this genus has been explicitly identified by Sibley and Ahlquist (1990) as being allied more closely to members of the subfamily Thraupinae. Its members are widely distributed, both ecologically and geographically, being found in woodland and scrub habitats of both the Andes Mountains and the lowlands of south-central South America (Ridgely and Tudor, 1989). About half the species are found below 1000 m above sea level (masl) (Table 1); most of these range widely east of the Andes in Brazil, Paraguay, Uruguay, Bolivia, and Argentina, and one (*P. hispaniolensis*) is found along the Pacific rim of Peru and southern Ecuador and is the only species of the genus found west of the continental divide. The remaining taxa occur at higher altitudes (up to 3500 masl) in the Andes of Peru, Bolivia, and Argentina and show more geographically restricted ranges than the lowland taxa. Further, plumage diversity in the genus is substantial (Table 1): some species are essentially black, gray, and white; others are gray and rufous, perhaps with some white; others are gray, black, white, and rufous; most are boldly patterned. Only one species (*hispaniolensis*) shows a clear sexual plumage dimorphism. The species

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TABLE 1

Descriptions and Distributions of *Poospiza* Taxa Used in the Present Study

Species	Current range and plumage type
	Highland taxa
alticola	Andes of n.c. Peru; 2900 to 4300 masl. Gray, black, white, and rufous.
baeri[a]	Andes of n.w. Argentina; extremely restricted range; 2000 to 3000 masl. Gray and rufous.
boliviana	Andes Mountains of w.c. Bolivia; ~1600 to 3000 masl. Gray, white, and rufous.
caesar[b]	Andes of s.e. Peru; 2900 to 3900 masl. Gray, black, white, and rufous.
erythrophrys	Andes of w.c. Bolivia and n.w. Argentina; 1200 to 3000 masl. Gray and rufous.
garleppi[a]	Andes of w. Bolivia in Cochabamba; 3000 to 3500 masl. Gray and rufous.
hypochondria	Andes of w. Bolivia and n.w. Argentina; 2500 to 4000 masl. Gray, white, and rufous.
whitii[c]	Andean slopes of n.w. Argentina and w. Bolivia; ~600 to 3500 masl. Gray, black, white, and rufous.
	Lowland taxa
hispaniolensis	Coastal w. Peru and s.w. Ecuador; typically below 1000 masl. Male black, gray, and white; female grayish-brown and streaked.
melanoleuca[d]	Interior valleys and slopes of Bolivian Andes and lowlands of s.e. Bolivia, w. Paraguay, and n. Argentina; to ~1800 in Bolivia. Black, gray, and white lower parts.
ornata	Lowlands of n.c. Argentina; below 1000 masl. Gray and rufous.
torquata	Interior slopes of Bolivian Andes and lowlands of n. Argentina; to ~1800 in Bolivia. Resembles *hispaniolensis.*

Note. Information derived from Ridgely and Tudor (1989) and Fjeldså and Krabbe (1990).

[a] Previously placed in the genus *Compsospiza.*

[b] Previously placed in the genus *Poospizopsis.*

[c] Traditionally subsumed within the species *P. nigrorufa,* but considered by Ridgely and Tudor (1989) to merit specific status based on disjunct range and differences in song and plumage.

[d] *P. melanoleuca* and *P. cinerea* of interior southern Brazil are sometimes considered to be conspecific.

are behaviorally quite diverse: though most species feed by foliage-gleaning in warbler-like fashion, some feed and spend substantial amounts of time on the ground (*P. nigrorufa, P. baeri, P. caesar*). The genus *Poospiza* now includes three taxa (the mountain-finches) which were previously placed in the genera *Compsopiza* (*baeri* and *garleppi*) and *Poospizopsis* (*caesar*) (Ridgely and Tudor, 1989; Fjeldså and Krabbe, 1990).

As part of a larger study of the relationships among, and affinities of, these putative tanager-finches as evidenced by DNA sequence characters, we have assembled cytochrome *b* sequence for 12 species of *Poospiza* and for representatives of 7 other neotropical "traditional" emberizine genera. Burns (1997) has evaluated the evolutionary relationships of 47 of 57 thraupine genera using the mitochondrial cytochrome *b* gene. Using these combined data, we investigate the relationships among species of *Poospiza,* test for monophyly, and examine the affinities of the genus to other representatives of the family Emberizidae. Finally, given a phylogeny recently proposed by Fjeldså (1992), based on plumage characters and biogeographic range, we have an explicit hypothesis to test with data emerging from our analyses of mitochondrial cytochrome *b* sequence.

MATERIALS AND METHODS

Taxon Sampling and Sample Sources

Samples sequenced expressly for this study were either collected by the authors during expeditions to northern Argentina in 1992 or 1994 (either blood or liver tissue), collected by colleagues in Cuba (*Melopyrrha nigra*), or derived from the collections of the Louisiana State Museum or the Zoological Museum, University of Copenhagen. In total, we obtained samples for 12 recognized warbling-finch taxa (species and details of sample provenances are provided in Appendix 2). For 5 of these, additional individuals were included in the analysis as a partial check for the exemplar

effect (e.g., Zink *et al.*, 1998): *Poospiza alticola, P. torquata, P. hypochondria, P. melanoleuca,* and *P. whitii.* We sequenced representatives for an additional 6 neotropical emberizine genera: *Atlapetes torquata,* **Coryphospingus cucullatus,* **Embernagra platensis, Melopyrrha nigra,* **Phrygilus alaudinus,* and **Saltatricula multicolor* (those marked with * are hypothetically thraupines).

To cytochrome *b* sequences obtained from these samples we added published sequences from *Tiaris obscura* (an emberizine; Sato *et al.*, 1999; GenBank Accession No. AF108808) and representative species from 47 thraupine genera (Burns, 1997; GenBank Accession Nos. AF006211–AF006258). We included two outgroup taxa: *Vireo olivaceus* (Vireonidae; GenBank Accession No. X74260; Helm-Bychowski and Cracraft, 1993) and *Corvus frugilegus* (Corvidae; GenBank Accession No. Y18522; Harild and Arnason, 1999).

DNA Extraction, Amplification, and Sequencing Protocols

Total genomic DNA was extracted from small plugs of liver tissue or from approximately 10 μL of blood in 450 μL of an iminodiacetic acid chelating resin suspension (5% Chelex; Sigma). Samples in Chelex solution were incubated overnight in a 56°C water bath. Samples were then vortexed at maximum speed for 15 s, incubated at 95°C for 15 min, vortexed again for 15 s, and then spun at 12,000 rpm for 5 min. Extracted samples were stored at −20°C until subsequent analyses.

All PCR amplifications were performed in a Perkin–Elmer 9600 thermocycler. A negative control was included for all reaction cocktails. An approximately 1.1-kb fragment of cytochrome *b* was amplified using a shortened version of L14841 (Kocher *et al.*, 1989; 5′-CCATCCAACATCTCAGCATGATGAAA-3′) and a universal avian primer H16065 (Tim Birt unpublished; 5′-GTCTTCAGTTTTTGGTTTACAAGAC-3′). To generate light single-stranded product we used a biotinylated version of L14841 paired with nonmodified H16065 and for heavy single-stranded product the converse. Each PCR contained 2 μl of sample and 48 μl of reaction cocktail with 2 mM $MgCl_2$, 200 μM dNTPs, 1 μM each primer, 1× Gibco BRL react buffer, and 0.25 units of Gibco BRL *Taq* polymerase. The amplification profile was as follows: 3 min at 95°C; 35 cycles of 1 min at 95°C, 1 min at 50°C, and 1 min at 72°C; final extension of 3 min at 72°C. Amplified products were cleaned and single-stranded template was isolated using super-magnetic polystyrene beads (Dynabeads M-280 Streptavidin; Dynal) according to the manufacturer's instructions.

Light single-stranded products were sequenced with shortened versions of H15149 (Kocher *et al.*, 1989; 5′-CCCTCAGAATGATATTTGTCCTCA-3′), H15547 (Edwards *et al.*, 1991), and H15767 (Lanyon, 1994). Heavy strand products were sequenced with L15114 (Edwards *et al.*, 1991) and a primer of our design (L15147; 5′-CATGAGGCCAAATATCCTTCTGAGG-3′). Sequencing was performed using the United States Biochemical Sequenase Version 2.0 Protocol with incorporation of α-^{35}S-labeled ATP (10 mCi/mL). All samples were denatured at 90°C for 2 min prior to loading on a 6% polyacrylamide gel. Each sample was subjected to PAGE for short (2-h) and long (4.5-h) durations. Gels were dried and then exposed on Kodak Biomax film for 2–10 days, depending on the intensity of the signal. Autoradiographs were scored by hand.

Phylogenetic Analyses

All sequences were aligned using GeneWorks (IntelliGenetics, Inc.) and double-checked by eye. Phylogenetic analyses were performed in PAUP* Version 4.0 (Swofford, 1998) except where noted. To test whether the cytochrome *b* data set contained structure that was different from random (i.e., was potentially phylogenetically informative), we used (1) a permutation tail probability test (Faith, 1991; Faith and Cranston, 1991) as implemented in PAUP* using 100 random matrices and (2) a relative apparent synapomorphy analysis (RASA; Lyons-Weiler *et al.*, 1996). To evaluate levels of saturation, we plotted *p*-distance (Nei, 1987) calculated for transitions only versus an overall *p*-distance that included all substitutions.

We performed the phylogenetic analyses in two stages. We first evaluated relationships among included *Poospiza* taxa only, so that we could compare (1) topologies resulting from different phylogenetic methods and (2) cytochrome *b* tree topologies to those derived from another mitochondrial gene (16S; Lougheed *et al.*, unpublished; GenBank Accession Nos. AY005180–AY005197) to diminish the chances that we have included paralogous copies of cytochrome *b* in our analyses (e.g., see Hu and Thilly, 1994; Friesen and Anderson, 1997; also cf. Quinn, 1997). The second phase of our analyses involved examinations of *Poospiza* together with other emberizines and all thraupines from Burns (1997).

We evaluated relationships among included *Poospiza* taxa with outgroup taxa included singly and in combination and with two different weighting schemes used in parsimony analysis: (1) all substitutions weighted equally and (2) third-position transversions weighted five times transitions (based on the TS/TV ratio for included *Poospiza* taxa; see Burns, 1997 for a discussion and justification of this approach). Heuristic searches were conducted using stepwise addition and 200 random addition replicates with the TBR branch-swapping option enforced. Relative support for nodes in resulting trees was evaluated using 1000 bootstrap replicates each with 10 random additions per replicate. To assess the impact of alternative phylogenetic algorithms on tree topology, we

also performed neighbor-joining analyses using Kimura (1980) two-parameter distances and maximum-likelihood analyses using the Hasegawa–Kishino–Yano (1985) two-parameter model for unequal base frequencies (assuming equal rates and using empirically derived base frequencies).

To search for the most-parsimonious tree topology among all included emberizid taxa, we used the heuristic search option with random stepwise addition and 25 replicates again with TBR branch-swapping. Relative support for nodes in resulting trees was evaluated using 100 heuristic bootstrap replicates. Differences in replicate number between the *Poospiza* only and the analyses including all taxa result from increased computational requirements of the latter. Analyses were performed using each outgroup alone and with both included. As before, two weighting schemes were employed: (1) all substitutions weighted equally and (2) third-position transversions weighted five times transitions.

To explicitly test the hypothesis of monophyly of *Poospiza,* we constrained tree topology in our parsimony analyses and qualitatively compared constrained (monophyletic) and nonconstrained most-parsimonious tree lengths. We also performed a topology-dependent PTP test (Faith, 1991) in which a T-PTP test statistic (calculated by subtracting minimum length under a monophyly constraint from minimum tree length with no constraint) was compared to a null distribution of length differences generated using 100 randomly permuted data sets.

RESULTS

We obtained 849 bp (283 complete codons) of cytochrome *b* sequence for all taxa (see Appendix 2 for GenBank Accession Nos.). Overall base composition was markedly skewed toward C (0.358) and deficient in G (0.137), with approximately equal proportions of A and T (0.264 and 0.240, respectively). These values are similar to those found in cytochrome *b* in other avian studies (e.g., Moore and DeFilippis, 1997). Substitutions were strongly skewed toward third positions (270 of 378 or 71.4% of variable sites for the ingroup). No insertions or deletions or stop codons were detected. Mean uncorrected pairwise divergence (±SD) between the two outgroup and all ingroup taxa was 15.7 ± 1.1%, between thraupine genera 10.7 ± 1.4%, between emberizine genera 10.2 ± 0.8%, between thraupines and emberizines 10.3 ± 1.3%, and between examined warbling-finch taxa 8.0 ± 1.4%. Intraspecific divergence was low (<0.7%) for four of the five species for which we surveyed multiple individuals. However, divergence between the two examined *P. torquata* specimens was 4.4%, as high as some of the interspecific comparisons within the genus. Mean pairwise TS/TV ratio for *Poospiza* only was 4.90 and for all ingroup taxa was 2.31. The plots shown in Fig. 1 show clear evidence for saturation above approximately 10% divergence as, beyond this level, the scatter of points lies well below the line x = y. Separate plots by codon position indicate that this is due primarily to saturation of third position sites (Fig. 1). However, results from both our PTP and RASA tests indicate that there is significant phylogenetic signal in our data set (PTP < 0.01; $t_{\text{RASA,2552 df}} = 28.829$, $P < 0.0001$).

Across all maximum-parsimony analyses, regardless of weighting or outgroup combination used, four groupings of warbling-finch species were always recovered and consistently had bootstrap support of >50%: (1) *P. hypochondria, P. caesar;* (2) *P. torquata, P. melanoleuca, P. alticola, P. erythrophys;* (3) *P. baeri, P. garleppi;* and (4) *P. ornata, P. boliviana* (Figs. 2 and 3). Analyses using maximum-likelihood and neighbor-joining methods for *Poospiza* alone consistently recovered these same four groups (results not shown). Phylogenies constructed using 475 bp of the 16S rRNA gene for *Poospiza* taxa (S. C. Lougheed *et al.,* unpublished) were almost identical in all regards to those derived from cytochrome *b* (Fig. 2). This together with the sequence characteristics outlined in the preceding paragraph make it unlikely that we have included paralogous nuclear copies of cytochrome *b* in our analyses. The placement of both *P. hispaniolensis* and *P. whitii* varied markedly across analyses. *P. hispaniolensis* appeared to be basal in most analyses where only members of the warbling-finch genus were considered (Fig. 2), but was usually found with *P. ornata* and *P. boliviana* in analyses including other emberizid genera (e.g., Fig. 3). Various affinities for *P. whitii* were suggested, depending on included taxa and weighting scheme used (e.g., Figs. 2 and 3). All species for which we assayed sequence variation for two or more individuals were monophyletic, including *P. torquata* for which intraspecific divergence was high.

For analyses that included all ingroup taxa (*Poospiza* + other emberizids), no tree topology resulting from any considered outgroup/weighting scheme combination suggested monophyly of the warbling-finches. Rather, two thraupine taxa always appeared as part of clades containing a subset of *Poospiza* taxa. *Nephelornis oniellei* was consistently basal to the clade containing *P. alticola, P. erythrophrys, P. torquata,* and *P. melanoleuca.* The placement of *Cypsnagra hirundinacea* as basal to *P. caesar* and *P. hypochondria* also was stable across all analyses. Increased weighting of transversions over transitions (i.e., 5×) increased bootstrap support for these nodes. For most trees, placement of other thraupine taxa also suggested a relationship with the warbling-finches: *Pyrrhocoma ruficeps, Thylpopsis sordida, Cnemoscopus rubirostris,* and *Hemispingus atropileus* (e.g., Fig. 3). Although we included 8 genera of "traditional" emberizines and 47 genera of "traditional" thraupines, in no analysis was

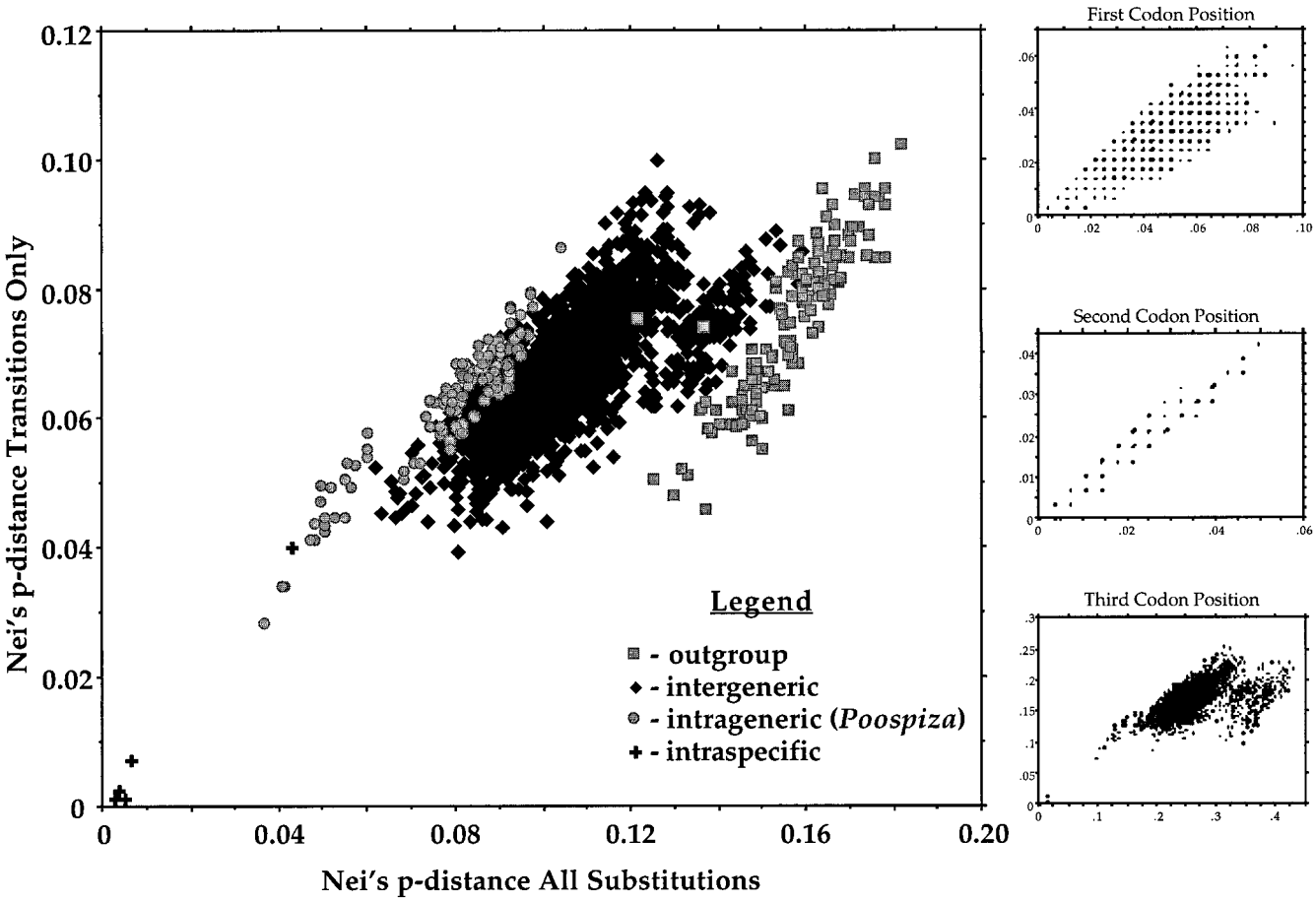

FIG. 1. Saturation plot of cytochrome *b* (all codon positions) showing the relationship between uncorrected sequence divergence (*p*-distance) across all substitutions to divergence considering transitions only. Small plots to the right show the same relationship but for each codon position separately.

there a suggestion of monophyly or even close evolutionary affinities of all taxa from each of these currently recognized emberizid subfamilies.

Conclusions of lack of monophyly for *Poospiza* are strengthened by results of our analyses, which constrained constituent species to form a single clade. For example, lengths of the shortest trees from an unweighted heuristic search (both outgroups) with this topological constraint were 22 steps longer than those resulting from an unconstrained analysis (3046 versus 3068 steps, respectively; T-PTP < 0.01). A similar result obtains regardless of outgroup or weighting strategy.

DISCUSSION

Phylogenetics and the Question of Monophyly

We may draw two main, related conclusions from our phylogenetic analyses. First, the genus *Poospiza* appears paraphyletic with several predominantly Andean tanager genera implicated as sister taxa of some clades of warbling-finches (Fig. 3). Second, examined members of the genus *Poospiza* are more closely allied to some thraupine lineages than they are to the other "traditional" emberizine genera included in our analyses. We discuss these in turn below.

Our phylogenetic analyses and topology-dependent permutation tail probability tests strongly suggest that *Poospiza* taxa do not comprise a monophyletic clade. Burns (1997) found that a clade composed of *Cnemoscopus rubirostris, Cypsnagra hirundinacea, Hemispingus atropileus, Nephelornis oniellei, Pyrrhocoma ruficeps,* and *Thylpopsis sordida* was one of the few that was robustly supported in his thraupine phylogeny (e.g., a 98% bootstrap value from an analysis with third codon position transversions weighted six times transitions). These same thraupine taxa were consistently interspersed across a clade containing warbling-finches regardless of outgroup(s) or weighting scheme used. Some of these taxa comprise monotypic genera (e.g., *Nephelornis, Cnemoscopus*) and were of unknown affinities (notably *Nephelornis;* see Lowery and Tall-

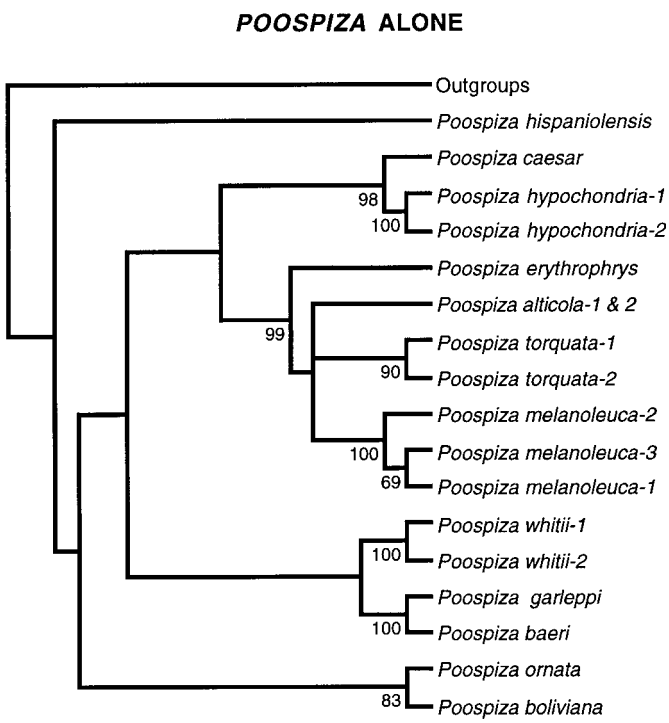

FIG. 2. Strict consensus of two equally parsimonious trees (length 586 steps) resulting from a heuristic search of 849 bp of cytochrome *b* DNA sequence data with equal weighting and 200 random addition replicates (*Poospiza* only). Analyses shown used both *Vireo olivaceus* and *Corvus frugilegus* as outgroups. Bootstrap support for retained nodes is indicated for values ≥50%.

man, 1976) until Burns' (1997) phylogenetic study. It is noteworthy, then, that warbling-finches are implicated as part of this Andean thraupine radiation (see below).

In no phylogeny resulting from our analyses (e.g., Fig. 3) did "traditional" emberizines or thraupines form two distinct monophyletic clades. For thraupines this is, perhaps, unsurprising as Burns (1997) has already suggested that at least two genera (*Chlorophonia* and *Euphonia*) may well be more closely related to oscine passerines outside of the traditional limits of the family Emberizidae. In the present study, we added representatives of eight neotropical "traditional" emberizine genera (including *Poospiza*) to Burns' (1997) data set, yet in no tree did these form a monophyletic group. Indeed, a tree (equal weighting and with both outgroups) constrained for "traditional" emberizine monophyly was 55 steps longer than the most parsimonious topologies without such a constraint (3102 versus 3046 steps, respectively), with at least 20,000 trees shorter than the constrained tree. Present results thus add to the growing picture revealed by molecular studies that current avian classifications often do not properly represent either true phylogenetic relationships nor monophyly (e.g., *Agelaius,* Lanyon, 1994; galliforms, Kimball *et al.,* 1999; *Icterus,* Omland *et al.,* 1999).

Conclusions of a close relationship among certain thraupine and "traditional" emberizine taxa are not new. Based on DNA–DNA hybridization studies, Bledsoe (1988) and Sibley and Ahlquist (1985, 1990) suggested that a series of neotropical genera traditionally considered emberizines (New World sparrows) are more closely allied to some tanager taxa. Indeed Sibley and Ahlquist (1990) went so far as to suggest that the majority of neotropical "finch-billed tanagers" are thraupines. Among these tanager-finches, they include the genera *Poospiza, Volatinia, Emberizoides, Diuca, Oryzoborous,* and *Sicalis,* among several others (see Appendix 1). Bledsoe (1988) concludes that convergence, especially of feeding specializations, is characteristic of the nine-primaried New World oscine assemblage. Our analyses corroborate these views and suggest that a generalized "finch" morphology has arisen multiple times within the family Emberizidae. These findings suggest that the relationships among all Thraupinae and Emberizinae need to be completely reevaluated in future studies, perhaps using a gene that does not saturate as quickly as cytochrome *b* so that better resolution of deeper nodes may be achieved.

Comparison to a Previous Phylogenetic Perspective

We know of only one other attempt to assess the evolutionary relationships among the warbling-finches. Fjeldså (1992) presented a phenogram of the 17 taxa in this genus based on plumage, behavior, and geographic range (his Fig. 14, redrawn here in Fig. 4). Although not a cladistic analysis, the tree presented by Fjeldså presents an explicit hypothesis of evolutionary affinities to which we can compare our phylogenetic hypotheses. Setting aside the issue of apparent paraphyly of the genus, it is difficult to find any support in our results for Fjeldså's phylogeny. Comparison of Fig. 2 to Fig. 4 makes plain that only one (*baeri–garleppi*) of Fjeldså's sister taxon pairs is found here. The differences between the two phylogenetic hypotheses include (1) our very deep separations between *torquata* and *hispaniolensis* and between *ornata* and *erythrophrys* and (2) our finding of strong associations of (a) *caesar* with *hypochondria,* (b) *alticola, melanoleuca, torquata,* and *erythrophrys,* and (c) *boliviana* with *ornata.* Using our cytochrome *b* data, a heuristic search of *Poospiza* taxa alone (equal weighting and no outgroups as the Fjeldså phenogram specifies no root) yields two equally parsimonious trees of length 405 steps. A topology constrained to that of Fjeldså yields a tree that is 17% longer (474 steps). Such fundamental incongruence between the two topologies suggests that one (or both) suites of characters do not reflect actual evolutionary affinities of the considered taxa. Many studies have shown that plumage characters are quite evolutionarily labile (e.g., Arctander and Fjeldså, 1994; Burns, 1998; Greenburg *et al.,* 1998) and as such are subject to much parallelism and convergence. This ob-

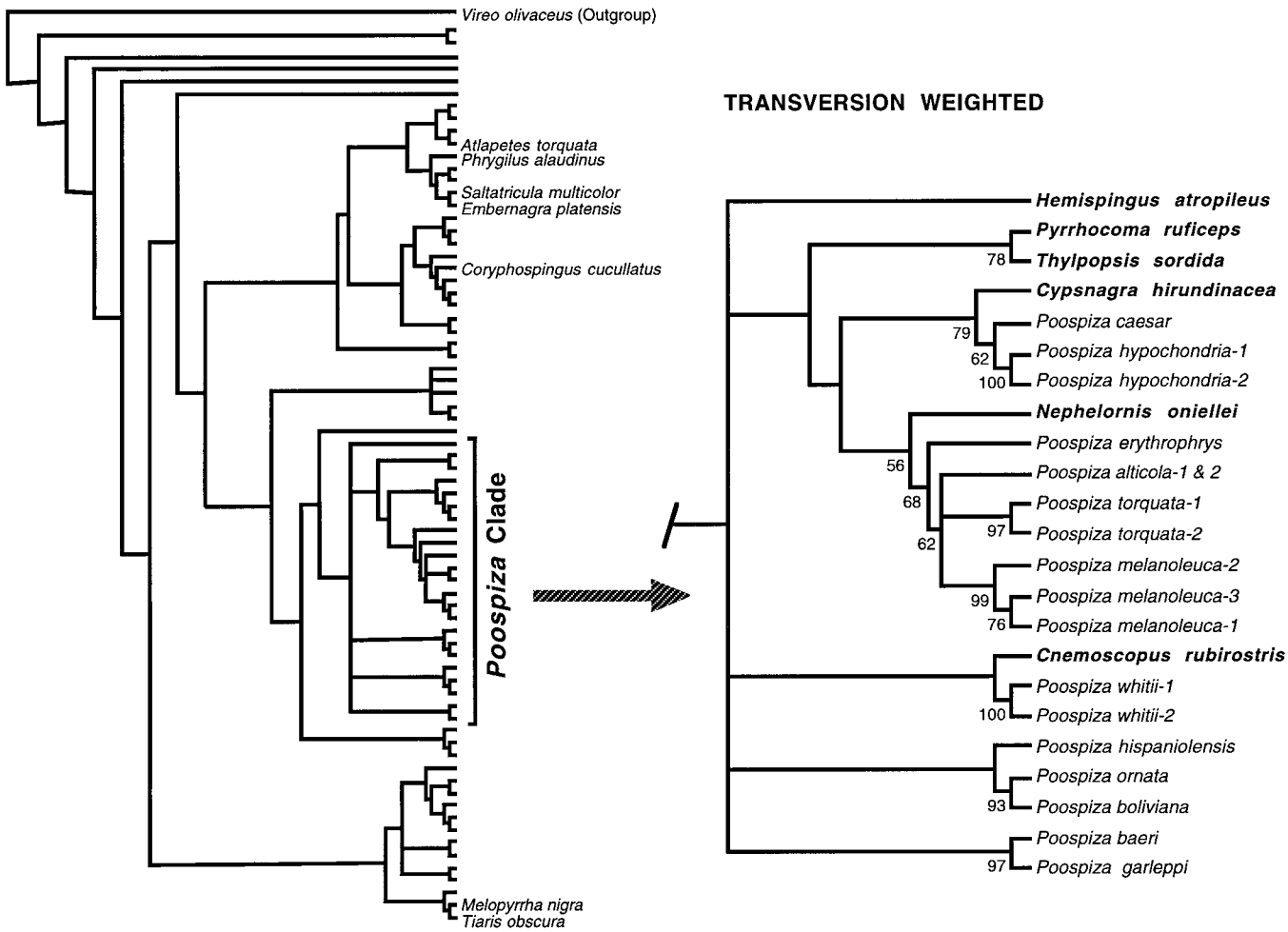

FIG. 3. Strict consensus of six equally parsimonious trees (length 5841 steps; CI = 0.214; RI = 0.378) resulting from a heuristic search with third position transversions weighted five times transitions and *Vireo olivaceus* included as an outgroup (left). Only included emberizine taxa are labeled as Burns (1997) has discussed the phylogeny of thraupines in detail. At right a detail of the clade containing all *Poospiza* species with bootstrap support indicated for values ≥50%. All non-*Poospiza* taxa in this clade (boldface) are traditionally considered members of the subfamily Thraupinae. Tree derives from an analysis of 849 bp of cytochrome *b* DNA sequence data.

servation suggests that the sequence-based phylogeny in Fig. 3 probably more accurately reflects the evolutionary affinities of *Poospiza* with each other (and with other emberizids).

Impact of Missing Taxa, Density of Taxon Sampling, and Outgroup Choice

The strict consensus trees presented in Figs. 2 and 3 are reasonably well resolved with relatively few polytomies. However, proportionately few nodes received bootstrap support exceeding 50%. In our analyses we have used (1) a subset of recognized warbling-finch taxa, (2) representatives of only a portion of all emberizid taxa, and (3) two outgroup taxa that might be considered relatively distant from ingroup taxa. Thus, it is important to comment on the robustness of conclusions derived from our phylogenetic analyses.

Dense taxon sampling may have an impact on tree topology because long branches may be subdivided as ingroup taxa are added (Felsenstein, 1978; Huelsenbeck and Hillis, 1993; Lecointre *et al.*, 1993; Milinkovitch *et al.*, 1996; Omland *et al.*, 1999). We have sampled 12 of 17 *Poospiza* species recognized by Ridgely and Tudor (1989) and thus lack 5: *P. cinerea, P. lateralis, P. thoracica, P. nigrorufa,* and *P. rubecula.* Inclusion of these additional warbling-finch taxa may well further resolve relationships among considered taxa and alter tree topology. It is also probable that the topology presented in Fig. 3 will change with the addition of other thraupines and emberizines. Regardless, it seems unlikely to change our conclusion that *Poospiza* and some thraupines have close evolutionary affinities. Whereas sequence divergence is not an infallible or universal means for assessing taxonomic rank (Johnson and Zink, 1983), it does provide a rough metric for evaluating phylogenetic distinctiveness. Divergence between some thraupines and warbling-

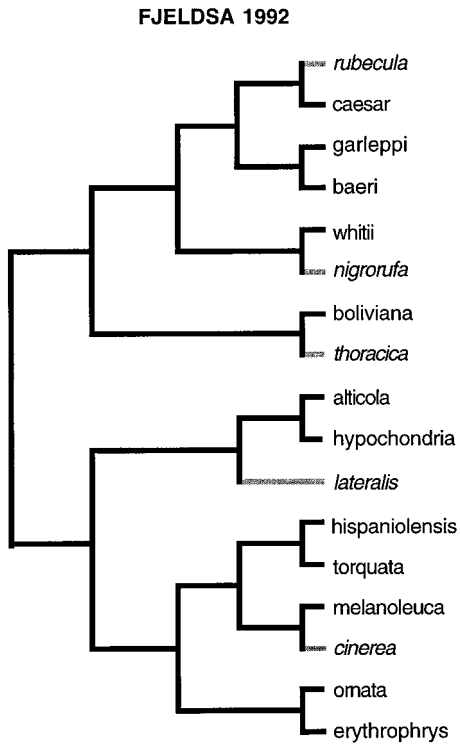

FIG. 4. Fjeldså's (1992) hypothetical phylogeny of the genus *Poospiza* based on plumage morphology and geographic range. Taxa shown in italics and with branches in gray are not included in our analyses.

finches is smaller than for pairwise comparisons between some warbling-finch species. For example, mean sequence divergence between *Nephelornis oniellei* and *Poospiza melanoleuca* is 6.5% and between *Cypsnagra hirundinacea* and *Poospiza hypochondria* is 5.3%, below the average pairwise divergence for *Poospiza* taxa alone (8.0%).

Monophyly at the specific level is an important aspect of building reliable phylogenetic hypotheses (Omland, 1997). Sampling single individuals of species that are polyphyletic or paraphyletic may influence tree topology (Melnick *et al.*, 1993; Omland *et al.*, 1999). All five species for which we sequenced more than one individual were monophyletic in our analyses (Figs. 2 and 3). However, *P. torquata* showed quite substantial divergence (larger than that between *P. garleppi* and *P. baeri*) between individuals derived from disjunct portions of the species range (Bolivia and Argentina; intersample distance >800 km). The "species-level" sequence divergence between taxa that are virtually indistinguishable to the eye implies that each merits specific status. Certainly if *melanoleuca, erythrophrys,* and *alticola* or *whitii* and *nigrorufa* are recognized as distinct species, then the present evidence strongly suggests that Argentine "*torquata*" and Bolivian "*torquata*" should also be considered distinct (sister) species. Paynter and Storer (1970), in listing these two populations as subspecies, show them to have been originally described as distinct species: those from Bolivia as *P. torquata* and those from Argentina as *P. pectoralis.* Our results would lend support to the idea of reinstating this specific distinction. Other warbling-finch taxa (e.g., *P. lateralis*) also occupy disjunct areas within their known range and future work on this genus should attempt to include multiple exemplars from a greater selection of species. It may well be that there is greater phylogeographic division within some of these "species" than is suggested by traditional morphological studies.

Outgroup choice for New World sparrows and tanagers is problematic, as the evolutionary affinities of most taxa are poorly known and often controversial (e.g., Isler and Isler, 1987; Burns, 1997). Outgroup taxa that are too distant from the ingroup may confound attempts of phylogenetic reconstruction because homoplasy will have overwritten much of the meaningful signal for deducing character polarities (Hillis *et al.*, 1990; Wheeler, 1990; Smith, 1994). Inclusion of such distant outgroup taxa may result in incorrect root placement and erroneous conclusions regarding relationships among ingroup taxa because of long-branch attraction (Wheeler, 1990; Smith *et al.*, 1992). A number of empirical studies have shown that selection of different outgroups may alter interpretations of affinities of ingroup taxa (e.g., Weller *et al.*, 1992; Smith, 1994). In the present study, for all analyses we used two outgroups (both singly and combined) unequivocally outside of the predominantly New World emberizid radiation with little impact on tree topology as regards the affinities and lack of monophyly of *Poospiza.* Moreover, reanalysis of our data without explicit identification of outgroups does not change our conclusions regarding the paraphyly of *Poospiza* or the constituent members of the *Poospiza*/thraupine clade shown in Fig. 3. Finally, with reanalysis of ingroup taxa only (all thraupines and "traditional" emberizines including *Poospiza*), it is not possible to root the network such that *Poospiza* is monophyletic.

Biogeographical Considerations

Various authors have recently commented upon the importance of the Andes mountains in the generation of a significant proportion of the current species complement in South America (e.g., Fjeldså, 1994; Burns, 1997; Roy *et al.*, 1997). For some taxa, diversification was probably driven by the appearance of new life zones and vicariance events during uplift of the Andes (e.g., *Leptopogon;* Bates and Zink, 1994). For other avian taxa (e.g., *Scytalopus;* Arctander and Fjeldså, 1994), the deeply incised topography of western South America coupled with cyclical climatic–vegetational changes have been implicated in speciation. An explicit historical biogeographic model of diversification awaits the inclusion of the remaining five members of

Poospiza and clarification of basal relationships within the warbling-finch/thraupine clade. However, it seems clear that the montane region of western South America has played a role in diversification of this genus and affiliated thraupines. Species diversity of the warbling-finches and of *Cnemoscopus, Cypsnagra, Hemispingus, Nephelornis, Pyrrhocoma,* and *Thylpopsis* is primarily concentrated in the topographically complex mountain regions of Peru, Bolivia, and Argentina. Even many of the warbling-finches that we have classified as having a "lowland" range (e.g., *P. melanoleuca, P. ornata,* and *P. torquata*) may be found on lower altitude slopes and in interior valleys of the Andes.

Estimating the timing of diversification among warbling-finches and associated Andean thraupines requires a calibration for rate of sequence divergence in cytochrome *b.* If we assume the widely applied 2% divergence per million years (Shields and Wilson, 1987), the mean overall sequence divergence of 8.30 ± 1.1% between lineages in this clade implies an average age of diversification of 4.15 ± 0.55 my. However, given that our plots in Fig. 1 show evidence of saturation, calculations of diversification times based on overall divergence may be underestimates. Thus, it may be more appropriate to use the calibration of Irwin *et al.* (1991) of 0.5% third codon position transversion divergence per million years. Mean third position transversion divergence was 4.7 ± 1.3%, implying an age of 9.4 ± 2.6 my. Either estimate places much of the diversification within this largely Andean clade well before the Pleistocene, perhaps within the late Miocene and Pliocene, a period coincident with major orogenic activity in central-western South America (Marshall and Sempere, 1993; Arctander and Fjeldså, 1994).

APPENDIX 1

The Larger Taxonomic Context of This Study

The nine-primaried oscines have long been a taxonomically troublesome group, in terms of their relationships with other groups, such as Old World Sparrows, Cardueline finches, and others, and with regard to their internal organization (see extensive discussion provided in Sibley and Alquist, 1990, p. 683 *et seq.*) The "official picture" has stabilized, at least for the time being, as shown below:

Family Emberizidae	
Parulinae	Wood warblers
Coeribinae	Bananaquits
Thraupinae	Tanagers
Catamblyrhynchinae	Plush-capped finch
Cardinalinae	Cardinals, Grosbeaks
Emberizinae	Buntings, Sparrows
Icterinae	Blackbirds, Grackles, etc.

Although some parts of this subfamilial grouping are well agreed upon (Parulinae, Icterinae), the limits of the Thraupinae, Cardinalinae, and Emberizinae are still far from clear. There is no taxonomic character confined to "the tanagers," whether or not they include the so-called Plush-capped finch, *Catamblyrhynchus;* the distinctiveness of the cardinals and grosbeaks is lost once one includes such South American taxa as *Saltator;* all "true emberizine" characters break down once the entire array of tanagers and New World seedeaters are considered together. Sibley and Ahlquist (also Sibley and Monroe, 1990) assert that much of the confusion surrounding this group has its explanation in wholesale evolutionary convergence, in the neotropical region, on the morphological syndrome which we may refer to as "the seedeater." Their suggestion is plainly expressed: "It may be that, with few exceptions, the finch-billed Emberizinae of South America are members of the Thraupini, not of the Emberizini." (Sibley and Ahlquist, 1990, p. 698).

In place of this received taxonomy, Sibley and Monroe (1990) place the conventional Emberizidae as a subfamily of their family Fringillidae, constituted thus:

Family Fringillidae	typical genera
Peucedraminae	*Peucedramus*
Fringillinae	
Fringillini	*Fringilla*
Carduelini	*Carduelis, Carpodacus, Loxia*
Drepanidini	*Himatione*
Emberizinae	
Emberizini	*Emberiza, Calcarius, Zonotrichia*
Parulini	*Vermivora, Dendroica, Geothlypis*
Thraupini	*Piranga, Tachyphonus, Habia*
Cardinalini	*Spiza, Pheucticus, Saltator*
Icterini	*Cacicus, Icterus*

The South American seedeater genera which Sibley and Monroe (1990) relocate from the conventional Emberizinae to their new tanager group Thraupini are *Amaurospiza, Catamenia, Charitospiza, Coryphaspiza, Coryphospingus, Diuca, Dolospingus, Donacospiza, Emberizoides, Embernagra, Haplospiza, Idiopsar, Incaspiza, Lophospingus, Melanodera, Oryzoborus, Phrygilus, Piezorhina, Poospiza, Rhodospingus, Saltatricula, Sicalis, Sporophila, Tiaris, Volatinia, Xenospingus.*

APPENDIX 2

Collecting Localities and Tissue Sources for the Emberizine Taxa Sequenced in This Study

Taxon	Locality[a]	Tissue	Collection[b]	Accession No.	Catalogue[c]
Poospiza alticola 1	Ancash, PE.	Blood	ZMUC	AY005198	0665
Poospiza alticola 2	Ancash, PE.	Blood	ZMUC	AY005199	0664
Poospiza baeri	Tafí del Valle, Tucumán, AR.	Blood	QUMEL	AY005200	na
Poospiza boliviana	La Paz Department, BO.	Liver	LSUM	AY005201	B1198
Poospiza caesar	Andamarca, Ayacucho, PE.	Blood	ZMUC	AY005202	0667
Poospiza erythrophrys	Finca El Rey, Salta, AR.	Liver	QUMEL	AY005203	na
Poospiza garleppi	Cochabamba Department, BO.	Liver	LSUM	AY005204	B106745
Poospiza hispaniolensis	Lambayeque Department, PE.	Liver	LSUM	AY005205	B5205
Poospiza hypochondria 1	Cochabamba Department, BO.	Liver	LSUM	AY005206	B106736
Poospiza hypochondria 2	Cochabamba, BO.	Blood	ZMUC	AY005207	0671
Poospiza melanoleuca 1	Quimili, Santiago del Estero, AR.	Blood	QUMEL	AY005208	na
Poospiza melanoleuca 2	Monteagudo, Tucumán, AR.	Blood	QUMEL	AY005209	na
Poospiza melanoleuca 3	Palmarcito, Chuquisaca, BO.	Blood	ZMUC	AY005210	05031
Poospiza whitii 1	Santa Cruz Department, BO.	Liver	LSUM	AY005211	B6573
Poospiza whitii 2	Sopachuy, Chuquisaca, BO.	Blood	ZMUC	AY005212	05057
Poospiza ornata	Amanao, Catamarca, AR.	Blood	QUMEL	AY005213	na
Poospiza torquata 1	Lujan, Santiago del Estero, AR.	Blood	QUMEL	AY005214	na
Poospiza torquata 2	Chuquisaca, BO.	Blood	ZMUC	AY005215	5036
Atlapetes torquata	La Angostura, Tucumán, AR.	Blood	QUMEL	AY005216	na
Saltatricula multicolor	Quimili, Santiago del Estero, AR.	Blood	QUMEL	AY005217	na
Melopyrrha nigra	Cayo Coco, CU.	Blood	QUMEL	AY005219	na
Coryphospimgus cucullatus	Lujan, Santiago del Estero, AR.	Blood	QUMEL	AY005221	na
Embernagra platensis	Yavi, Jujuy, AR.	Blood	QUMEL	AY005220	na
Phrygilus alaudinus	Tafí del Valle, Tucumán, AR.	Blood	QUMEL	AY005218	na

[a] AR, Argentina; BO, Bolivia; CA, Canada; PE, Peru; CU, Cuba.
[b] LSUM, Louisiana State University, Museum of Natural Science collection; QUMEL, Queen's University Molecular Ecology Laboratory collection; ZMUC, Zoological Museum, University of Copenhagen.
[c] Catalogue number; na, catalogue number not assigned.

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