



The Yellow-green Bush-tanager is neither a bush-tanager nor a sparrow: Molecular phylogenetics reveals that *Chlorospingus flavovirens* is a tanager (Aves: Passeriformes; Thraupidae)

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Abstract

Molecular phylogenetic analyses of the genus *Chlorospingus* (Aves: Emberizidae) indicate that the genus is not monophyletic because *Chlorospingus flavovirens* is actually a member of the tanager family (Thraupidae), in which its closest relatives are members of the genus *Bangsia*. We thus propose that *C. flavovirens* be transferred to Thraupidae and to the genus *Bangsia*.

Key words: Andes, Chocó, Emberizoidea, Passerellidae, polyphyly

Introduction

Recent molecular studies have been essential to improving our understanding of the phylogenetic relationships and diversification of Neotropical birds (e.g. McGuire *et al.* 2007, 2014; Tello *et al.* 2009; Lovette *et al.* 2010; Derryberry *et al.* 2011; Barker *et al.* 2015). Genetic data have revolutionized the taxonomy and classification of the Emberizoidea, a passerine clade commonly known as the New World nine-primaried oscines, which comprises more than 830 species in the families Icteridae (blackbirds), Cardinalidae (cardinals), Emberizidae (sparrows, including both the Passerellidae and Emberizidae of Barker *et al.* 2013), Thraupidae (tanagers), and Parulidae (wood-warblers; Burns *et al.* 2014, 2016; Klicka *et al.* 2014; Barker *et al.* 2013, 2015; Remsen *et al.* 2016). The tanagers in particular have been subject to extensive taxonomic revision, with many taxa traditionally placed in this family having been transferred to other families such as Emberizidae, Cardinalidae and Fringillidae (finches), and vice versa (Chesser *et al.* 2014; Remsen *et al.* 2016).

An example of taxonomic changes involving the tanagers and other emberizoids is the genus *Chlorospingus* Cabanis, 1851, long considered to belong in the tanager family but recently transferred to the Emberizidae based on molecular phylogenetic evidence (Klicka *et al.* 2007, 2014; Remsen *et al.* 2016). The genus comprises nine species restricted to Neotropical cloud-forests ranging from Mexico to Argentina (Isler & Isler 1999; Hilty 2011). Weir *et al.* (2008) showed that one of the most geographically variable species, *C. ophthalmicus* (now *C. flavopectus* (Lafresnaye, 1840)), is paraphyletic with respect to three other *Chlorospingus* species: *C. tacarcunae* Griscom, 1924, *C. inornatus* (Nelson, 1912) and *C. semifuscus* Sclater & Salvin, 1873. This result suggested that the classification of species in the genus requires revision, but this has not been completed due to insufficient taxon sampling.

As part of a project to reconstruct the phylogeography of the South American populations of *C. flavopectus* and their affinities with other species in the genus (Avendaño 2010), we expanded sampling to include several previously unstudied taxa, including the poorly known Yellow-green Bush-tanager (*C. flavovirens* (Lawrence,

1867)) from western Colombia and Ecuador. Preliminary phylogenetic analyses we conducted based on mitochondrial DNA sequences surprisingly suggested that this species is not a member of the *Chlorospingus* clade nor of the Emberizidae, a result later suggested as well by a comprehensive phylogeny of the family (Klicka *et al.* 2014). Here, we report on additional analyses that demonstrate conclusively that the Yellow-green Bush-tanager has been misplaced in *Chlorospingus* and in the Emberizidae, and suggest taxonomic changes to make classification consistent with phylogeny.

Materials and methods

We studied two specimens (ICN 37481 and ICN 37740) of *C. flavovirens* collected by F. G. Stiles and O. Acevedo-Charry in 2009–2010 at the Río Nambí Nature Reserve, vereda El Barro, Corregimiento de Altaquer, municipality of Barbacoas, Nariño department, Colombia. Genomic DNA from these specimens was extracted from toepads using the Bioline Isolate Genomic DNA Kit, following the manufacturer's protocol. Based on methods described in Cadena *et al.* (2007), we amplified three mitochondrial genes (ATPase 6 & 8—842 bp; NADH dehydrogenase subunit 2—ND2, 1041 bp) in laboratories at Universidad de los Andes and Universidad de los Llanos, Colombia. DNA sequencing was performed by Macrogen Inc., South Korea. We also sequenced a fraction of the cytochrome *b* gene—*cyt b* (777 bp) from a third specimen (deposited at the American Museum of Natural History, catalogue number AMNH 824756) collected by S. L. Hilty in 1975 at Alto Yunda, 3.5 Km S La Cascada, Anchicayá, Valle del Cauca department, Colombia (Hilty 1977). Laboratory work on this specimen was conducted independently at facilities of the University of Minnesota (see protocols in Barker *et al.* 2013).

We first conducted phylogenetic analysis based on sequences of the ATPase 6 & 8 genes available for all *Chlorospingus* species including *C. flavovirens*, plus additional representatives of the Thraupidae (16 species), Emberizidae (16 species), Cardinalidae (4 species), Parulidae (5 species), Icteridae (4 species), and Fringillidae (2 species). As outgroups for this data set we used sequences of *Ploceus cucullatus* Statius Muller, *Peucedramus taeniatus* Du Bus, and *Motacilla alba* Linnaeus, which are all members of the superfamily Passeroidea (Sibley & Ahlquist 1990) and thus are believed to be close relatives of the nine-primaried oscines (Klicka *et al.* 2000), as well as *Bombycilla cedrorum* Vieillot, a more distant relative. GenBank accession numbers of the ATPase data set and DNA sequences of *C. flavovirens* are listed in the Appendix.

Because the analysis based on ATPase genes found that *C. flavovirens* is nested in a thraupid clade referred to as the 'core tanagers' in the subfamily Thraupinae (Burns & Naoki 2004; see below), we sought to precisely establish the systematic relationships of *C. flavovirens* with a denser sampling scheme in the Thraupidae. For this purpose, we analyzed sequences of two additional mitochondrial genes (ND2 and *cyt b*), for which there is comprehensive sampling of Thraupidae taxa (Sedano & Burns 2010; Burns *et al.* 2014; Barker *et al.* 2015). We analyzed available sequences (ND2: 108 individuals, *cyt b*: 111 individuals) of most Thraupinae species (99 out of 103; Klicka *et al.* 2007; Burns *et al.* 2014). In addition, one or two species per genus ($n=72$) from other Thraupidae subfamilies were also included (ND2: 67 sequences of 65 genera; *cyt b*: 73 sequences of 71 genera). Because Cardinalidae is the sister taxon to tanagers (Barker *et al.* 2013), we used four representatives of this clade to root trees: *Cardinalis cardinalis* Linnaeus, *Piranga ludoviciana* Wilson, *Pheucticus tibialis* Lawrence, and *Passerina ciris* Linnaeus (GenBank accession numbers: EF530007, EF529902, EF529998, AF290109, JX569837, JX569838, AF301459, EF529883).

We conducted separate maximum-likelihood (ML) and Bayesian phylogenetic analyses for each gene, and also concatenated analyses including sequences from both loci. Because for two of the specimens of *C. flavovirens* we had only ND2 data and for the other we had only *cyt b* data, in the concatenated analyses we included a chimeric sequence assembled from specimens ICN 37740 (ND2) and AMNH 824756 (*cyt b*). The best-fit model of evolution for each mitochondrial gene was GTR + I + G according to the Akaike information criterion implemented in jModeltest v2.1.6 (Darriba *et al.* 2012); ML and Bayesian analyses were partitioned by codon position. ML inference was implemented using RAxML v8.1.11 (Stamatakis 2014), which applies a GTR + Γ model of DNA evolution. The most likely tree was computed simultaneously with 1000 bootstrap replicates, which were run independently several times. We also conducted Bayesian analyses using BEAST v1.7.1 (Drummond *et al.* 2012). We used a Yule speciation prior, an UPGMA starting tree, and a relaxed uncorrelated lognormal clock for each gene tree. A substitution rate of 0.0105 mean substitutions per million years along each branch was used

(Weir & Schluter 2008; Burns *et al.* 2014). Four independent analyses were conducted with 200 million generations and sampling every 5000 generations. We used Tracer v1.5 (Rambaut & Drummond 2007) to assess convergence across independent runs and examine effective sample size values for all parameters; in all cases these were >200. The first 20 million generations and 4000 trees for each run were discarded as burn-in, log and tree files were combined using LogCombiner v1.7.1 (Drummond *et al.* 2012), and we produced a maximum clade credibility in TreeAnnotator v1.7.1 (Drummond *et al.* 2012). For the ATPase 6 & 8 genes, the Bayesian analysis consisted of 30 million generations sampling every 1000 generations, and the first 7.5 million generations and 7500 trees were discarded as burn-in. ML and Bayesian analyses were implemented on the XSEDE computing cluster, accessed via the CIPRES Science Gateway v3.1 (Miller *et al.* 2010).

Finally, we used Bayes factor analysis (Kass & Raftery 1995; Bergsten *et al.* 2013) to compare alternative hypotheses about the phylogenetic position of *C. flavovirens*. We calculated the marginal likelihood of alternative hypotheses (models) using the concatenated data set after specifying equally informed priors (constraints) on the topology. The marginal likelihood of each model was calculated using the stepping-stone sampling method implemented in MrBayes on XSEDE (3.2.6) accessed via the CIPRES Science Gateway v3.1 (Miller *et al.* 2010). For each model, we ran two independent Markov chain Monte Carlo (MCMC) analyses for 10×10^6 million generations sampling every 1000 generations, with 1 million generations discarded as burn-in. Convergence of the stepping-stone MCMC sampling among independent runs was successful, with an average deviation of split frequencies always <0.04. We used the arithmetic mean of the estimated marginal likelihood for each model across runs to calculate the Bayes factor.

Results and discussion

Analyses based on all three mitochondrial genes suggested that the Yellow-green Bush-tanager is not closely related to species of *Chlorospingus* or to any other emberizid, but instead, is deeply nested within the Thraupidae. For the ATPase 6 & 8 genes (Fig. 1), all *Chlorospingus* species formed a well-supported clade (posterior probability = 0.96; ML bootstrap = 50%; supports hereafter in this order) within the Emberizidae (or more specifically the Passerellidae, following the taxonomy of Barker *et al.* 2013), whereas *C. flavovirens* was included in a distantly related but weakly supported clade containing tanagers and cardinals. Within this clade, however, the species was included in a strongly supported clade (1.0; 64%) containing typical Thraupinae taxa (e.g. *Buthraupis*, *Tangara*). ND2 analyses clearly showed *C. flavovirens* within the core tanager clade (1.0; 70%; Fig. 2A). Moreover, sequences of this gene strongly suggested the species is sister to *Bangsia arcaei* Sclater & Salvin (1869) (1.0; 94%); the clade formed by *C. flavovirens* and *B. arcaei* was sister to a clade including the remaining species of *Bangsia* Penard (1.0; 98%). Relationships inferred based on the *cyt b* gene were not as strongly supported, especially within the core tanagers (Fig. 2B). Although support was not strong in analyses based on this gene, *C. flavovirens* was also found to be a member of the core tanagers; in contrast to the ND2 topology, it was not recovered as sister to *B. arcaei*, but rather as the sister group of *Bangsia*, albeit with weak support. The concatenated analyses resulted in topologies and support values similar to those obtained in the ND2 analyses (Fig. 3): *C. flavovirens* was nested within the *Bangsia* clade (0.99; 81%) as the sister taxon to *B. arcaei* (1.0; 93%).

We used estimates of marginal likelihoods based on the concatenated data set to contrast the null hypothesis where *C. flavovirens* is sister to *B. arcaei* to the alternative hypothesis where *C. flavovirens* is sister to a clade formed by all species of *Bangsia* using the Bayes factor. Estimates of the marginal likelihood were -82045.67 for the null hypothesis and -82519.12 for the alternative hypothesis, resulting in an absolute difference (i.e. Bayes factor) of 473.45. Because Bayes factors larger than 150 should be interpreted as very strong evidence in favor of the better model (Kass & Raftery 1995; Bergsten *et al.* 2013), this analysis strongly favors the hypothesis that, given our mtDNA data, *C. flavovirens* is sister to *B. arcaei*.

Chlorospingus flavovirens was originally described as *Buarremon flavovirens* (Lawrence, 1867). It was later transferred to *Chlorospingus* Cabanis, 1851 by Sclater (1885) based on its short and strong beak, more typical of *Chlorospingus* species. Since then, it has been consistently considered a *Chlorospingus*, sharing similar plumage patterns (particularly with some species; e.g. *C. tacarcunae*, *C. inornatus*), habitat and behavior with members of this group (Isler & Isler 1999; Hilty 2011; see Fig. 1). Our results conclusively show that *C. flavovirens* is actually a tanager distantly related to true *Chlorospingus*, for which the type species is the taxon now known as *C.*

flavopectus ophthalmicus (Du Bus, 1847). Accordingly, the species must be transferred to the subfamily Thraupinae within the Thraupidae.

Examples of morphological similarity between phylogenetically distant taxa are not rare among Emberizoids, and this is one of the reasons why classification in groups like tanagers, emberizids and cardinalids has been subject to extensive revision following molecular phylogenetic analyses (Burns *et al.* 2014, 2016; Klicka *et al.* 2014; Barker *et al.* 2015; Remsen *et al.* 2016). However, the similarity between *C. flavovirens* and true *Chlorospingus* that had thus far misled taxonomists who considered them congeneric represents a remarkable case of evolutionary convergence in plumage, morphology, and behavior between taxa belonging to different families.

In addition to being transferred to the Thraupidae, *C. flavovirens* should be placed in a different genus to make classification consistent with phylogeny. The genus name *Buarremon* Bonaparte, 1850 in which the species was originally described is not available because the type species is *Embernagra torquata* Lafresnaye and d'Orbigny, 1837, (i.e., *Arremon torquatus*; Cadena & Cuervo 2010), an emberizid distantly related to *C. flavovirens*. Because no generic name is available for *C. flavovirens*, based on our results we see three alternatives: (1) creating a monotypic genus for *C. flavovirens*, (2) placing *C. flavovirens* and the closely allied *B. arcaei* in a genus separate from the other species of *Bangsia*, or (2) merging *C. flavovirens* and *Bangsia* in a single genus. We favor the third option for reasons outlined below.

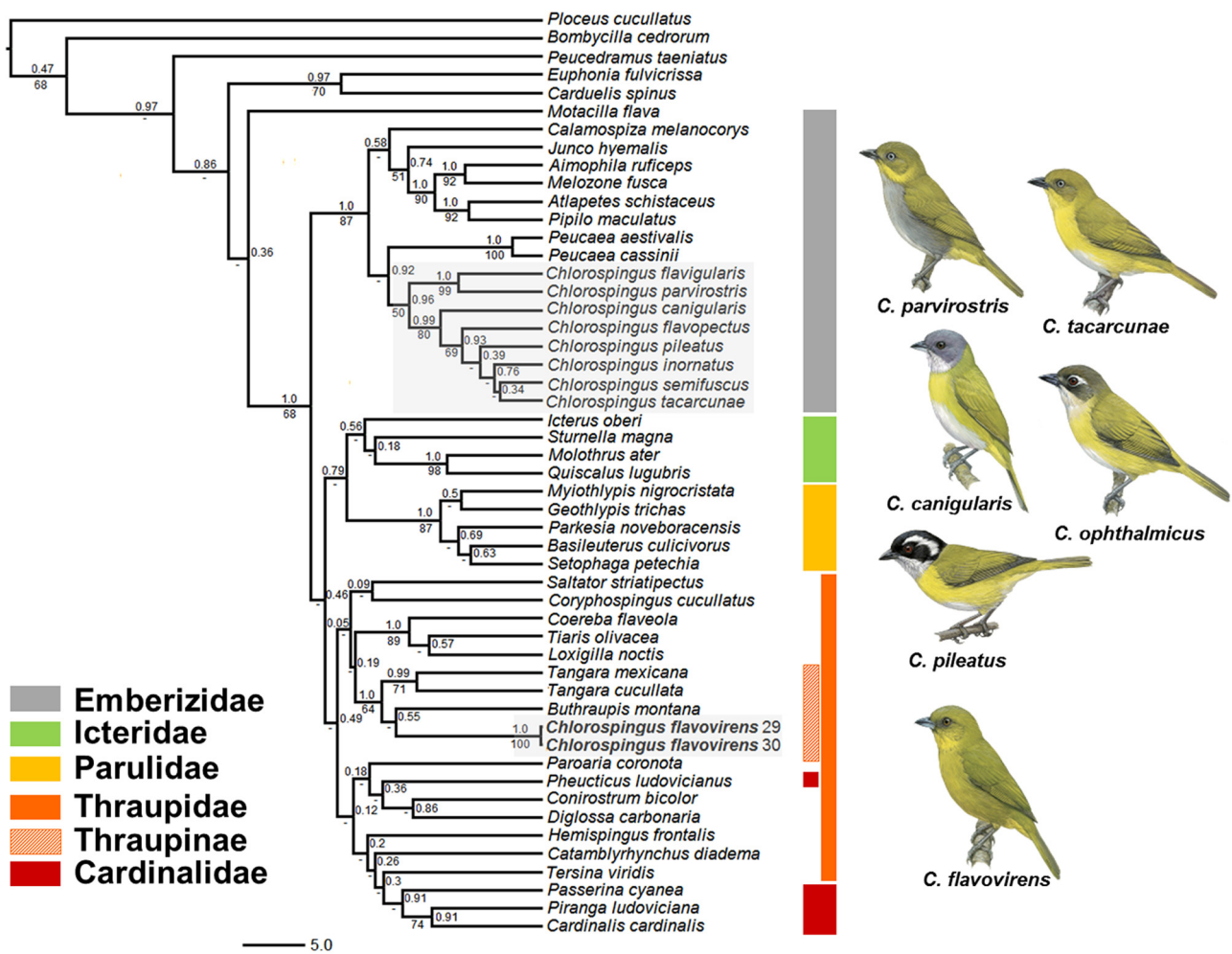


FIGURE 1. Maximum clade credibility tree reconstructed in BEAST showing relationships of *Chlorospingus flavovirens* and representatives of six families of nine-primaried oscines, based on ATPase 6 & 8 genes. The phylogeny indicates that *Chlorospingus flavovirens* is more closely related to tanagers (Thraupidae) than to other *Chlorospingus* species (Emberizidae). For each node, the posterior probability from the BEAST analysis is given above the branch leading to that node, and the maximum likelihood value from the RAxML analysis is given below the branch. Nodes that lacked bootstrap support based on 1000 maximum-likelihood replicates are indicated by “–”. Illustrations are from *C. flavovirens* and some selected *Chlorospingus* species (courtesy of Lynx Edicions; *Handbook of the Birds of the World*, Vol. 16, 2011). Numbers in front on taxon names correspond to sample ID (see Supplementary file).

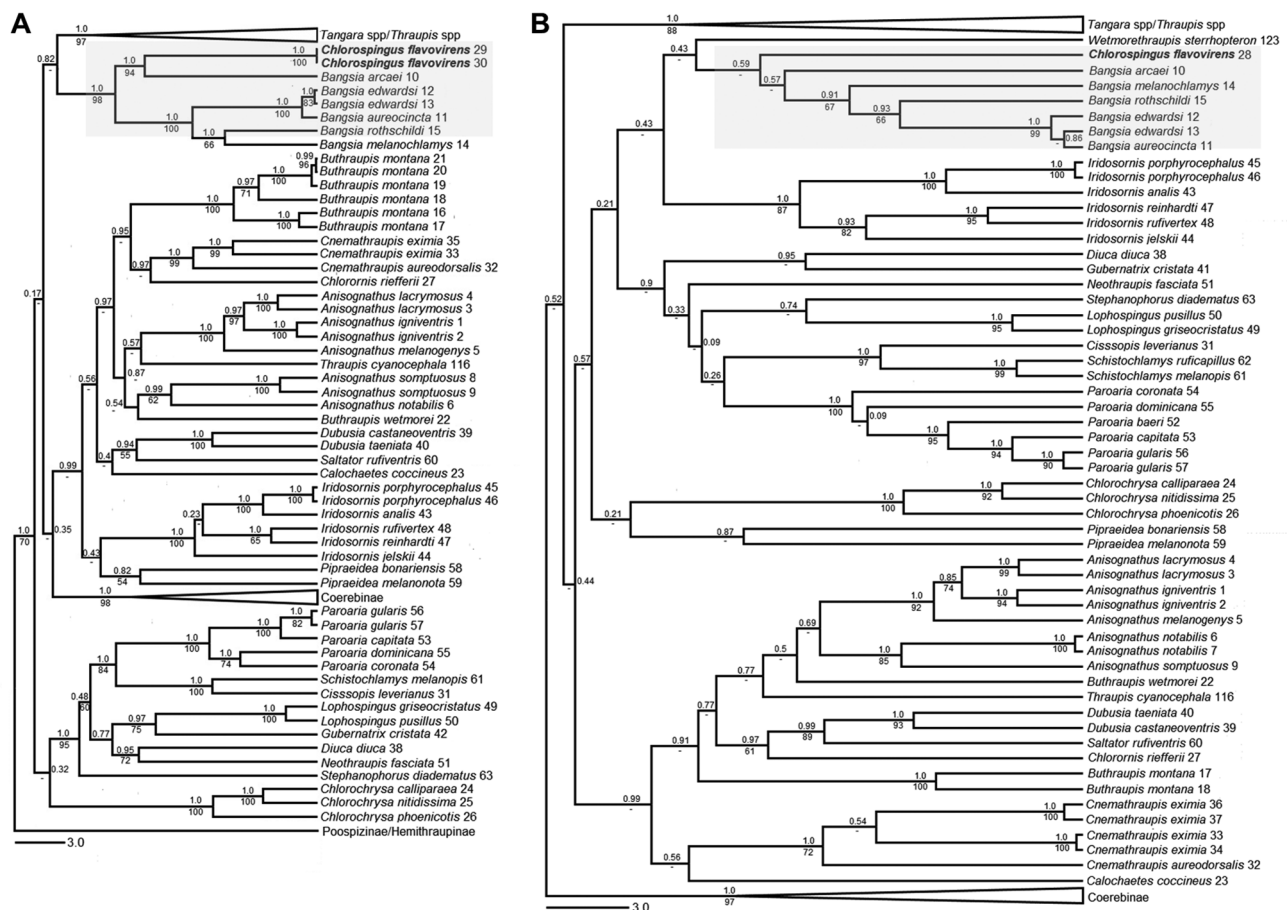


FIGURE 2. Maximum clade credibility trees reconstructed in BEAST for the core tanagers (Thraupinae) based on ND2 (A) and Cyt *b* (B) genes. While the ND2 topology indicates that *Chlorospingus flavovirens* is closely related to *Bangsia arcaeii*, the Cyt *b* topology points to *C. flavovirens* as sister to all *Bangsia* species, although this relationship is weakly supported. For each node, the posterior probability from the BEAST analysis is given above the branch leading to that node, and the maximum likelihood value from the RAxML analysis is given below the branch. Nodes that lacked bootstrap support based on 1000 maximum-likelihood replicates are indicated by “-”. Numbers in front on taxon names correspond to sample ID (see Supplementary file).

Creating a monotypic genus for *C. flavovirens* would recognize the phenotypic and evolutionary distinctiveness of this taxon. However, given our finding of its close relation with *B. arcaeii*, which is the type species of *Bangsia* (Ridgway, 1893), this would require naming an additional genus for the remaining four species now included in this genus. This would result in recognizing three genera and in changing the genus of *C. flavovirens* and of four species of *Bangsia*, a solution that would involve substantial changes to the existing classification. In addition, this alternative would imply recognizing two monotypic genera (one for *C. flavovirens*, one for *B. arcaeii*); we favor not doing so because monotypic genera convey no information about phylogenetic relationships. Of course, classifying species in monotypic genera does convey phylogenetic information in cases where it highlights deeply divergent lineages with no close relatives (e.g., *Sapayoa* Hartert or *Donacobius* Swainson among Neotropical passerines), but we argue this is not the case for *C. flavovirens*.

The second alternative (i.e. merging *C. flavovirens* and *B. arcaeii* in *Bangsia*) would prevent the naming of a new genus for the former, but again this would require naming a new genus for the remaining four species of *Bangsia*. Moreover, although the ND2 data and the concatenated analyses strongly show that *C. flavovirens* is sister to *B. arcaeii*, this was not supported by the *cyt b* data. An important consideration regarding this and the former alternatives, both of which imply separating *B. arcaeii* from other species of *Bangsia*, is that this has no apparent phenotypic basis given the relatively conserved plumage and morphology across these species. Although Penard (1919) noted some differences in bill shape and primary length between *B. arcaeii* and its congeners, neither we nor Penard could draw reliable conclusions about the taxonomic validity of these characters due to the scarcity of specimens.

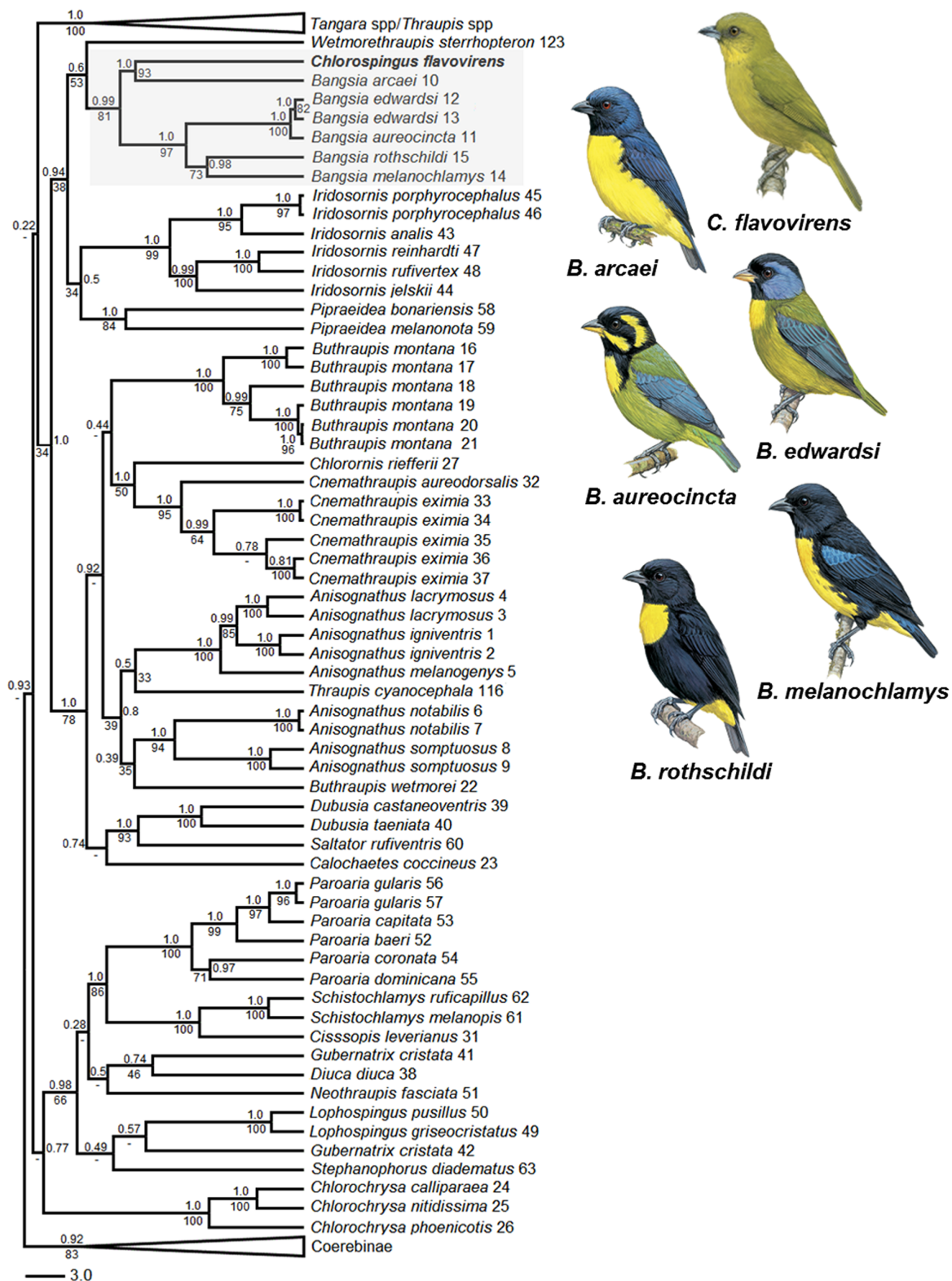


FIGURE 3. Maximum clade credibility tree reconstructed in BEAST for the Core Tanagers (Thraupinae) based on concatenated ND2 and Cyt b sequences. The phylogeny indicates that *Chlorospingus flavovirens* is nested within a clade of *Bangsia* species, and most closely related to *Bangsia arcaei*. For each node, the posterior probability from the BEAST analysis is given above the branch leading to that node, and the maximum likelihood value from the RAxML analysis is given below the branch. Nodes that lacked bootstrap support based on 1000 maximum-likelihood replicates are indicated by “-”. Illustrations are from *C. flavovirens* and *Bangsia* species (courtesy of Lynx Edicions; *Handbook of the birds of the world*, Vol. 16, 2011). Numbers in front on taxon names correspond to sample ID (see Supplementary file).

Finally, merging *C. flavovirens* and *Bangsia* in a single genus would avoid naming two new genera and would imply changing the name of only one species, thus maximizing taxonomic stability. In addition, this treatment would be consistent with all of our analyses, which unequivocally place *C. flavovirens* in a clade with species of *Bangsia* regardless of its position within such clade. Despite our findings showing strong support for the position of *C. flavovirens* as sister to *Bangsia*, we do not deny the possibility that *C. flavovirens* may be sister to *Bangsia* as suggested by the *cyt b* data; however, if this were to be confirmed with additional analyses considering other characters (i.e. nuclear DNA data), our proposal to merge *C. flavovirens* and *Bangsia* would still render a classification consistent with phylogeny. Moreover, we suggest that this treatment is more informative about the evolutionary relationships of the taxa involved despite implying the recognition of a phenotypically heterogeneous genus. Although differences in plumage coloration between *C. flavovirens* and species currently included in *Bangsia* are rather striking (Fig. 3), all these taxa are generally similar in size and proportions, so one may think of *C. flavovirens* as a taxon lacking complex plumage patterns and some of the colors present in relatively close relatives such as *B. edwardsi* (Elliot, 1865) or *B. aureocincta* (Hellmayr, 1910). Finally, we note that *C. flavovirens* occupies the center of the geographic distribution of *Bangsia*, reflecting a shared history of diversification in northwestern South America among members of this clade (Sedano & Burns 2010).

In summary, to make classification consistent with our current understanding of phylogeny, we suggest that the taxon heretofore referred to as *Chlorospingus flavovirens* (Emberizidae) should be transferred to the Thraupidae and referred to as *Bangsia flavovirens*. To avoid confusion with members of the genus *Chlorospingus*, we further suggest that its English name should be changed to Yellow-green Tanager. We encourage further studies involving a broader gene sampling, together with morphological and vocal analyses to improve our understanding of the systematic relationships and evolution of phenotypic diversity in this group.

Acknowledgements

We are very grateful to F. Gary Stiles and Orlando Acevedo-Charry for collecting the specimens of *C. flavovirens* used in this paper and for allowing us to access to the ornithological collection of Instituto de Ciencias Naturales (ICN). Other collectors and institutions that helped with tissue samples and access to their collections were: Jhon Jairo Calderón Leyton, Universidad de Nariño; Juan Diego Palacio, Claudia Alejandra Medina, Socorro Sierra and Fernando Forero, Instituto Alexander von Humboldt; María del Pilar Rivas and Fernando Ayerbe-Quiñones, Museo de Historia Natural, Universidad del Cauca; and Paul Sweet, American Museum of Natural History. This study was supported by The Facultad de Ciencias at Universidad de los Andes, Beca Colombia Biodiversa of Fundación Alejandro Ángel Escobar, the Dirección de Investigaciones of Universidad de los Llanos (Proyecto CAMVZ-21-2012), and the National Science Foundation (DEB-0316092). Lynx Edicions kindly provided permission to use images from the *Handbook of Birds of the World*. We thank Kevin J. Burns, Edward C. Dickinson and F. Gary Stiles for discussions on tanager taxonomy, and James Van Remsen, Jr. and two anonymous reviewers for comments that improved early versions of the manuscript.

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APPENDIX. GenBank accession numbers of DNA sequences.

ATPase data set. Ingroup (n=46): AF279695, AF109415, AF132376, AF132427, AF279694, AF382975, AF382981, AF382986, AF447313, AF447314, AF447315, AF447321, AF447322, AF447324, AF447325, AF447333, AF447341, AF447344, AF447346, AF447348, AF447357, AF447359, AF468612, AF468617, AF468618, AF468624, AF468634, AF468636, AF468637, AF468643, AY115224, AY115225, AY387460, EF567562, EU427581, EU427638, EU427641, EU427643, EU427645, FJ817125, GU932045, GU932068, GU932136, JQ219038. Outgroup: (n=4). AF447347, AY259479, EF486794, JN411179.

C. flavovirens. ND2: KX180147, KX180148. Cyt b: KX180149.