

# Article



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# A genus-level classification of the family Thraupidae (Class Aves: Order Passeriformes)

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#### **Abstract**

The tanagers (Thraupidae) are a major component of the Neotropical avifauna, and vary in plumage colors, behaviors, morphologies, and ecologies. Globally, they represent nearly 4% of all avian species and are the largest family of songbirds. However, many currently used tanager genera are not monophyletic, based on analyses of molecular data that have accumulated over the past 25 years. Current genus-level classifications of tanagers have not been revised according to newly documented relationships of tanagers for various reasons: 1) the lack of a comprehensive phylogeny, 2) reluctance to lump existing genera into larger groups, and 3) the lack of available names for newly defined smaller groups. Here, we present two alternative classifications based on a newly published comprehensive phylogeny of tanagers. One of these classifications uses existing generic names, but defines them broadly. The other, which we advocate and follow here, provides new generic names for more narrowly defined groups. Under the latter, we propose eleven new genera (*Asemospiza*, *Islerothraupis*, *Maschalethraupis*, *Chrysocorypha*, *Kleinothraupis*, *Castanozoster*, *Ephippiospingus*, *Chionodacryon*, *Pseudosaltator*, *Poecilostreptus*, *Stilpnia*), and resurrect several generic names to form monophyletic taxa. Either of these classifications would allow taxonomic authorities to reconcile classification with current understanding of tanager phylogenetic relationships. Having a more phylogenetically accurate classification for tanagers will facilitate the study and conservation of this important Neotropical radiation of songbirds.

Key words: tanager, taxonomy, phylogeny, genus, systematics

#### Introduction

The tanagers (Order Passeriformes: Family Thraupidae) are the largest radiation of Neotropical birds, encompassing a diverse array of plumage colors, behaviors, morphologies, and ecologies (Storer 1969; Webster 1988; Isler & Isler 1999; Hilty 2011). This phenotypic diversity has made the construction of an accurate taxonomy of the group difficult, with little agreement on the limits of the family as a whole or on relationships within the family. The traditional view of tanagers is best exemplified by the classification of Storer (1970). In this classification, the tanagers include 242 mostly colorful, fruit-eating birds in 57 genera. However, over two decades of genetic work (e.g., Bledsoe 1988; Sibley & Ahlquist 1990; Burns 1997; Lougheed et al. 2000; Yuri & Mindell 2002) has shown that many of these species are more closely related to other groups and that many other additional species belong with the tanagers. In addition, studies of subsets of the tanagers (e.g., Burns & Racicot 2009; Sedano & Burns 2010; Campagna et al. 2011; Mason & Burns 2013; Shultz & Burns 2013) uncovered relationships at the species level and showed that many genera were not monophyletic. Some of these changes were incorporated into the taxonomies of Dickinson & Christidis (2014) and Clements et al. (2015). Nonetheless, the comprehensive phylogenies needed to construct a new tanager classification have only recently become available. Barker et al. (2013) sampled nearly every genus of the nine-primaried oscines, including the Emberizidae, Icteridae, Parulidae, Cardinalidae, and Thraupidae, and based their phylogenies on six molecular markers. These include two mtDNA gene regions: cytochrome b (cyt b) and nicotinamide adenine dehydrogenase subunit 2 (ND2). In addition, they included a protein-coding nuclear gene, recombination activating gene 1 (RAG1), and three

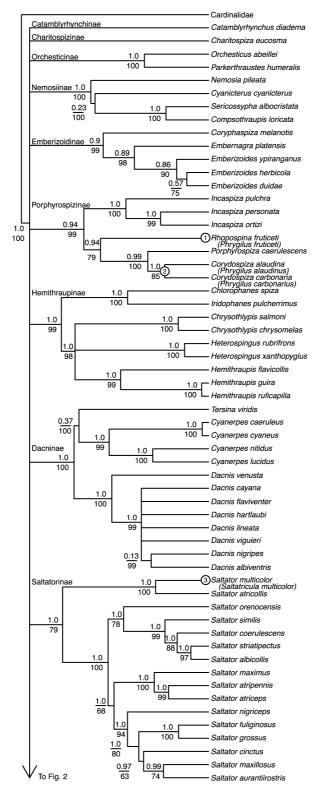
introns: the ninth intron of the sex-linked aconitase 1 (ACO1-I9), myoglobin intron 2 (MB-I2), and β-fibrinogen intron 5 (FGB-I5). Burns *et al.* (2014) and Barker *et al.* (2015) extended these results by producing a species-level phylogeny of tanagers. They included the same molecular markers as Barker *et al.* (2013) and sampled 95% of the species of tanagers. These studies were able to define the limits of tanagers for the first time and showed that tanagers include 372 species, representing roughly 4% of all avian diversity. As currently composed, the Thraupidae are the second largest family of birds and the largest family of songbirds (Clements *et al.* 2015). These phylogenies also revealed that many currently recognized genera are paraphyletic and polyphyletic and that some of the morphological characters used to unite species into certain genera actually represent parallel or convergent evolution. Burns *et al.* (2014) provided a subfamily-level classification of the tanagers and some recommendations for how to reconcile generic names with the tree. However, they did not provide a comprehensive, genus-level classification of tanagers. Therefore, we provide such a classification in this paper. We present two alternative classifications: one which includes broader genera and does not require new generic names, and another which preserves most traditional generic names, but requires the introduction of new genera and the resurrection of older names.

#### Methods

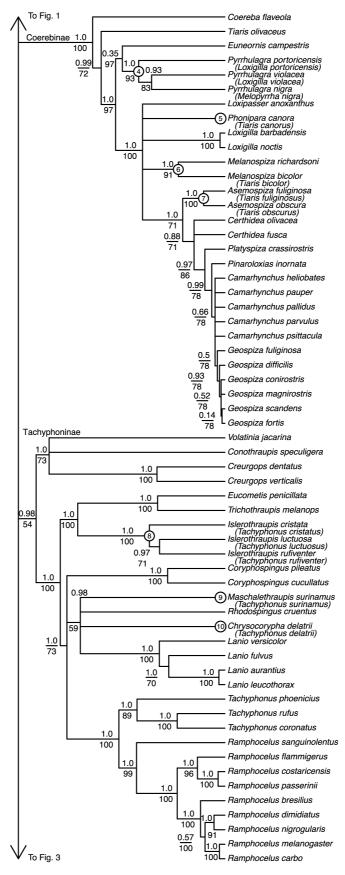
We use the trees of Burns *et al.* (2014) as our best estimate of tanager phylogeny, basing named categories on strongly supported nodes only. That is, we made taxonomic changes only when required by nodes supported by greater than 70% bootstrap replicates in the maximum likelihood analyses or 0.95 posterior probability in the Bayesian analyses. Thus, in the interest of taxonomic stability, we did not split any existing genera if they were strongly supported as monophyletic. In addition, support for a few genera (*Anisognathus*, *Certhidea*, and *Sicalis*) was equivocal. Because there was neither support for or against monophyly in these cases, we retained the current genus assignment, pending further data. Throughout, we use the species-level taxonomy of Clements *et al.* (2015) as our baseline classification, which incorporates the recommendations of the two geographically relevant taxonomic committees, the South American Classification Committee (Remsen *et al.* 2015) and the North American Classification Committee (American Ornithologists' Union 1983 and supplements).

#### Results

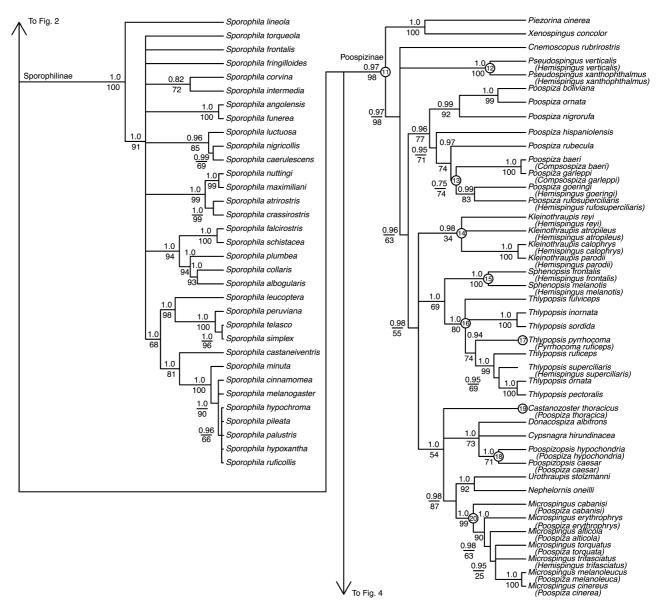
As our first approach toward producing a classification with monophyletic genera, we created a taxonomy by including species in broader genera where generic names are available (Table 1, alternative 2). One advantage of this approach is that the resulting classification emphasizes relationships among species. In other words, the emphasis is placed on species' shared evolutionary history rather than highlighting morphologically distinct taxa in monospecific genera. Traditional classifications of tanagers have many monospecific genera, likely because the distinct morphology of many species led to uncertainty surrounding their taxonomic relationships. For example, 43 of the 92 total genera in the Clements et al. (2015) classification are monospecific. New genetic data, however, have greatly enhanced our understanding of the relationships of these taxa, so a classification based on broader genera can accurately reflect relationships among close relatives. Another advantage of this approach is that it requires the adoption of no new generic names and relatively few resurrected genera. A disadvantage is that many familiar, well-known genera are subsumed into broader groupings. In addition, many of these genera contain more phenotypic diversity than do typical passerine genera. For example, this classification requires the lumping of all genera of Darwin's finches into a broad genus that also includes many of their close relatives. Previous studies of tanagers (e.g., Burns & Racicot 2009; Sedano & Burns 2010), have suggested the use of such broader genera. For example, Sedano & Burns (2010) suggested a broader definition of Tangara that includes many species in the genus Thraupis. However, these suggestions have not been widely adopted by subsequent classifications (Clements et al. 2015; Remsen et al. 2015). Therefore, in this paper we provide an alternative approach (Table 1, alternative 1) that still minimizes the introduction of new and resurrected generic names while retaining most generic names currently used in the tanagers. The logic for many of these recommendations was provided in Burns et al. (2014). In places where more detail is needed, or our recommendations differ from Burns et al. (2014), we provide more information in the comments section.



**FIGURE 1.** Maximum clade credibility tree from the Bayesian analyses of Burns *et al.* (2014). Subfamilies Catamblyrhynchinae, Charitospizinae, Orchesticinae, Nemosiinae, Emberizoidinae, Porphyrospizinae, Hemithraupinae, Dacninae, and Saltatorinae shown. Branch lengths are proportional to the number of nucleotide substitutions, and only strongly supported nodes (>70 maximum likelihood bootstrap or >0.95 posterior probability) are shown. Nodes that fail to meet either support threshold are collapsed to polytomies. The posterior probability from the Bayesian analysis is given above the branch leading to each node, and the maximum likelihood bootstrap value is given below that branch. Circled numbers correspond to recommended changes described in the text. Names along the backbone represent the subfamily classification proposed in Burns *et al.* (2014). Names at terminals correspond to classification alternative 1 (from Table 1). Names in parentheses are used in Clements *et al.* (2015). Sister clades and polytomies are arranged from least to most speciose.



**FIGURE 2.** Maximum clade credibility tree from the Bayesian analyses of Burns *et al.* (2014). Subfamilies Coerebinae and Tachyphoninae shown. Labeling and format as in Fig. 1.



**FIGURE 3.** Maximum clade credibility tree from the Bayesian analyses of Burns *et al.* (2014). Subfamilies Sporophilinae and Poospizinae shown. Labeling and format as in Fig. 1.

In total, we recommend the following 32 changes to reconcile the new tree's topology with the classification of tanagers in accord with alternative 1. Each numbered recommendation is indicated on the best estimate of tanager phylogeny (Figs. 1–5):

1. Recognize a monospecific *Rhopospina* Cabanis, 1851 (type = *Fringilla fruticeti* Kittlitz, 1833, currently *Phrygilus fruticeti*), for *Phrygilus fruticeti* (Fig. 1). Because *Rhopospina* is feminine in gender and *Phrygilus* is masculine, the subspecies *Phrygilus fruticeti peruvianus* Zimmer, 1924, becomes *Rhopospina fruticeti peruviana*.

Comments. *Phrygilus* is polyphyletic, and the type species of *Phrygilus* (*P. gayi*) is distantly related to several species of *Phrygilus* (Burns *et al.* 2014, Fig. 4). Thus, a new genus-level taxonomy is needed for *P. fruticeti* as well as several other species of *Phrygilus* (see recommendations 2, 22, and 24 below).

2. Recognize *Corydospiza* Sundevall, 1872 [type = *Fringilla alaudina* Kittlitz, 1833, currently *Phrygilus alaudinus* (Kittlitz, 1883)], for *Phrygilus carbonarius* d'Orbigny & Lafresnaye, 1837, and *P. alaudinus* (Kittlitz, 1833) (Fig. 1). Because *Corydospiza* is feminine in gender and *Phrygilus* is masculine, the name *Phrygilus carbonarius* becomes *Corydospiza carbonaria*, *P. alaudinus* becomes *C. alaudina*, *P. a. alaudinus* becomes *C. a. alaudina*, *P. a. alaudinus* 

*bipartitus* Zimmer, 1924, becomes *C. a. bipartita*, and *P. a. excelsus* Berlepsch, 1907, becomes *C. a. excelsa*. Other subspecific names in this genus are invariable.

- 3. Merge *Saltatricula* Burmeister, 1861 (type = *Saltator multicolor* Burmeister, 1860, currently *Saltatricula multicolor*), into *Saltator* Vieillot, 1816 (type = *Tanagra maxima* Statius Müller, 1776, currently *Saltator maximus*) (Fig. 1), reverting to the original.
- 4. Recognize *Pyrrhulagra* Bonaparte, 1850 (type = *Loxia portoricensis*) Daudin, 1800, currently *Loxigilla portoricensis*), for *Loxigilla portoricensis*, *Melopyrrha nigra* (Linnaeus, 1758), and *Loxigilla violacea* (Linnaeus, 1758) (Fig. 2).

Comments. Burns *et al.* (2014) recommended merging these three species into *Melopyrrha*. However, *Pyrrhulagra* Bonaparte, 1850, has priority over *Melopyrrha* Bonaparte, 1853 (type = *Loxia nigra* Linnaeus, 1758, currently *Melopyrrha nigra*), and cannot be considered a *nomen oblitum*. Having priority, *Pyrrhulagra* needs to be used for these species, as *Pyrrhulagra portoricensis*, *P. nigra*, and *P. violacea*.

- 5. Recognize a monospecific *Phonipara* Bonaparte, 1850 (type = *Loxia canora* Gmelin, 1789, currently *Tiaris canorus*), for *Tiaris canorus* (Fig. 2). Because *Phonipara* is feminine in gender and *Tiaris* is masculine, *Tiaris canorus* becomes *Phonipara canora*.
- 6. Merge *Tiaris bicolor* (Linnaeus, 1766) into *Melanospiza* Ridgway, 1897 (type = *Loxigilla richardsoni* Cory, 1886, currently *Melanospiza richardsoni*) (Fig. 2). Both *M. richardsoni* and *M. bicolor* share pink feet and legs and overall dark plumage without facial markings.
- 7. Asemospiza, new genus (Fig. 2)

Type species. Fringilla fuliginosa Wied, 1831, currently recognized as Tiaris fuliginosus.

Included species. *Asemospiza fuliginosa* (Wied, 1831) and *A. obscura* (d'Orbigny & Lafresnaye, 1837), the latter currently recognized as *T. obscurus*. Because the name *Asemospiza* is feminine in gender and *Tiaris* is masculine, the endings of the adjectival specific epithets change, as do the following adjectival subspecific names: *T. f. fuliginosus* becomes *A. f. fuliginosa*, *T. f. fumosus* (Lawrence, 1874) becomes *A. f. fumosa*, *T. o. obscurus* becomes *A. o. obscura*, and *T. o. pacificus* (Koepcke, 1963) becomes *A. o. pacifica*. Other subspecific names currently used in this genus are invariable.

Diagnosis. Like several other species within Coerebinae, these two species have small conical bills. However, neither *A. fuliginosa* nor *A. obscura* has the markings of many of these species. They lack the yellow facial markings found in *Tiaris olivaceus* and *Phonipara* or the greenish upperparts found in *Melanospiza bicolor* and *Loxipasser* Bryant, 1866. They also lack the orange to reddish facial markings of the bullfinches (*Pyrrhulagra portoricensis*, *P. violacea*, and *Loxigilla* Lesson, 1831), which are also conical-billed species classified in the Coerebinae. Instead, the two species of *Asemospiza* are mostly unmarked. Males of *A. fuliginosa* are uniformly black, but differ thus from the other species in Coerebinae that are mostly black: they lack the pink feet of *Melanospiza*, the white wing markings of *Pyrrhulagra nigra*, or the white undertail markings of *Geospiza*. Females of *A. fuliginosa* and *A. obscura* are similar to each other: both are unpatterned, mostly brown, and slightly darker above than below. In addition to these morphological characters, we have identified 10 unreversed molecular synapomorphies across two genes (numbered by their position in the gene alignment). These are, for cyt *b*: C147G, C195T, C325T, C358A, A417G, and C750T; for ND2: C211T, C345T, C367T, C507A. The two species are also the only members of the Coerebinae restricted to South America. Cladistically, we define this genus as the descendants of the common ancestor of *Asemospiza fuliginosa* and *A. obscura*.

Etymology. *Asemospiza* is formed from the Greek ἄσημος, "unmarked," in reference to the unstreaked drab plumage of the two component species, and Greek  $\sigma\pi$ ίζα, the chaffinch *Fringilla coelebs*, commonly used in ornithology in the coining of names of finch-like birds. Its gender is feminine, in accord with Greek grammar.

Comments. The genus *Tiaris* Swainson, 1827 (type = *Tiaris pusillus* Swainson, 1827, currently *Tiaris olivaceus*), includes five species representing four distinct clades within the subfamily Coerebinae (Fig. 2). No species or set of species of *Tiaris* forms an exclusive clade with the type species; hence we make this recommendation and recommendations 4, 5, and 6 above. Two of the five species, *T. fuliginosus* and *T. obscurus*,

form a strongly supported monophyletic group (PP = 1.0, ML bootstrap = 100%) and are geographic replacements of each other (Bates 1997). These two species form the sister clade to the Darwin's finches (PP = 1.0, ML bootstrap = 71%). Therefore, unless these two species are merged into a broad genus that includes all the Darwin's finches, a new genus is needed for their clade, and there being no generic name available, we provide *Asemospiza* for this purpose.

# 8. Islerothraupis, new genus (Fig. 2)

Type species. Tanagra cristata Linnaeus, 1766 (currently Tachyphonus cristatus).

Included species. *Islerothraupis cristata*, *I. luctuosa* (d'Orbigny & Lafresnaye, 1837), and *I. rufiventer* (Spix, 1825), currently recognized as *Tachyphonus cristatus*, *T. luctuosus*, and *T. rufiventer*. Because the name *Islerothraupis* is feminine in gender and *Tachyphonus* is masculine, the endings of two of the specific epithets change to *cristata* and *luctuosa*, as do the following subspecific names: *T. c. cristatus* becomes *I. c. cristata*, *T. c. cristatellus* Sclater, 1862, becomes *I. c. cristatella*, *T. c. brunneus* (Spix, 1825) becomes *I. c. brunnea*, *T. l. luctuosus* becomes *I. l. luctuosa*, and *T. l. nitidissimus* Salvin, 1870, becomes *I. l. nitidissima*. Other specific and subspecific names in this genus are invariable with respect to this change.

Diagnosis. Morphologically, males of these species share glossy black plumage that contrasts with a yellow to bright orange crest or crown patch, as well as a white shoulder patch (either on the outermost scapulars or the upperwing coverts). *Tachyphonus surinamus* has these characters as well; however, *T. surinamus* also has pectoral and flank patches that contrast with otherwise black undersides. Additionally, we have identified five unreversed molecular synapomorphies across three genes shared by the proposed *Islerothraupis* (numbered by their position in the gene alignment). These are, for cyt *b*: C348A and C360A; for ND2: A661T and T847G; for FGB-I5: C399T. Cladistically, we define this genus as the descendants of the common ancestor of *Islerothraupis cristata* and *Islerothraupis rufiventer*.

Etymology. We are pleased to name this clade for Morton L. and Phyllis R. Isler, who published the definitive work on tanagers (Isler & Isler 1999). This detailed, illustrated monograph is an exhaustive treatment of species classified in the Thraupidae at the time, including their identification, ecology, distribution, habitat, and behavior. Although the Islers' more recent work has been on antibrds (e.g., Isler *et al.* 1998, 2007, 2014; Zimmer & Isler 2003), their tanager monograph remains a testament of their dedication to expanding our knowledge of Neotropical birds. We form the genus name from their last name, Isler, and the Greek  $\theta \rho \alpha u \pi i \varsigma$ , "a kind of finch mentioned by Aristotle" (Jobling 2010:385), commonly used in ornithology to coin tanager names. Its gender is feminine.

Comments. Molecular phylogenies (Burns & Racicot 2009; Burns *et al.* 2014) show that all species of the traditional genus *Tachyphonus* Vieillot, 1816, belong to the subfamily Tachyphoninae; however, the genus is polyphyletic with respect to the genera *Eucometis* Sclater, 1856, *Trichothraupis* Cabanis, 1850, *Coryphospingus* Cabanis, 1851, *Rhodospingus* Sharpe, 1888, *Lanio* Vieillot, 1816, and *Ramphocelus* Desmarest, 1805 (Fig. 2). *Tachyphonus cristatus*, *T. luctuosus*, and *T. rufiventer* form a strongly supported clade (PP = 1.0; ML bootstrap = 100%) that is not closely related to the type species of *Tachyphonus* (*Tangara rufa* Boddaert, 1783, currently recognized as *Tachyphonus rufus*). Instead, the clade containing *Tachyphonus cristatus*, *T. luctuosus*, and *T. rufiventer* is the sister clade to a clade containing the two monospecific genera *Eucometis* and *Trichothraupis*. Support for this placement is high (PP = 1.0; ML bootstrap = 100%). Unless a broad genus containing all five of these species is used, a new generic name is needed for the group that includes *T. cristatus*, *T. luctuosus*, and *T. rufiventer*. Accordingly, we provide *Islerothraupis* for this purpose.

#### 9. Maschalethraupis, new genus (Fig. 2)

Type species. Turdus surinamus Linnaeus, 1766 (currently Tachyphonus surinamus).

Included species. Monospecific; includes only *Maschalethraupis surinamus*, currently recognized as *Tachyphonus surinamus*. The name *Maschalethraupis* is feminine, but *surinamus*, which lacks a Latin ending that unambiguously identifies the word as an adjective, may be construed as either an adjective or a noun in apposition, and so should be treated as a noun and left unchanged (Article 31.2.2 of the International Code of Zoological Nomenclature 1999). None of the name endings of the subspecies of *M. surinamus* recognized by Hellmayr (1936) or Storer (1970) is affected by reclassification in *Maschalethraupis*.

Diagnosis. This genus is diagnosed by the species characters of *Turdus surinamus* Linnaeus, 1766.

Etymology. The name is formed from the Greek μασχάλη, "armpit," alluding to the male's contrasting

underwing coverts and pectoral tuft emerging from under the bend of the wing, and Greek  $\theta\rho\alpha\nu\pi$ i $\varsigma$ , "a kind of finch mentioned by Aristotle" (Jobling 2010:385), commonly used in ornithology to coin tanager names. Its gender is feminine

Comments. In addition to *Islerothraupis*, two more generic names are needed to reconcile the polyphyly of *Tachyphonus* with a classification in which genera are monophyletic. *Tachyphonus surinamus* forms a strongly supported clade (PP = 1.0) with *Tachyphonus delatrii*, *Rhodospingus* (1 species), and *Lanio* (4 species) (Fig. 2). Burns *et al.* (2014) did not find strong support for the placement of *T. surinamus* within this morphologically diverse clade. Therefore, unless a broad genus containing all six of these species is used (and which would be exceptionally heterogeneous in terms of plumage and morphology), a new genus name is needed for *T. surinamus*. Accordingly, we provide *Maschalethraupis* for this purpose.

# 10. Chrysocorypha, new genus (Fig. 2)

Type species. Tachyphonus delatrii Lafresnaye, 1847.

Included species. Monospecific; includes only *Chrysocorypha delatrii*, currently recognized as *Tachyphonus delatrii*.

Diagnosis. This genus is diagnosed by the specific characters of *Tachyphonus delatrii* Lafresnaye, 1847.

Etymology. The name, feminine in gender, is formed from the Greek χρυσός, "gold," and Greek κορυφή, "crown" or "top of the head," in allusion to the male's tawny crest.

Comments. As explained in the previous section, *Tachyphonus delatrii* forms a strongly supported clade with *T. surinamus*, *Lanio*, and *Rhodospingus* (Fig. 2). As is the case with *T. surinamus*, molecular phylogenies indicate that *T. delatrii* is not closely related to any one of these species in particular. Thus, unless a broad and exceptionally heterogeneous genus subsumes all six species involved, a new generic name is needed for *T. delatrii*. Accordingly, we provide *Chrysocorypha* for this purpose.

# 11. Poospizinae, new subfamily (Fig. 3)

Type genus. Poospiza Cabanis, 1847.

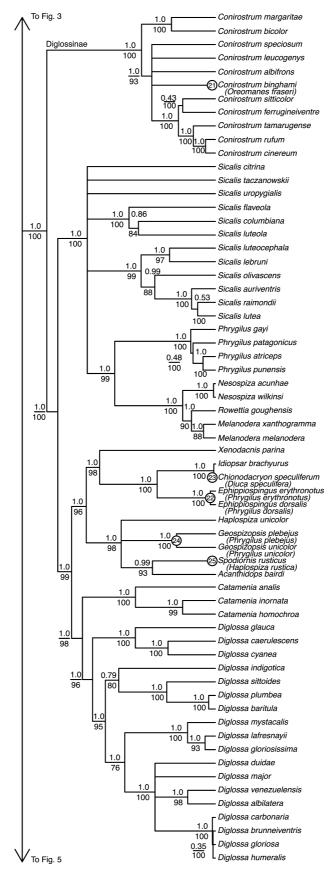
Included genera. *Cnemoscopus* Bangs & Penard, 1919, *Compsospiza* Berlepsch, 1893, *Cypsnagra* Lesson, 1831, *Donacospiza* Cabanis, 1851, *Hemispingus* Cabanis, 1851, *Nephelornis* Lowery & Tallman, 1976, *Piezorina* Lafresnaye, 1843, *Poospiza* Cabanis, 1847, *Pyrrhocoma* Cabanis, 1851, *Thlypopsis* Cabanis, 1851, *Urothraupis* Taczanowski & Berlepsch, 1885, *Xenospingus* Cabanis, 1867.

Diagnosis. We do not know any morphological characters that unite this diverse group. Instead, we have identified seven unreversed molecular synapomorphies across four genes. These are, for ND2: C1003A; for ACO1: A768G; for MBI2: G110A and T190C; for RAG1: T253C, C568G and A1984G. Cladistically, we define this subfamily as the descendants of the common ancestor of *Xenospingus concolor* and *Poospiza melanoleuca*.

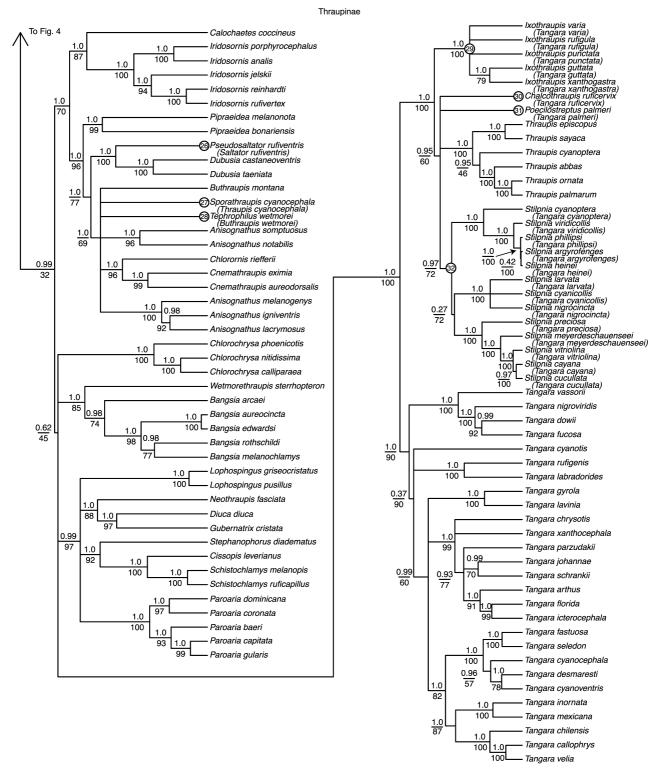
Comments. This subfamily name was originally used by Wolters (1980), but as he provided no description it is there a *nomen nudum*. Although Burns *et al.* (2014) described this subfamily, they failed to explicitly designate Poospizinae as a new subfamily name. Here we correct this omission and indicate Poospizinae as a new subfamily.

The genus names used within this subfamily require extensive revision. In particular, the large genera *Hemispingus* Cabanis, 1851, and *Poospiza* Cabanis, 1847, are polyphyletic with respect to each other and with respect to eight other genera (Fig. 3). Thus, we make recommendations 12 to 20 below to bring the classification of this subfamily into alignment with the topology of our phylogenetic tree.

- 12. Recognize *Pseudospingus* Berlepsch & Stolzmann, 1896 (type = *Dacnis xanthophthalma* Taczanowski, 1874, currently *Hemispingus xanthophthalmus*), for *Hemispingus xanthophthalmus* and *H. verticalis* (Lafresnaye, 1840) (Fig. 3), as *Pseudospingus xanthophthalmus* and *P. verticalis*.
- 13. Merge two species of *Hemispingus* [*Hemispingus rufosuperciliaris* Blake & Hocking, 1974, and *H. goeringi* (Sclater & Salvin, 1871)] and the two species of *Compsospiza* Berlepsch, 1893 (type = *Compsospiza garleppi* Berlepsch, 1893) into a more restricted *Poospiza* (type = *Emberiza nigrorufa* d'Orbigny & Lafresnaye, 1837, currently *Poospiza nigrorufa*) than is currently recognized, as *Poospiza rufosuperciliaris*, *P. goeringi*, *P. baeri*, and *P. garleppi*. In addition to the above four species, this revised version of *Poospiza* includes the following five species currently recognized as belonging to *Poospiza*: *P. hispaniolensis* Bonaparte, 1850, *P. rubecula* Salvin, 1895, *P. nigrorufa*, *P. boliviana* Sharpe, 1888, and *P. ornata* (Landbeck, 1865).



**FIGURE 4.** Maximum clade credibility tree from the Bayesian analyses of Burns *et al.* (2014). Subfamily Diglossinae shown. Labeling and format as in Fig. 1.



**FIGURE 5.** Maximum clade credibility tree from the Bayesian analyses of Burns *et al.* (2014). Subfamily Thraupinae shown. Labeling and format as in Fig. 1.

Comments. Burns *et al.* (2014) recommended a different approach for the taxonomy of this clade. They advocated restricting *Poospiza* to *P. boliviana*, *P. ornata*, and *P. nigrorufa* only, retaining *Compsospiza*, applying the available name *Orospingus* Riley, 1922, to *Hemispingus goeringi* and *H. rufosuperciliaris*, and creating two new generic names, one for *Poospiza hispaniolensis* and one for *Poospiza rubecula*. In this paper, we present an alternative, simpler approach that does not require two additional new generic names.

# 14. Kleinothraupis, new genus (Fig. 3)

Type species. Arremon atropileus Lafresnaye, 1842 (as "atro-pileus," currently Hemispingus atropileus).

Included species. *Kleinothraupis reyi* (Berlepsch, 1895), *K. atropileus* (Lafresnaye, 1842), *K. calophrys* (Sclater & Salvin, 1876), and *K. parodii* (Weske & Terborgh, 1974) (currently recognized as *Hemispingus reyi*, *H. atropileus*, *H. calophrys*, and *H. parodii*).

Diagnosis. Morphologically, three of these species (*K. atropileus*, *K. calophrys*, and *K. parodii*) share a superciliary stripe. *K. reyi* lacks this character, but has similar, carotenoid-based plumage (Shultz & Burns 2013). The sequence of *K. reyi* reported in Burns *et al.* (2014) is only a 200 base pair fragment of cyt *b* sequenced from a toe pad. Thus, we have less confidence in the placement of *K. reyi* in this genus, but tentatively place it here because of its carotenoid coloration, the topology of the phylogenetic tree (Fig. 3), and the high posterior probability supporting this clade. Cyt *b* is the only gene sampled from all four species in this clade, and the 200 base pair section in common does not show any unreversed synapomorphies. Two species, *K. atropileus* and *K. calophrys*, were both sampled for ND2 and have three unreversed synapomorphies (numbered by their position in the gene alignment): C114A, A810T, and A991G. Cladistically, we define this genus as the descendants of the common ancestor of *Kleinothraupis calophrys* and *K. atropileus*.

Etymology. We are pleased to name this genus for Nedra K. Klein (1951–2001), an avian systematist and evolutionary biologist (Hackett 2002, 2004). Nedra published several papers involving tanagers (Seutin *et al.* 1994; Burns *et al.* 2002, 2003), though she was probably best known for her work on wood-warblers (Parulidae) (e.g., Klein & Brown 1994; Klein *et al.* 2004). Given that she worked on both tanagers and warblers, and given the morphological similarity of the species in this genus to warblers, we are pleased to name this genus in her honor. The genus name is formed from Nedra's surname (Klein) and the Greek θραυπίς. The name *Kleinothraupis* is feminine in gender. The only specific or subspecific epithet affected by reclassification in *Kleinothraupis* is *atropileus intermedius* Carriker, 1934, listed by Storer (1970) as a synonym of *Hemispingus a. auricularis*; if recognized, it becomes *K. a. intermedia*. The name *atropileus* is a noun in apposition and invariable.

Comments. The clade containing *Hemispingus reyi*, *H. atropileus*, *H. calophrys*, and *H. parodii* is strongly supported (PP = 0.98) and is the sister clade to a large clade containing 24 species in eight currently recognized genera. Unless a broad genus that includes both clades is recognized, a new generic name is needed for the first clade (*Hemispingus reyi*, *H. atropileus*, *H. calophrys*, *H. parodii*). Accordingly, we provide *Kleinothraupis* for this purpose.

Some classifications (Hilty *et al.* 2011; Dickinson & Christidis 2014) treat the two subspecies of *Kleinothraupis atropileus* (*K. a. atropileus* and *K. a. auricularis*) as species (*K. atropileus* and *K. auricularis*), though Clements *et al.* (2015) treated them as subspecies. Therefore, although our sample represents *K. a. auricularis*, we list it as *K. atropileus*. García-Moreno & Fjeldså (2003) sequenced ND2 from both forms and found *K. auricularis* to be sister to a clade containing *K. atropileus* and *K. parodii*. Thus, regardless of whether these taxa are treated as subspecies or species, both belong in *Kleinothraupis*.

15. Recognize *Sphenopsis* Sclater, 1862 (type = *Sphenopsis ignobilis* Sclater, currently *Hemispingus frontalis*), for *Hemispingus melanotis* (Sclater, 1855) and *H. frontalis* (Tschudi, 1844) (Fig. 3), as *Sphenopsis melanotis* and *S. frontalis*.

Comments. Burns *et al.* (2014) recommended using *Sphenops* Sclater, 1861, for this clade, but the original spelling of this genus is *Sphenopsis* Sclater, 1860, *Sphenops* being an unnecessary emendation.

16. Merge *Pyrrhocoma* Cabanis, 1851 (type = *Tachyphonus ruficeps* Strickland, 1844, currently *Pyrrhocoma ruficeps*), and *Hemispingus superciliaris* Cabanis, 1851 (type = *Arremon superciliaris* Lafresnaye, 1840), into *Thlypopsis* Cabanis, 1851 (type = *Nemosia fulvescens* Strickland, 1844, a junior synonym of *Nemosia sordida* d'Orbigny & Lafresnaye, 1837, currently *Thlypopsis sordida*) (Fig. 3). For *H. superciliaris*, the name becomes *Thlypopsis superciliaris*; see below for a new name for *Pyrrhocoma*.

Comments. *Hemispingus superciliaris* and the sole species of *Pyrrhocoma* are embedded within a strongly supported clade (PP = 1.0, ML bootstrap = 80) containing all six species of *Thlypopsis*. The type species of each of these three genera are contained within this clade. Therefore, maintaining all three names would require naming several additional new genera. Instead, we recommend merging all the species in this clade into a single genus. All three genera were proposed simultaneously in the same publication. Because most of the species in this clade

belong to *Thlypopsis*, we act as first revisers in selecting *Thlypopsis* Cabanis, 1851, to take precedence over *Pyrrhocoma* Cabanis, 1851, and *Hemispingus* Cabanis, 1851, as the name of this genus. When *Pyrrhocoma* is merged with *Thlypopsis*, *Pyrrhocoma ruficeps* Strickland, 1844, becomes a junior homonym of *Thlypopsis ruficeps* d'Orbigny & Lafresnaye, 1837. Therefore, we introduce the following replacement name for *Pyrrhocoma ruficeps* when it is included in the genus *Thlypopsis*:

# 17. Thlypopsis pyrrhocoma, new name (Fig. 3)

Type. Pyrrhocoma ruficeps Strickland, 1844

Included taxa. Monotypic; includes only Pyrrhocoma ruficeps. No subspecies of this species are recognized.

Etymology. The name is formed from the Greek  $\pi$ ύρρος, "flame-colored" or "red," as applied to hair, and the Greek κόμη, "hair of the head," in allusion to the male's rufous head. The name is to be construed as a noun in apposition. We intend adoption of the former generic name as the new specific epithet to communicate past taxonomic connections.

18. Recognize *Poospizopsis* Berlepsch, 1893 (type = *Poospiza caesar* Sclater & Salvin, 1869), for *Poospiza caesar* and *P. hypochondria* (d'Orbigny & Lafresnaye, 1837) (Fig. 3), which now become *Poospizopsis caesar* and *Poospizopsis hypochondria*.

#### 19. Castanozoster, new genus (Fig. 3)

Type species. Fringilla thoracica Nordmann, 1835 (currently Poospiza thoracica).

Included species. Monospecific; includes only *Castanozoster thoracicus*, currently recognized as *Poospiza thoracica*. Because the name *Castanzoster* is masculine in gender and *Poospiza* is feminine, the ending of the adjectival specific epithet changes.

Diagnosis. This genus is diagnosed by the specific characters of Fringilla thoracica Nordmann, 1835.

Etymology. The name is formed from the Greek καστανό ("chestnut," both the nut and the color) and Greek ζωστήρ ("belt"), alluding to the bold chestnut band across the bird's breast and down its flanks. Its gender is masculine.

Comments. *Poospiza thoracica* belongs to a clade of 14 other species representing six currently recognized genera in traditional classifications. Burns *et al.* (2014) did not find strong support for the placement of *P. thoracica* within this clade. Thus, unless a broad genus including all 14 of these species is recognized, a new generic name is needed for *P. thoracica*. Accordingly, we provide *Castanozoster* for this purpose.

20. Recognize *Microspingus* Taczanowski, 1874 (type species = *Microspingus trifasciatus* Taczanowski, 1874, currently *Hemispingus trifasciatus*), for *Hemispingus trifasciatus* and merge *Poospiza cabanisi* Bonaparte, 1850, *P. lateralis* (Nordmann, 1835), *P. erythrophrys* Sclater, 1881, *P. alticola* Salvin, 1895, *P. torquata* (d'Orbigny & Lafresnaye, 1837), *P. cinerea* Bonaparte, 1850, and *P. melanoleuca* (d'Orbigny & Lafresnaye, 1837) into *Microspingus* (Fig. 3) as *M. cabanisi*, *M. lateralis*, *M. erythrophrys*, *M. alticola*, *M. torquatus*, *M. cinereus*, and *M. melanoleucus*. Because the name *Microspingus* is masculine in gender and *Poospiza* is feminine, the adjectival specific names *P. torquata*, *P. cinerea*, and *P. melanoleuca* become *M. torquatus*, *M. cinereus*, and *M. melanoleucus*, respectively. Gender endings for additional names of subspecies recognized by Storer (1970) are not affected by the reclassification of these species in *Microspingus*.

Comments. Burns *et al.* (2014) did not include *P. lateralis* (Nordmann, 1835) among the species they sampled. *Poospiza cabanisi* was recently split from *P. lateralis* (Assis *et al.* 2007); thus, the two species are likely closely related. Therefore, we suggest placing *P. lateralis* in *Microspingus*, pending further systematic analysis.

# 21. Merge Oreomanes Sclater, 1860, into Conirostrum d'Orbigny & Lafresnaye, 1838 (Fig. 4).

Comments. As discussed in Burns et al. (2014), Oreomanes fraseri is best viewed as a specialized Conirostrum, a finding previously suggested by the hybridization of Oreomanes and Conirostrum ferrugineiventre (Schulenberg 1985). If Oreomanes is merged into Conirostrum, Oreomanes fraseri Sclater, 1860 becomes a junior homonym of Conirostrum cinereum fraseri Sclater, 1859. Therefore, a different name needs to be applied to Oreomanes fraseri. Oreomanes binghami Chapman, 1919, is the next oldest name available for the species, and we accordingly apply that name to the species currently known as Oreomanes fraseri, which now becomes Conirostrum binghami.

# 22. Ephippiospingus, new genus (Fig. 4)

Type species. Phrygilus dorsalis Cabanis, 1883.

Included species. *Ephippiospingus dorsalis* (Cabanis, 1883) and *Ephippiospingus erythronotus* (Philippi & Landbeck, 1861), currently recognized as *Phrygilus dorsalis* and *Phrygilus erythronotus*.

Diagnosis. In at least some plumages, these two species share an upper back and mantle that are colored differently from the rest of the body, giving a saddle-like appearance. In adult *E. dorsalis*, the saddle is rufous, but in juveniles, the saddle is duller and streaked. Juveniles of *E. erythronotus* are similar to juveniles of *E. dorsalis* with a brown back contrasting with mostly gray plumage. Adults of *E. erythronotus* have slate gray backs. Additionally, we have identified 47 unreversed molecular synapomorphies across six genes (numbered by their position in the gene alignment). These are, for cyt *b*: T161C, C228T, C237T, C289T, A291T, A366C, C372G, C384T, A402T, A414G, A444G, C462T, C577A, and C660T; for ND2: A31T, C37T, A61A, C147T, C156G, G202A, A225G, A234C, A252G, C378T, C381G, A447G, A475G, A528G, T584C, A589G, A672G, A690G, A810A, A834G, G953T, C958T, and C987A; for ACO1: C310T and C409Y; for FGB-I5: G190A, and A272G; for MB-I2: G475C; for RAG1: A183G, T205C, C1198T, T1723C, and T2425G. Cladistically, we define this genus as the descendants of the common ancestor of *Ephippiospingus dorsalis* and *Ephippiospingus erythronotus*.

Etymology. The name is formed from the Greek ἐφιππιον ("saddle") and Greek σπίγγος ("finch"), alluding to the contrasting rufous saddle on the back of *E. dorsalis* and the juvenile of *E. erythronotus* (whose name means "red-backed").

Comments. The traditional genus *Phrygilus* (the sierra-finches) is one of the most polyphyletic of all tanagers (Campagna *et al.* 2011; Burns *et al.* 2014). Among the sierra-finches, *P. dorsalis* and *P. erythronotus* form a strongly supported clade (PP = 1.0; ML bootstrap 100%) within the subfamily Diglossinae (Fig. 4). The type species of *Phrygilus* (*Fringilla gayi* Gervais, 1834, currently *Phrygilus gayi*) is also a member of the subfamily Diglossinae but is not closely related to *P. dorsalis* or *P. erythronotus*. Instead, these two species form a clade with *Diuca speculifera* (d'Orbigny & Lafresnaye, 1837) and *Idiopsar brachyurus* Cassin, 1867 (Fig. 4). The clade containing these four species is strongly supported (PP = 1.0, ML bootstrap = 100%); thus, all four species could be merged into a single genus, and *Idiopsar* would be the appropriate generic name to apply for this purpose (see discussion of *Diuca* in the next section). However, the four species are more diverse behaviorally and morphologically than is typical of genera currently used in the Thraupidae. In particular, *Idiopsar brachyurus* has a large, pointed bill that it uses to probe lichen and moss on boulders and *Polylepis* trees (Lloyd *et al.* 2005). Thus we propose maintaining *Idiopsar*, placing *Diuca speculifera* in a separate genus (see number 23 below), and applying a new generic name to the two sierra finches in this clade. Accordingly, we provide *Ephippiospingus* for the last two species.

#### 23. Chionodacryon, new genus (Fig. 4)

Type species. *Emberiza speculifera* d'Orbigny & Lafresnaye, 1837 (currently recognized as *Diuca speculifera*).

Included species. Monospecific, includes only *Chionodacryon speculiferum*. Because the name *Chionodacryon* is neuter in gender and *Diuca* is feminine, the ending of the adjectival specific epithet changes to agree, as does that of the subspecies *D. s. magnirostris*, which becomes *C. s. magnirostre*.

Diagnosis. This genus is diagnosed by the specific characters of *Emberiza speculifera* d'Orbigny & Lafresnaye, 1837.

Etymology. The name is formed from the Greek χιών ("snow") and Greek δάκρυον ("teardrop"), alluding to the large white spot below the bird's eye, one of the characters distinguishing *Chionodacryon speculiferum* from *Diuca diuca*. Its gender is neuter.

Comments. Burns *et al.* (2014) showed that the two species currently placed in *Diuca* are distantly related with *D. diuca* (Molina, 1782) in the Thraupinae and *D. speculifera* in the Diglossinae. The discovery that *D. diuca* and *D. speculifera* are not sister taxa leads to a nomenclatural conundrum. In introducing the generic name *Diuca*, Reichenbach (1850) illustrated the bill, head, tail, outer primaries, and foot but did not describe any characters as diagnostic, list any species, or designate a type species. Under Article 12.2.7 of the International Code of Zoological Nomenclature (ICZN 1999), generic names proposed in this way before 1931 may be available, and many of Reichenbach's names introduced similarly in the same work, *Avium Systema Naturale*, have been used continuously since 1850. In 1851, Cabanis (p. 135) proposed the name *Hedyglossa* as a substitute for *Diuca*, listing

*Diuca* as a synonym and listing *diuca* alone, not *speculifera*, as a component species. In 1855, Gray (p. 79) listed *Hedyglossa* as a synonym of *Diuca* instead and explicitly designated *speculifera* as type species of the latter.

The necessity of allocating *diuca* and *speculifera* to different genera reopens the question of the type species of *Diuca* because the species that is not the type may require a new genus. The issue is resolved by Article 67.2 of the International Code of Zoological Nomenclature (ICZN 1999), hereafter the Code. In the first explicit assignment of species to either of the relevant genera *Diuca* Reichenbach and *Hedyglossa* Cabanis, Cabanis (1851: 135) listed only one, *Fringilla diuca* Molina, 1782, which applies to both generic names, irrespective of Cabanis's treating *Diuca* as a synonym of *Hedyglossa*. Under Article 67.2.2 of the Code, *Fringilla diuca* thus becomes the only species eligible for fixation as the type for either of these generic names, effectively by monotypy (Article 69.3). Consequently, Gray's (1855) subsequent designation of *speculifera* as type species of *Diuca* is irrelevant, and if *speculifera* is to be assigned to a monospecific genus, a new generic name is needed for it. Accordingly we provide *Chionodacryon* here.

- 24. Recognize *Geospizopsis* Bonaparte, 1856 (type = *Passerculus geospizopsis* Bonaparte, 1853, currently considered a subspecies of *Phrygilus unicolor*), for *Phrygilus unicolor* (d'Orbigny & Lafresnaye, 1837) and *P. plebejus* Tschudi, 1844 (Fig. 4), which become *Geospizopsis unicolor* and *G. plebejus*.
- 25. Recognize a monospecific *Spodiornis* Sclater, 1866 (type = *Spodiornis jardinii* Sclater, 1866, a junior synonym of *Phrygilus rusticus* Tschudi, 1844, currently *Haplospiza rustica*), for *Haplospiza rustica* (Fig. 4). Because the name *Spodiornis* is masculine in gender and *Haplospiza* is feminine, the ending of adjectival specific epithets changes to agree: *H. rustica* becomes *S. rusticus*, *H. r. rustica* becomes *S. r. rusticus*, and *H. r. arcana* (Wetmore & Phelps, 1949) becomes *S. r. arcanus* (the last as originally described).
- 26. Pseudosaltator, new genus (Fig. 5).

Type species. Saltator rufiventris d'Orbigny & Lafresnaye, 1837.

Included species. Monospecific, includes only *Pseudosaltator rufiventris*.

Diagnosis. This genus is diagnosed by the specific characters of *Saltator rufiventris* d'Orbigny & Lafresnaye, 1837.

Etymology. The name is formed from the Greek ψευδής (false) and the generic name *Saltator*, alluding to the mistaken classification of this species in that genus. Its gender is masculine.

Comments. Several studies (Klicka *et al.* 2007; Barker *et al.* 2013; Burns *et al.* 2014) show that *Saltator rufiventris* is not closely related to other members of that genus. Burns *et al.* (2014) placed it within the subfamily Thraupinae as sister to two species of *Dubusia* with high support (PP = 1.0; ML bootstrap = 100%; Fig. 5). In addition, *S. rufiventris* is more similar in geographic range, plumage, and bill characteristics to *Dubusia* than it is to the other members of *Saltator*. The type species of the genus *Saltator* (*Tanagra maxima* Statius Müller, 1776, currently recognized as *Saltator maximus*) belongs to the clade containing the rest of the saltators. Thus *S. rufiventris* must be assigned to a different genus. Unless *S. rufiventris* and the two species of *Dubusia* are merged into a broader *Dubusia*, a new generic name needs to be applied to *S. rufiventris*. Accordingly, we provide *Pseudosaltator* for this purpose.

- 27. Recognize a monospecific *Sporathraupis* Ridgway, 1898 (type = *Aglaia cyanocephala* d'Orbigny & Lafresnaye, 1837, currently *Thraupis cyanocephala*), for *Thraupis cyanocephala* (Fig. 5), as *Sporathraupis cyanocephala*.
- 28. Recognize a monospecific *Tephrophilus* Moore, 1934 (type = *Tephrophilus wetmorei* Moore, 1934, currently *Buthraupis wetmorei*), for *Buthraupis wetmorei* (Fig. 5).
- 29. Recognize *Ixothraupis* Bonaparte, 1851 (type species = *Tanagra punctata* Linnaeus, 1766, currently *Tangara punctata*), for *Tangara punctata*, *T. varia* (Statius Müller, 1776), *T. rufigula* (Bonaparte, 1851), *T. xanthogastra* (Sclater, 1851), and *T. guttata* (Cabanis, 1850) (Fig. 5), which now become *Ixothraupis punctata*, *I. varia*, *I. rufigula*, *I. xanthogastra*, and *I. guttata*.

30. Recognize a monospecific *Chalcothraupis* Bonaparte, 1851 (type species = *Tanagra ruficervix* Prévost & Des Murs, 1846, currently *Tangara ruficervix*), for *Tangara ruficervix* (Fig. 5), as *Chalcothraupis ruficervix*.

#### 31. *Poecilostreptus*, new genus (Fig. 5).

Type species. Calospiza palmeri Hellmayr, 1909 (currently Tangara palmeri).

Included species. *Poecilostreptus palmeri* and *P. cabanisi* (Sclater, 1868), currently recognized as *Tangara palmeri* and *T. cabanisi*. Although the name *Poecilostreptus* is masculine in gender and *Tangara* is feminine, reassignment of these species to *Poecilostreptus* does not entail any changed ending in a specific epithet.

Diagnosis. Both species in this genus have black spots on their foreparts forming a collar, as well as black lores and a black forehead. Although widely separated geographically, the two species also share similarities in habitat and voice (Isler & Isler 1999).

Etymology. *Poecilostreptus* is formed from the Greek ποικίλος ("spotted" or "dappled") and στρεπτός ("collar"), alluding to the pattern of black spots across a whitish chest shared by *P. palmeri* and *P. cabanisi*.

Comments. The genus *Tangara* Brisson, 1760, as currently recognized, is the largest genus of Neotropical birds. Sedano & Burns (2009) and Burns *et al.* (2014) showed that some members of the genus *Thraupis* Boie, 1826, including the type species *T. episcopus* (Linnaeus, 1766), are embedded within *Tangara*. Both Sedano & Burns (2009) and Burns *et al.* (2014) suggested merging these species of *Thraupis* into *Tangara*, enlarging the genus to 55 species. However, this suggestion has not been widely adopted, likely because of reluctance to recognize a genus larger than is conventional for Class Aves, as well as the larger body size of these *Thraupis* species relative to *Tangara*. Therefore, we now propose dividing the large clade encompassing *Thraupis* and *Tangara* into smaller genera. For some of these clades, names are available (see 29, 30). However, *Tangara palmeri* and its presumed sister *T. cabanisi* require a new generic name if the genus *Thraupis* is to be preserved. *T. palmeri* belongs to a clade including these *Thraupis* species as well as 14 other species of *Tangara*. However, Burns *et al.* (2014) did not find strong support for the placement of *T. palmeri* within this clade. Thus, unless a broad genus is recognized to include these *Thraupis* species and some or all of the species currently in the genus *Tangara*, a new genus name needs to be erected for *T. palmeri* and its presumed sister *T. cabanisi* (see below). Accordingly, we provide *Poecilostreptus* for this purpose.

Burns *et al.* (2014) did not sample *Tangara cabanisi*, the presumed sister taxon to *T. palmeri*. These two species are similar in plumage, habitat, and voice (Isler & Isler 1999, Hilty *et al.* 2011), and Isler & Isler (1999) considered them to belong to the same species group. Thus, at least until genetic data addressing the position of *T. cabanisi* are obtained, we recommend including it in *Poecilostreptus*.

# 32. *Stilpnia*, new genus (Fig. 5).

Type species. Aglaia cyanoptera Swainson, 1834 (currently recognized as Tangara cyanoptera).

Included species. *Stilpnia larvata* (du Bus, 1846), *S. nigrocincta* (Bonaparte, 1838), *S. cyanicollis* (d'Orbigny & Lafresnaye, 1837), *S. preciosa* (Cabanis, 1850), *S. peruviana* (Desmarest, 1806), *S. meyerdeschauenseei* (Schulenberg & Binford, 1985), *S. vitriolina* (Cabanis, 1850), *S. cucullata* (Swainson, 1834), *S. cayana* (Linnaeus, 1766), *S. cyanoptera* (Swainson, 1834), *S. viridicollis* (Taczanowski, 1884), *S. phillipsi* (Graves & Weske, 1987), *S. argyrofenges* (Sclater & Salvin, 1876), and *S. heinei* (Cabanis, 1850) (Fig. 5). These species are currently placed in the genus *Tangara* Brisson, 1760. Although Burns *et al.* (2014) did not sample *T. peruviana*, the morphological similarities between this species and *T. preciosa* (Isler & Isler 1999, Hilty *et al.* 2011) imply that *T. peruviana* also belongs to this genus.

Diagnosis. Morphologically, these species can be separated from other members of the genus *Tangara* by their plumage patterns. Most species have either a cap or a hood that is set apart from the rest of the plumage. A black crown or cap is present in *S. cyanoptera*, *S. viridicollis*, *S. phillipsi*, *S. argyrofenges*, and *S. heinei*. In addition, all of these species except for *S. cyanoptera* have green or gold ear coverts and throats. In addition, females of all five of these species have dusky caps that contrast with green backs (Graves & Weske 1987; Isler & Isler 1999). A rufous crown or cap is present in *S. preciosa*, *S. vitriolina*, *S. cucullata*, and *S. cayana*. Although the crown of *S. meyerdeschauenseei* is not similarly rufous, it appears buffy and differs in color from the rest of the back (Schulenberg & Binford 1985). The three remaining species (*S. larvata*, *S. nigrocincta*, and *S. cyanicollis*) have blue or golden hoods that contrast with their black mantles, breasts, and eye masks (Isler & Isler 1999). Additionally, we have identified five molecular synapomorphies for cyt *b* (numbered by their position in the gene

alignment): C12T, A72G, A210G, C774A, and T801C. Cladistically, we define this genus as the descendants of the common ancestor of *Stilpnia cyanoptera* and *Stilpnia cucullata*.

Etymology. The name, feminine in gender, is derived from the Greek  $\sigma\tau\iota\lambda\pi\nu\eta$ , the feminine form of the adjective meaning "glittering" or "glistening," alluding to the glossiness of the plumage of these colorful tanagers. Comments. *Euschemon* Sclater, 1851 (type species *Tanagra flava* Gmelin, 1789, currently *Tangara cayana flava*), is preoccupied by *Euschemon* Doubleday, 1846, the name of an Australian butterfly, and so not available.

#### **Discussion**

The new molecular phylogenies present an opportunity to classify tanagers on the basis of character-based data and the criterion of monophyly for the first time. Our 32 recommended changes result in a classification (Table 1, alternative 1) in which all genera are monophyletic (Figs. 3–5). Compared to currently used classifications (e.g., Clements et al. 2015), it contains more genera (111 vs. 92), but roughly the same percentage of monospecific genera (48% vs. 46%). A total of 73 species would be assigned to a different genus, either a newly proposed name (32), a resurrected name (32), or lumped into an existing genus (9). A classification that includes broader genera (Table 1, alternative 2) results in fewer generic names (64) and a lower percentage of monospecific genera (24%). However, 97 species would have different generic names under this scheme. Of the two classifications, we firmly recommend alternative 1 and treat all new generic and replacement specific names introduced under it in this paper as valid (Article 11.5 of the Code). However, a hybrid approach might also be adopted, with aspects of one of these classifications used for some parts of the tree and aspects of the other classification used for others. Regardless, we consider that the classification presented by alternative 1 in this paper is the best possible at this time, and preferable to any of the current classifications which comprise numerous polyphyletic and paraphyletic genera. Whatever the approach to generic classification used by taxonomic authorities in the future, the names and recommendations provided here will allow such classifications to be reconciled with phylogeny and promote more accurate study of this remarkable Neotropical radiation.

**TABLE 1.** Sequential, linear classification of all tanagers. Current species-level taxonomy is taken from Clements *et al.* (2015). Species are arranged according to the phylogenetic structure of the tree (Figs. 1–5), starting from its base. For sister clades and polytomies, less speciose clades are listed first. Asterisks indicate species unsampled by Burns *et al.* (2014) and are placed in their most likely position, given available data. Double asterisks indicate species for which genetic data are available from studies other than Burns *et al.* (2014).

Current Taxonomy	Alternative 1	Alternative 2
Catamblyrhynchus diadema	Catamblyrhynchus	Catamblyrhynchus
Charitospiza eucosma	Charitospiza	Charitospiza
Orchesticus abeillei	Orchesticus	Orchesticus
Parkerthraustes humeralis	Parkerthraustes	Parkerthraustes
Nemosia pileata	Nemosia	Nemosia
Nemosia rourei*	Nemosia	Nemosia
Cyanicterus cyanicterus	Cyanicterus	Cyanicterus
Sericossypha albocristata	Sericossypha	Sericossypha
Compsothraupis loricata	Compsothraupis	Compsothraupis
Coryphaspiza melanotis	Coryphaspiza	Coryphaspiza
Embernagra platensis	Embernagra	Embernagra
Embernagra longicauda*	Embernagra	Embernagra
Emberizoides ypiranganus	Emberizoides	Emberizoides
Emberizoides herbicola	Emberizoides	Emberizoides
Emberizoides duidae	Emberizoides	Emberizoides
Incaspiza pulchra	Incaspiza	Incaspiza
Incaspiza personata	Incaspiza	Incaspiza

**TABLE 1.** (Continued)

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TABLE 1. (Continued)

Current Taxonomy	Alternative 1	Alternative 2
Tiaris olivaceus	Tiaris	Tiaris
Euneornis campestris	Euneornis	Tiaris
Loxigilla portoricensis	Pyrrhulagra	Tiaris
Loxigilla violacea	Pyrrhulagra	Tiaris
Melopyrrha nigra	Pyrrhulagra	Tiaris
Loxipasser anoxanthus	Loxipasser	Tiaris
Tiaris canorus	Phonipara	Tiaris
Loxigilla barbadensis	Loxigilla	Tiaris
Loxigilla noctis	Loxigilla	Tiaris
Melanospiza richardsoni	Melanospiza	Tiaris
Tiaris bicolor	Melanospiza	Tiaris
Tiaris fuliginosus	Asemospiza	Tiaris
Tiaris obscurus	Asemospiza	Tiaris
Certhidea olivacea	Certhidea	Tiaris
Certhidea fusca	Certhidea	Tiaris
Platyspiza crassirostris	Platyspiza	Tiaris
Pinaroloxias inornata	Pinaroloxias	Tiaris
Camarhynchus heliobates	Camarhynchus	Tiaris
Camarhynchus pauper	Camarhynchus	Tiaris
Camarhynchus pallidus	Camarhynchus	Tiaris
Camarhynchus parvulus	Camarhynchus	Tiaris
Camarhynchus psittacula	Camarhynchus	Tiaris
Geospiza fuliginosa	Geospiza	Tiaris
Geospiza difficilis	Geospiza	Tiaris
Geospiza conirostris	Geospiza	Tiaris
Geospiza magnirostris	Geospiza	Tiaris
Geospiza scandens	Geospiza	Tiaris
Geospiza fortis	Geospiza	Tiaris
Volatinia jacarina	Volatinia	Volatinia
Conothraupis speculigera	Conothraupis	Conothraupis
Conothraupis mesoleuca*	Conothraupis	Conothraupis
Creurgops dentatus	Creurgops	Creurgops
Creurgops verticalis	Creurgops	Creurgops
Eucometis penicillata	Eucometis	Trichothraupis
Trichothraupis melanops	Trichothraupis	Trichothraupis
Tachyphonus cristatus	Islerothraupis	Trichothraupis
Cachyphonus luctuosus	Islerothraupis	Trichothraupis
Tachyphonus rufiventer	Islerothraupis	Trichothraupis
Coryphospingus pileatus	Coryphospingus	Coryphospingus
Coryphospingus cucullatus	Coryphospingus	Coryphospingus
Tachyphonus surinamus	Maschalethraupis	Lanio
Rhodospingus cruentus	Rhodospingus	Lanio
Tachyphonus delatrii	Chrysocorypha	Lanio
Lanio versicolor	Lanio	Lanio
Lanio fulvus	Lanio	Lanio
Lanio aurantius	Lanio	Lanio
Lanio leucothorax	Lanio	Lanio

**TABLE 1.** (Continued)

Current Taxonomy	Alternative 1	Alternative 2
Tachyphonus phoenicius	Tachyphonus	Tachyphonus
Tachyphonus rufus	Tachyphonus	Tachyphonus
Tachyphonus coronatus	Tachyphonus	Tachyphonus
Ramphocelus sanguinolentus	Ramphocelus	Ramphocelus
Ramphocelus flammigerus	Ramphocelus	Ramphocelus
Ramphocelus costaricensis	Ramphocelus	Ramphocelus
Ramphocelus passerinii	Ramphocelus	Ramphocelus
Ramphocelus bresilius	Ramphocelus	Ramphocelus
Ramphocelus dimidiatus	Ramphocelus	Ramphocelus
Ramphocelus nigrogularis	Ramphocelus	Ramphocelus
Ramphocelus melanogaster	Ramphocelus	Ramphocelus
Ramphocelus carbo	Ramphocelus	Ramphocelus
porophila bouvronides*	Sporophila	Sporophila
Sporophila lineola	Sporophila	Sporophila
porophila torqueola	Sporophila	Sporophila
Sporophila corvina	Sporophila	Sporophila
Sporophila intermedia	Sporophila	Sporophila
Sporophila americana*	Sporophila	Sporophila
Sporophila fringilloides	Sporophila	Sporophila
Sporophila murallae*	Sporophila	Sporophila
porophila luctuosa	Sporophila	Sporophila
porophila caerulescens	Sporophila	Sporophila
Sporophila nigricollis	Sporophila	Sporophila
Sporophila ardesiaca*	Sporophila	Sporophila
Sporophila funerea	Sporophila	Sporophila
Sporophila angolensis	Sporophila	Sporophila
Sporophila nuttingi	Sporophila	Sporophila
Sporophila maximiliani	Sporophila	Sporophila
Sporophila crassirostris	Sporophila	Sporophila
porophila atrirostris	Sporophila	Sporophila
porophila schistacea	Sporophila	Sporophila
porophila falcirostris	Sporophila	Sporophila
Sporophila frontalis	Sporophila	Sporophila
Sporophila plumbea	Sporophila	Sporophila
Sporophila beltoni*	Sporophila	Sporophila
Sporophila collaris	Sporophila	Sporophila
porophila albogularis	Sporophila	Sporophila
Sporophila leucoptera	Sporophila	Sporophila
Sporophila peruviana	Sporophila	Sporophila Sporophila
Sporophila telasco	Sporophila	Sporophila
porophila simplex	Sporophila	Sporophila Sporophila
Sporophila castaneiventris	Sporophila	Sporophila Sporophila
Sporophila minuta	Sporophila	Sporophila Sporophila
Sporophila bouvreuil**	Sporophila Sporophila	Sporophila Sporophila
Sporophila nigrorufa*	Sporophila	Sporophila Sporophila
Sporophila hypoxantha	Sporophila	Sporophila Sporophila
Sporophila ruficollis	Sporophila Sporophila	Sporophila Sporophila

**TABLE 1.** (Continued)

TABLE 1. (Continued)		
Current Taxonomy	Alternative 1	Alternative 2
Sporophila pileata	Sporophila	Sporophila
Sporophila hypochroma	Sporophila	Sporophila
Sporophila cinnamomea	Sporophila	Sporophila
Sporophila palustris	Sporophila	Sporophila
Sporophila melanogaster	Sporophila	Sporophila
Piezorina cinerea	Piezorina	Piezorina
Xenospingus concolor	Xenospingus	Xenospingus
Cnemoscopus rubrirostris	Cnemoscopus	Cnemoscopus
Hemispingus verticalis	Pseudospingus	Pseudospingus
Hemispingus xanthophthalmus	Pseudospingus	Pseudospingus
Poospiza boliviana	Poospiza	Poospiza
Poospiza ornata	Poospiza	Poospiza
Poospiza nigrorufa	Poospiza	Poospiza
Poospiza hispaniolensis	Poospiza	Poospiza
Poospiza rubecula	Poospiza	Poospiza
Compsospiza baeri	Poospiza	Poospiza
Compsospiza garleppi	Poospiza	Poospiza
Hemispingus goeringi	Poospiza	Poospiza
Hemispingus rufosuperciliaris	Poospiza	Poospiza
Hemispingus reyi	Kleinothraupis	Cypsnagra
Hemispingus atropileus	Kleinothraupis	Cypsnagra
Hemispingus calophrys	Kleinothraupis	Cypsnagra
Hemispingus parodii	Kleinothraupis	Cypsnagra
Hemispingus frontalis	Sphenopsis	Cypsnagra
Hemispingus melanotis	Sphenopsis	Cypsnagra
Thlypopsis fulviceps	Thlypopsis	Cypsnagra
Thlypopsis inornata	Thlypopsis	Cypsnagra
Thlypopsis sordida	Thlypopsis	Cypsnagra
Pyrrhocoma ruficeps	Thlypopsis	Cypsnagra
Thlypopsis ruficeps	Thlypopsis	Cypsnagra
Hemispingus superciliaris	Thlypopsis	Cypsnagra
Thlypopsis ornata	Thlypopsis	Cypsnagra
Thlypopsis pectoralis	Thlypopsis	Cypsnagra
Poospiza thoracica	Castanozoster	Cypsnagra
Donacospiza albifrons	Donacospiza	Cypsnagra
Cypsnagra hirundinacea	Cypsnagra	Cypsnagra
Poospiza hypochondria	Poospizopsis	Cypsnagra
Poospiza caesar	Poospizopsis	Cypsnagra
Urothraupis stolzmanni	Urothraupis	Cypsnagra
Nephelornis oneilli	Nephelornis	Cypsnagra
Poospiza lateralis*	Microspingus	Cypsnagra
Poospiza cabanisi	Microspingus	Cypsnagra
Poospiza erythrophrys	Microspingus	Cypsnagra
Poospiza alticola	Microspingus	Cypsnagra
Poospiza torquata	Microspingus	Cypsnagra
Hemispingus trifasciatus	Microspingus	Cypsnagra
Poospiza melanoleuca	Microspingus	Cypsnagra

**TABLE 1.** (Continued)

Current Taxonomy	Alternative 1	Alternative 2
<sup>D</sup> oospiza cinerea	Microspingus	Cypsnagra
Conirostrum margaritae	Conirostrum	Conirostrum
Conirostrum bicolor	Conirostrum	Conirostrum
Conirostrum speciosum	Conirostrum	Conirostrum
Conirostrum leucogenys	Conirostrum	Conirostrum
Conirostrum albifrons	Conirostrum	Conirostrum
Oreomanes fraseri	Conirostrum binghami	Conirostrum
Conirostrum sitticolor	Conirostrum	Conirostrum
Conirostrum ferrugineiventre	Conirostrum	Conirostrum
Conirostrum tamarugense	Conirostrum	Conirostrum
Conirostrum rufum	Conirostrum	Conirostrum
Conirostrum cinereum	Conirostrum	Conirostrum
Sicalis citrina	Sicalis	Sicalis
Sicalis taczanowskii	Sicalis	Sicalis
Sicalis uropygialis	Sicalis	Sicalis
Sicalis flaveola	Sicalis	Sicalis
Sicalis columbiana	Sicalis	Sicalis
Sicalis luteola	Sicalis	Sicalis
Sicalis luteocephala	Sicalis	Sicalis
Sicalis lebruni	Sicalis	Sicalis
Sicalis mendozae*	Sicalis	Sicalis
Sicalis olivascens	Sicalis	Sicalis
Sicalis auriventris	Sicalis	Sicalis
Sicalis raimondii	Sicalis	Sicalis
Sicalis lutea	Sicalis	Sicalis
Phrygilus gayi	Phrygilus	Phrygilus
Phrygilus patagonicus	Phrygilus	Phrygilus
Phrygilus atriceps	Phrygilus	Phrygilus
Phrygilus punensis	Phrygilus	Phrygilus
Vesospiza acunhae	Nesospiza	Nesospiza
Nesospiza wilkinsi	Nesospiza	Nesospiza
Rowettia goughensis	Rowettia	Rowettia
Melanodera xanthogramma	Melanodera	Melanodera
Melanodera melanodera	Melanodera	Melanodera
Haplospiza unicolor	Haplospiza	Haplospiza
Phrygilus plebejus	Geospizopsis	Haplospiza
Phrygilus unicolor	Geospizopsis	Haplospiza
Haplospiza rustica	Spodiornis	Haplospiza
Acanthidops bairdi	Acanthidops	Haplospiza
Xenodacnis parina	Xenodacnis	Haplospiza
diopsar brachyurus	Idiopsar	Idiopsar
Diuca speculifera	Chionodacryon	Idiopsar
Phrygilus erythronotus	Ephippiospingus	Idiopsar
Phrygilus dorsalis	Ephippiospingus	Idiopsar
Catamenia analis	Catamenia	Catamenia
Catamenia inornata	Catamenia	Catamenia
Catamenia homochroa	Catamenia	Catamenia

**TABLE 1.** (Continued)

Current Taxonomy	Alternative 1	Alternative 2
Diglossa glauca	Diglossa	Diglossa
Diglossa caerulescens	Diglossa	Diglossa
Diglossa cyanea	Diglossa	Diglossa
Diglossa indigotica	Diglossa	Diglossa
Diglossa sittoides	Diglossa	Diglossa
Diglossa plumbea	Diglossa	Diglossa
Diglossa baritula	Diglossa	Diglossa
Diglossa mystacalis	Diglossa	Diglossa
Diglossa lafresnayii	Diglossa	Diglossa
Diglossa gloriosissima	Diglossa	Diglossa
Diglossa duidae	Diglossa	Diglossa
Diglossa major	Diglossa	Diglossa
Diglossa venezuelensis	Diglossa	Diglossa
Diglossa albilatera	Diglossa	Diglossa
Diglossa carbonaria	Diglossa	Diglossa
Diglossa brunneiventris	Diglossa	Diglossa
Diglossa gloriosa	Diglossa	Diglossa
Diglossa humeralis	Diglossa	Diglossa
Calochaetes coccineus	Calochaetes	Calochaetes
ridosornis porphyrocephalus	Iridosornis	Iridosornis
ridosornis analis	Iridosornis	Iridosornis
ridosornis jelskii	Iridosornis	Iridosornis
ridosornis reinhardti	Iridosornis	Iridosornis
ridosornis rufivertex	Iridosornis	Iridosornis
Pipraeidea melanonota	Pipraeidea	Pipraeidea
Pipraeidea bonariensis	Pipraeidea	Pipraeidea
Saltator rufiventris	Pseudosaltator	Pipraeidea
Dubusia castaneoventris	Dubusia	Pipraeidea -
Dubusia taeniata	Dubusia	Pipraeidea -
Buthraupis montana	Buthraupis	Pipraeidea
Thraupis cyanocephala	Sporathraupis	Pipraeidea -
Buthraupis wetmorei	Tephrophilus	Pipraeidea -
Chlorornis riefferii	Chlorornis	Pipraeidea
Enemathraupis eximia	Cnemathraupis	Pipraeidea
Enemathraupis aureodorsalis	Cnemathraupis	Pipraeidea
1nisognathus somptuosus	Anisognathus	Pipraeidea
Inisognathus notabilis	Anisognathus	Pipraeidea
Anisognathus melanogenys	Anisognathus	Pipraeidea
Inisognathus igniventris	Anisognathus	Pipraeidea
1nisognathus lacrymosus	Anisognathus	Pipraeidea
Chlorochrysa phoenicotis	Chlorochrysa	Chlorochrysa
Chlorochrysa nitidissima	Chlorochrysa	Chlorochrysa
Chlorochrysa calliparaea	Chlorochrysa	Chlorochrysa
Vetmorethraupis sterrhopteron	Wetmorethraupis	Wetmorethraupis
Bangsia arcaei	Bangsia	Bangsia
Bangsia aureocincta	Bangsia	Bangsia
Bangsia edwardsi	Bangsia	Bangsia

**TABLE 1.** (Continued)

Current Taxonomy	Alternative 1	Alternative 2
Bangsia rothschildi	Bangsia	Bangsia
Bangsia melanochlamys	Bangsia	Bangsia
ophospingus griseocristatus	Lophospingus	Lophospingus
ophospingus pusillus	Lophospingus	Lophospingus
Neothraupis fasciata	Neothraupis	Neothraupis
Diuca diuca	Diuca	Diuca
Gubernatrix cristata	Gubernatrix	Gubernatrix
Stephanophorus diadematus	Stephanophorus	Stephanophorus
Cissopis leverianus	Cissopis	Cissopis
Schistochlamys melanopis	Schistochlamys	Schistochlamys
Schistochlamys ruficapillus	Schistochlamys	Schistochlamys
Paroaria coronata	Paroaria	Paroaria
Paroaria dominicana	Paroaria	Paroaria
Paroaria nigrogenis**	Paroaria	Paroaria
Paroaria baeri	Paroaria	Paroaria
Paroaria capitata	Paroaria	Paroaria
Paroaria gularis	Paroaria	Paroaria
Tangara varia	Ixothraupis	Tangara
angara rufigula	Ixothraupis	Tangara
angara punctata	Ixothraupis	Tangara
angara guttata	Ixothraupis	Tangara
angara xanthogastra	Ixothraupis	Tangara
angara ruficervix	Chalcothraupis	Tangara
angara cabanisi*	Poecilostreptus	Tangara
angara palmeri	Poecilostreptus	Tangara
Thraupis episcopus	Thraupis	Tangara
Thraupis sayaca	Thraupis	Tangara
hraupis glaucocolpa*	Thraupis	Tangara
Thraupis cyanoptera	Thraupis	Tangara
hraupis abbas	Thraupis	Tangara
hraupis ornata	Thraupis	Tangara
Thraupis palmarum	Thraupis	Tangara
angara cyanoptera	Stilpnia	Tangara
angara viridicollis	Stilpnia	Tangara
angara phillipsi	Stilpnia	Tangara
angara argyrofenges	Stilpnia	Tangara
angara heinei	Stilpnia	Tangara
angara larvata	Stilpnia	Tangara
Cangara cyanicollis	Stilpnia	Tangara
Cangara nigrocincta	Stilpnia	Tangara
angara peruviana*	Stilpnia	Tangara
angara preciosa	Stilpnia	Tangara
Tangara meyerdeschauenseei	Stilpnia	Tangara
Tangara vitriolina	Stilpnia	Tangara
Tangara cayana	Stilpnia	Tangara
Tangara cucullata	Stilpnia	Tangara
Tangara vassorii	Tangara	Tangara

TABLE 1. (Continued)

Current Taxonomy	Alternative 1	Alternative 2	
Tangara nigroviridis	Tangara	Tangara	
Tangara dowii	Tangara	Tangara	
Tangara fucosa	Tangara	Tangara	
Tangara cyanotis	Tangara	Tangara	
Tangara rufigenis	Tangara	Tangara	
Tangara labradorides	Tangara	Tangara	
Tangara gyrola	Tangara	Tangara	
Tangara lavinia	Tangara	Tangara	
Tangara chrysotis	Tangara	Tangara	
Tangara xanthocephala	Tangara	Tangara	
Tangara parzudakii	Tangara	Tangara	
Tangara johannae	Tangara	Tangara	
Tangara schrankii	Tangara	Tangara	
Tangara arthus	Tangara	Tangara	
Tangara florida	Tangara	Tangara	
Tangara icterocephala	Tangara	Tangara	
Tangara fastuosa	Tangara	Tangara	
Tangara seledon	Tangara	Tangara	
Tangara cyanocephala	Tangara	Tangara	
Tangara desmaresti	Tangara	Tangara	
Tangara cyanoventris	Tangara	Tangara	
Tangara inornata	Tangara	Tangara	
Tangara mexicana	Tangara	Tangara	
Tangara chilensis	Tangara	Tangara	
Tangara callophrys	Tangara	Tangara	
Tangara velia	Tangara	Tangara	

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