PHYLOGENETIC RELATIONSHIPS OF THE CINNAMON TYRANT, *NEOPIPO CINNAMOMEA*, TO THE TYRANT FLYCATCHERS (TYRANNIDAE)[1]

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Abstract. A cladistic analysis of 14 binary morphological and nest architecture characters was conducted to investigate the relationship of *Neopipo cinnamomea*, formerly placed in the manakins (Pipridae), to the *Empidonax* assemblage of tyrant flycatchers (Tyrannidae; Lanyon 1986, 1988a). The results demonstrate that *Neopipo cinnamomea* is not a manakin, but a member of the *Myiophobus* group of tyrannids, which includes *Myiophobus, Myiobius* (including *Terenotriccus erythrurus*), *Pyrrhomyias,* and *Hirundinea* (Lanyon 1986, 1988a). Detailed illustrations and formal descriptions of the syringeal morphology of *Neopipo cinnamomea* and related genera are presented. Two alternative, maximally parsimonious phylogenetic hypotheses were identified (length = 20; Consistency Index = 0.70). In both hypotheses, *Myiophobus* is the sister group to the other five genera, and the monophyly of *Myiobius* including *M. erythrurus* is supported. The two alternative hypotheses differ in the hypothesized relationships among *Neopipo, Pyrrhomyias* and *Hirundinea*. In the first, *Neopipo* and *Pyrrhomyias* constitute a monophyletic group, and *Hirundinea* is its sister group. In the second, *Hirundinea* and *Pyrrhomyias* form a clade with *Neopipo* as its sister group. These findings strongly confirm that *Neopipo* is not a member of the Pipridae. It is recommended that *Neopipo cinnamomea* be referred to as the Cinnamon Tyrant, and that it be included in the *Myiophobus* group within the *Empidonax* assemblage of the Tyrannidae. The hypothesis that *Neopipo cinnamomea* is strikingly convergent with the tyrannid *Myiobius erythrurus* is falsified. Some similarities in plumage between these species are apparently homologous traits that evolved early in the radiation of the *Myiophobus* group.

Key words: Phylogeny; syrinx; Tyrant Flycatcher; manakin; Neopipo cinnamomea; *convergence.*

INTRODUCTION

The Cinnamon Tyrant (*Neopipo cinnamomea*) is a small suboscine passerine bird that ranges throughout the Amazonian Basin. It is rare and locally distributed in terra firmae forest and sandy-belt woodlands (Hilty and Brown 1986, Ridgely and Tudor 1994). This poorly known species has traditionally been included in the manakin family (Pipridae) since its description by Lawrence (1868), and has been referred to as the Cinnamon Manakin (Hellmayr 1929, Hilty and Brown 1986) or the Cinnamon Tyrant-Manakin (Monroe and Sibley 1993, Ridgely and Tudor 1994). Although *Neopipo* has been recognized as atypical within the manakins for over a century, it was not removed from the family until Prum (1990) documented that it lacked a derived syringeal character shared by all the true piprids, and a derived hindlimb artery trait shared by all

manakins and cotingas. Prum (1990) concluded that *Neopipo* was likely to be a tyrant flycatcher (Tyrannidae).

The few writings about *Neopipo cinnamomea* have focused on the extreme morphological similarities between it and the Ruddy-tailed Flycatcher, *Myiobius* (formerly *Terenotriccus*) *erythrurus*, in the tyrant flycatchers (Tyrannidae; Hilty and Brown 1986, Ridgely and Tudor 1994). For example, Hilty and Brown (1986) describe *Neopipo* as "remarkably like Ruddy-tailed [Flycatcher]" but having a "manakinlike shape with large eyes, large rounded head and slightly hunched posture." Indeed, according to the traditional classification, these two genera would constitute a detailed and striking case of plumage convergence. Are these similarities between *Neopipo cinnamomea* and *Myiobius erythrurus* an amazing case of convergence or really an instance of homology?

To test this hypothesis of convergence, we investigated the phylogenetic relationships of *Neopipo* to the diverse family of tyrant flycatchers. Although a completely resolved phylogeny of the

tyrannids has not been established, and continued questions arise about the monophyly of the tyrannids (Sibley and Ahlquist 1985, 1989; S. M. Lanyon 1985; McKitrick 1985; Prum 1990), W. E. Lanyon (1984a, 1984b, 1986, 1988a, 1988b, 1988c) has proposed resolved phylogenetic hypotheses for several diverse tyrannid clades encompassing almost the entire family. Lanyon's (1984a, 1984b, 1986, 1988a, 1988b, 1988c) phylogenetic hypotheses are based on cranial and syringeal morphology, plumage, and nest architecture characters. According to Lanyon (1986), the monophyly of the *Empidonax* assemblage, which includes 109 species in 33 genera, is supported by a derived configuration of the nasal septum: the presence of a trabecular plate along the ventral edge of the ossified nasal septum. Unfortunately, only a single skeletal specimen of *Neopipo* is currently available (LSU 90006), but the septum in this specimen is not well preserved and it is not possible to evaluate whether *Neopipo* shares this feature. However, syringeal evidence strongly supports the placement of *Neopipo* in one clade within the *Empidonax* assemblage. One lineage in Lanyon's (1986, 1988a) *Myiophobus* group that includes *Myiobius* (including *Terenotriccus*), *Pyrrhomyias,* and *Hirundinea* is supported by the derived loss of the pair of intrinsic syringeal muscles, the Mm. obliquus ventrales (Ames 1971; Lanyon 1986, 1988a). These intrinsic syringeal muscles are also absent in *Neopipo cinnamomea* (Prum 1990), supporting the placement of *Neopipo* in this restricted clade among the many possibilities within the Tyrannidae.

Following a review of the systematic history of *Neopipo cinnamomea,* we present a phylogenetic analysis of Lanyon's (1988a) *Myiophobus* group including *Neopipo.* The analysis incorporates new characters from the syringes of these taxa, and characters from syringeal morphology, plumage, and nest architecture that were recognized by Lanyon (1986, 1988a).

SYSTEMATIC HISTORY AND COMMENTS

Lawrence (1868) described the species *Pipra?* [sic] *cinnamomea.* He placed the species provisionally in *Pipra,* the only major manakin genus at that time, based on its fused or syndactyl outer toes. Sclater and Salvin (1869) independently described the same taxon as *Neopipo rubricunda.* Subsequently, they recognized that Lawrence had previously described this species as *cinnamomea.* Following the rules of priority, Sclater and Salvin (1873) retained the senior specific synonym, *cinnamomea,* in their new genus, and recognized *Neopipo cinnamomea.*

Sclater (1888) assembled the first complete classification to the species and genera of Pipridae, and he based this classification on male plumage coloration, tail and bill shape, and syndactyly. Despite its dull, nearly monomorphic plumage, Sclater (1888) retained *Neopipo* in the Pipridae because of its syndactyly, and placed *Neopipo cinnamomea* in the subfamily Piprinae along with most of the true piprids recognized today (Prum 1990).

Ridgway (1907) reclassified the tyrannids, piprids, and cotingids (Cotingidae) based on a strict interpretation of a few morphological characters, including bill shape, syndactyly, and the condition of the hindlimb arteries (which were actually known for very few taxa; Garrod 1876, Prum 1990). Following Sclater (1888), Ridgway left the aberrant, syndactyl *Neopipo* in the Pipridae. Interestingly, Ridgway (1907) placed two partially syndactyl genera in the tyrannids in violation of his typical strict interpretation of this trait. These two genera—*Terenotriccus* (= *Myiobius erythrurus*) and *Rhynchocyclus*—are both strikingly similar to two genera of aberrant piprids—*Neopipo* and *Sapayoa*—which were placed in the Pipridae solely on the basis of their syndactyly.

McConnell (1911) described the new species *Neopipo helenae,* from the Guianas, based on plumage differences from the nominate *cinnamomea.* Hellmayr (1929) recognized the new form as a subspecies of *Neopipo cinnamomea,* and included the genus in the Pipridae, following previous authors. Hellmayr's (1929) classification of the Pipridae remained basically unchanged by Snow (1975, 1979), except for rearrangement of the sequence of genera and species. However, Snow (1975) emphasized the aberrant plumage of *Neopipo,* and questioned its placement in the Pipridae.

Based on a phylogenetic analysis of morphological characters, Prum (1990) recommended the removal of six genera from the traditional Pipridae (Hellmayr 1929; Snow 1975, 1979), including *Neopipo, Sapayoa, Schiffornis, Piprites, Neopelma,* and *Tyranneutes.* All six of these genera lack the derived, dorsal fusion of the B1 and B2 syringeal elements that is shared by all other traditional piprid genera (Prum 1990, 1992).

Furthermore, *Neopipo* and *Sapayoa* also lack the derived enlarged femoral artery shared by cotingas and manakins, and have elaborate medial syringeal cartilages, implying that they are tyrannids (Prum 1990).

In his first treatment of the *Empidonax* assemblage, Lanyon (1986) proposed that *Myiophobus* was the sister group of *Hirundinea* and *Pyrrhomyias,* and he referred to these three genera as the *Myiophobus* group. Lanyon (1986) further concluded that the traditional genus *Myiophobus* is polyphyletic. He suggested that *fasciatus, inornatus, flavicans,* and *pulcher* constitute *Myiophobus,* and that *roraimae, phoenicomitra,* and *ochraceiventris* were unrelated to these species. He hesitated to create a new genus for these latter species until further information was available to resolve their relationships. We follow Lanyon's strict limits to *Myiophobus.*

In a subsequent paper, Lanyon (1988a) hypothesized that *Myiobius* and *Terenotriccus erythrurus* belonged within the *Myiophobus* group as the sister group to *Hirundinea-Pyrrhomyias* clade. Lanyon (1988a) recommended that the monotypic genus *Terenotriccus* be synonymized with *Myiobius* because of the weight of the derived syringeal and behavioral characters uniting them. We disagree with Lanyon that genera should be delimited based on a priori assumptions about "generic" or "specific" level characters. However, we agree that placing *erythrurus* back in *Myiobius* appropriately communicates the monophyly of this group, and eliminates a monotypic, nonfunctional generic name. We follow Lanyon's taxonomy here, and place *erythrurus* in *Myiobius.*

METHODS

Observations of the syringeal morphology of a wide variety of tyrannoid species were made from cleared and double-stained specimens prepared by W. E. Lanyon (1986, 1988a) and borrowed from various institutions, and from additional syringeal material that was cleared and double-stained by the authors. Clearing and double-staining of syringeal specimens was performed following the protocol of Cannell (1988) with a few changes. Cannell recommends using 10% KOH solution to clear material (in steps 7 and 9 of the procedure). This concentration is much too strong for small syringes and will completely destroy a small specimen in a few hours. We recommend use of a 0.5% KOH solution which clears muscle and tissue quite adequately, and does not damage small specimens. Illustrations of syringes were made using a Wild M5A dissecting scope and a camera lucida. Observations of external morphology were made from study skins housed in the University of Kansas Museum of Natural History, Lawrence, Kansas, and the American Museum of Natural History, New York.

A list of the ingroup specimens observed and complete descriptions of their syringes are presented in the Appendix. Syringeal terminology follows Prum (1992). King (1989) and Brackenbury (1989) have proposed an alternative functional terminology for syringeal supporting elements based on the position of elements relative to the tracheobronchial junction. Because the position of the tracheobronchial junction can evolve independently relative to homologous syringeal elements, a functional terminology can lead to errors in homologizing syringeal elements. This system poses a direct impediment to comparative analysis of syringeal evolution and systematics (Prum 1992).

Monophyly of the ingroup—Lanyon's (1988a) expanded *Myiophobus* group plus *Neopipo cinnamomea*—was accepted a priori based on the presence of one or more complete, ossified bronchial elements (character 1, below; Lanyon 1986, 1988a). Within the ingroup, 13 different morphological characters were analyzed. Nine of these characters (1, 2, 5, 7, 8, 10, 11, 12, and 13) were based on Lanyon's (1986, 1988a) analyses of the phylogeny of the *Myiophobus* group, and five other original characters (3, 4, 6, 9, 10, and 13) were identified here. Character variation in the ingroup was polarized by outgroup comparison (Wiley 1981, Maddison et al. 1984). Based on Lanyon's (1986) phylogeny of the *Empidonax* assemblage, two successive outgroups were used to polarize character variation. The first outgroup is a clade that includes most of the taxa in the *Empidonax* assemblage—*Ochthornis, Satrapa,* and the *Empidonax, Knipolegus,* and *Muscisaxicola* groups. The second outgroup is the *Ochthoeca* group, the sister group to the rest of the *Empidonax* assemblage.

The data were assembled in a matrix of 14 binary characters and were analyzed cladistically using the computer programs PAUP 3.0 (branch-and-bound), and MacClade 3.0 (Table 1). Primitive, derived, and unknown character states are coded as 0, 1, and ? respectively.

CHARACTERS

(1) One or two complete, ossified, bronchial A elements. One or two complete, double, and ossified A elements around each bronchus are present in all of the ingroup taxa (Figs. 1, 2). Lanyon (1988a) found this character to be unique to this clade within the *Empidonax* assemblage, and he used this derived feature to support the monophyly of the *Myiophobus* group. All of the taxa in the first outgroup have complete A2 or A3 elements that are medially cartilaginous (Lanyon 1986). All of the genera within the *Ochthoeca* group entirely lack complete A elements around the bronchi. *Neopipo* is distinct within the ingroup because its A2 and A3 are combined into a single complex, complete element around each bronchus. A2 is double and medially incomplete, but the ventral ends of A2 are medially fused to the right and left ventral ends of A3 (Figs. 1A, B). However, the detailed, derived character proposed by Lanyon (1986) is shared by *Neopipo*. Complete, ossified A elements in support of the bronchi are not found in the first outgroup or the *Ochthoeca* group, so the presence of one or two complete, ossified A elements around the bronchi is hypothesized to be derived in *Neopipo, Myiobius, Hirundinea, Pyrrhomyias,* and *Myiophobus.*

(2) Double, complete, and independent ossified A2 and A3. Lanyon (1988a) hypothesized that the double, complete, ossified A2 and A3 elements supporting the bronchi is derived in *Myiobius,* including *erythrurus* (Fig. 2). Although ossification was medially incomplete in two of the six specimens of *Myiobius barbatus* examined (KU 65451, KU 66933), ossification was complete in all eight specimens of three other species examined in these genera (Fig. 2). Double, complete, ossified A2 and A3 elements are not present in *Neopipo, Hirundinea, Pyrrhomyias, Myiophobus,* or the first or second outgroups. Following Lanyon (1988a), the presence of two complete and ossified rings in support of each bronchus is hypothesized to be derived in *Myiobius.*

(3) Medial fusion of A2 and A3. In *Neopipo, Hirundinea,* and *Pyrrhomyias,* the A2 elements are double and medially incomplete, and their ventral ends are fused to the medial surface of A3 (Figs. 1, 2). In *Neopipo,* the fusion of A2 and A3 elements is complete, forming a unique, complex element described above (Character 1) and

in Appendix. The A2 and A3 elements in all other ingroup and outgroup taxa are independent and unfused. Medial fusion of A2 and A3 elements is hypothesized to be derived in these three genera.

(4) Wide pessulus dorsally fused to the first, single, complete, tracheal element. In *Neopipo* and *Pyrrhomyias,* the pessulus is dorsally fused to A5, which is the first single, dorsally complete tracheal A element (Fig. 1). None of the other ingroup or outgroup taxa exhibit this character. This feature is hypothesized to be derived in *Neopipo* and *Pyrrhomyias.*

(5) Narrow strand of cartilage between the ventral ends of B2 and B3. In *Pyrrhomyias* and *Hirundinea,* there is a unique strand of cartilage located between the ventral ends of the medially incomplete B2 and B3 elements within the tympaniform membrane (Figs. 1C–F; Lanyon 1986, 1988a). All other ingroup and outgroup taxa possess some type of medial accessory cartilages within the tympaniform membrane, but none have the accessory elements located between ventral ends of the B2 and B3 elements. The presence of narrow strands of internal cartilages between the B2 and B3 elements is, therefore, hypothesized to be derived in *Pyrrhomyias* and *Hirundinea.*

(6) Medial accessory elements broad, flat, and ossified. In *Neopipo,* the medial accessory elements are broad, ossified plates that extend caudally from the dorsal tips of the medially incomplete A1 and A2 elements into the medial tympaniform membrane (Figs. 1A, B). None of the other ingroup or outgroup taxa have ossified medial cartilages with this morphology. This character is hypothesized to be an autapomorphy of *Neopipo.*

(7) Loss of Mm. obliquus ventrales. Myiobius, Hirundinea, and *Pyrrhomyias* lack Mm. obliquus ventrales, which are a pair of intrinsic syringeal muscles that are present in *Myiophobus,* all outgroup taxa, and all other tyrannids, including *Sapayoa aenigma* (Ames 1971; Lanyon 1984a, 1984b, 1985, 1986, 1988a, 1988b, 1988c; McKitrick 1985; Prum 1990). Lanyon (1986, 1988a) hypothesized that the absence of Mm. obliquus ventrales is a derived loss in these genera. *Neopipo* also lacks these intrinsic syringeal muscles (Prum 1990). Given the evidence that the ingroup taxa are all members of the tyrannid clade, the loss of that intrinsic syringeal muscle
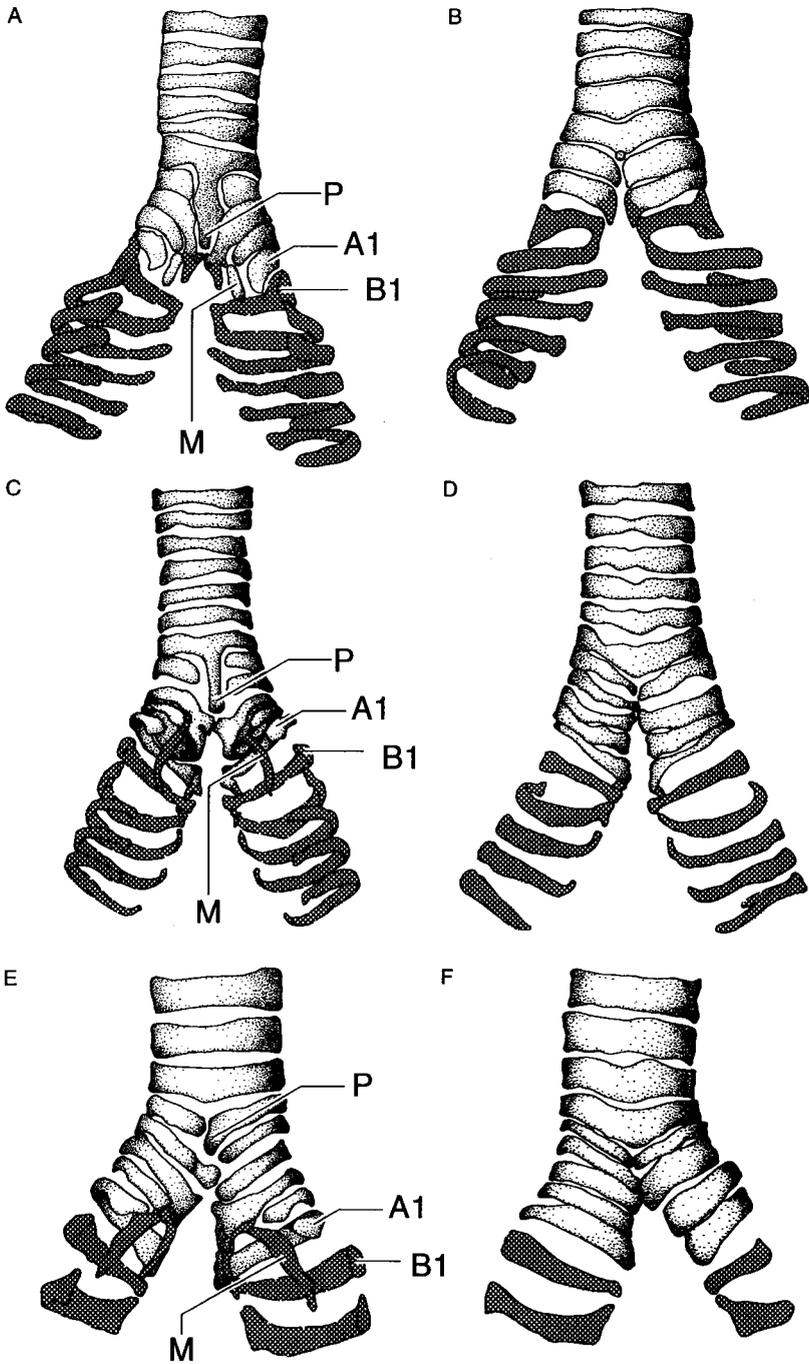
FIGURE 1.   Supporting elements of syrinx of: *Neopipo cinnamomea*, (A) dorsal, and (B) ventral views; *Pyrrhomyias cinnamomea*, (C) dorsal, and (D) ventral views; and *Hirundinea ferruginea*, (E) dorsal, and (F) ventral views. Abbreviations: A1, B1—A1 and B1 syringeal elements; M—medial cartilages; and P—pessulus.
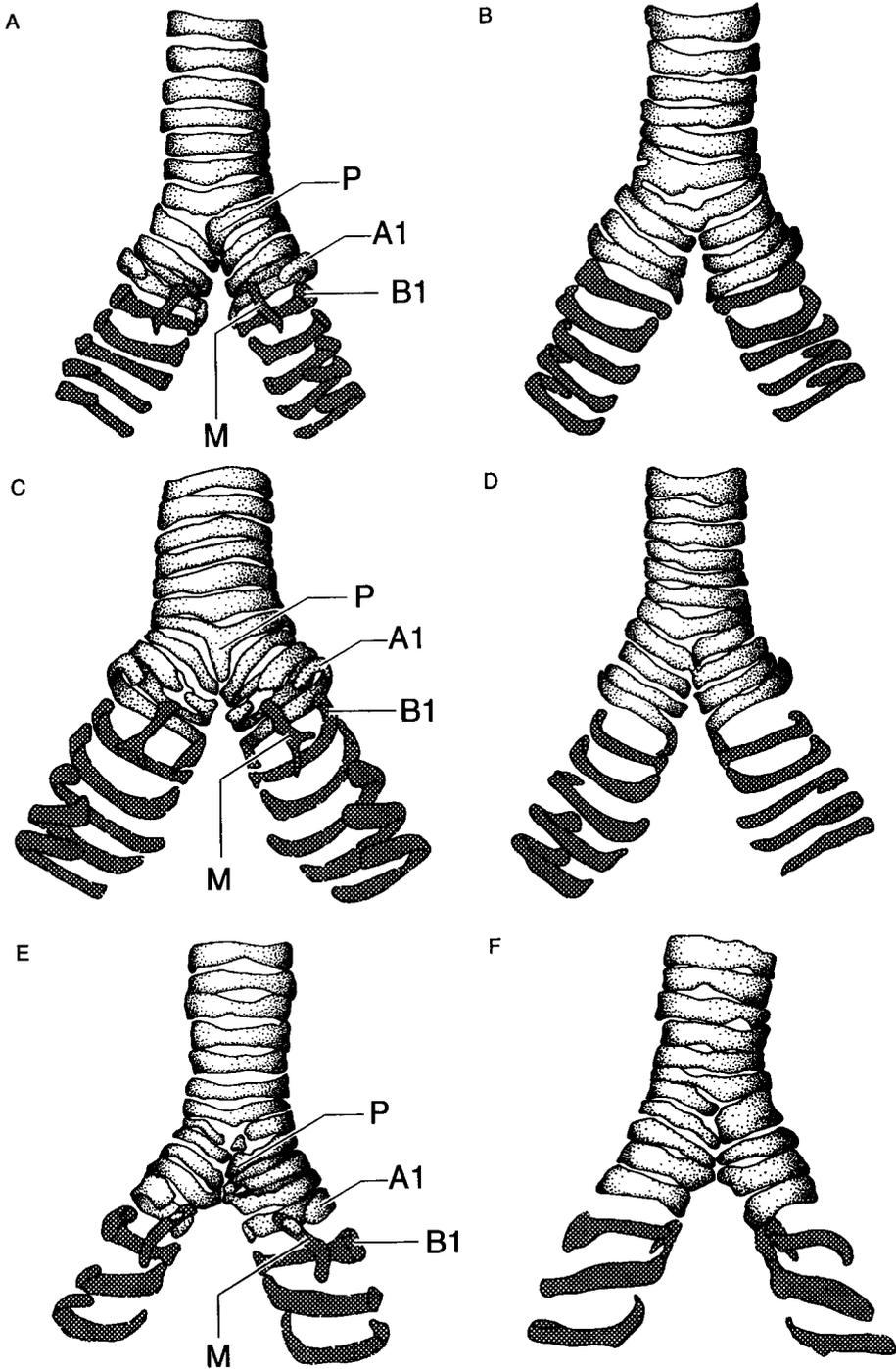
FIGURE 2. Supporting elements of syrinx of: *Myiophobus erythrurus,* (A) dorsal, and (B) ventral views; *Myiobius barbatus,* (C) dorsal, and (D) ventral views; and *Myiophobus fasciatus,* (E) dorsal, and (F) ventral views. Abbreviations: A1, B1—A1 and B1 syringeal elements; M—medial cartilages; and P—pessulus.

A.
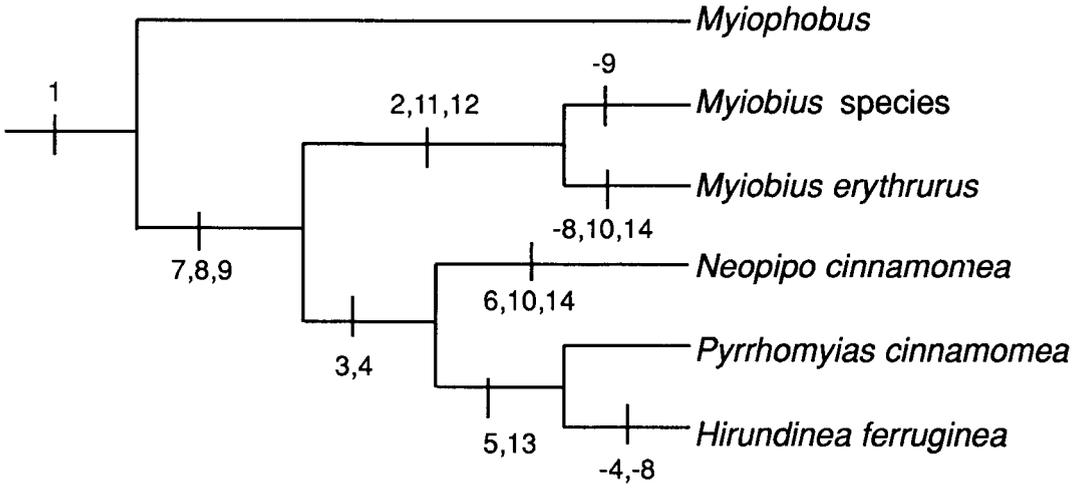
B.
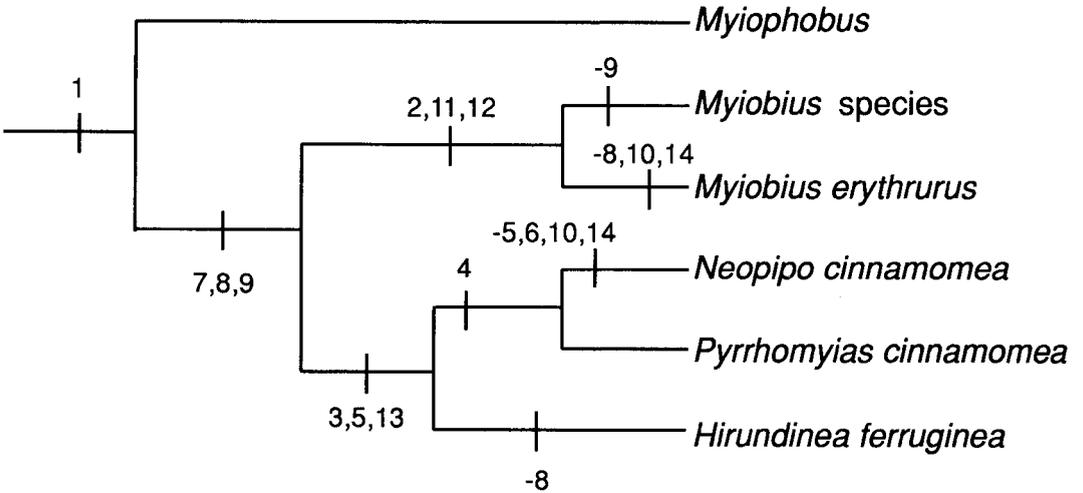
FIGURE 3. Two alternative resolutions of the phylogeny of the *Myiophobus* group of tyrannids including *Neopipo cinnamomea*. The two resolutions differ as follows: (A) *Neopipo* as the sister group to a *Pyrrhomyias-Hirundinea* clade. (B) *Hirundinea* as the sister group to a *Neopipo-Pyrrhomyias* clade. Both hypotheses are equal length (20 steps), and maximally parsimonious (CI = 0.70). Optimized hypotheses for the evolution of the 14 binary characters analyzed are shown on both phylogenetic hypotheses. Ambiguous optimizations are shown as accelerated transitions: Character 4 (A), Character 5 (B), and Character 9 (A&B).

is hypothesized to be derived in *Neopipo, Myiobius, Hirundinea,* and *Pyrrhomyias.*

(8) *Plumage with concealed crown patch.* *Myiobius,* excluding *M. erythrurus, Pyrrhomyias,* and *Myiophobus* all have a yellow or rufous col-

ored crown patch that can be concealed from view by longer, dark head plumes (Lanyon 1988a). *Neopipo* has a bright yellow crown patch (or orange rufous in females) that may also be concealed. *Myiobius erythrurus, Hirundinea,*

members of the first outgroup, and most of the *Ochthoeca* group lack a concealed crown patch, and have generally dark, solid plumage on the crown. The concealed crown patch of *Myiobius*, *Pyrrhomyias*, *Myiophobus*, excluding *erythrurus*, and *Neopipo* is hypothesized to be derived. A few species of *Ochthoeca* have concealed central crown patches that are hypothesized to be independently evolved.

(9) *Rufous underparts. Neopipo, Myiobius erythrurus, Hirundinea,* and *Pyrrhomyias* all have prominent rufous underparts. The plumage of the underparts of *Myiobius*, excluding *M. erythrurus, Myiophobus*, the first outgroup, and the *Ochthoeca* group ranges from bright yellow, olive or dusty gray to light or dark brown. Rufous underparts exist in a few species of *Myiotheretes* and *Ochthoeca* in both the first and second outgroups, but these plumages are quite different in detail, and are hypothesized to be independently derived in those taxa. The presence of rufous underparts is hypothesized to be derived in *Neopipo, Myiobius erythrurus, Hirundinea,* and *Pyrrhomyias.*

(10) *Rufous tail. Neopipo* and *Myiobius erythrurus* both have a distinctive rufous tail. The ingroup taxa and almost all of the outgroup species generally have black or brown tails (except in *Myiotheretes*). The rufous tail of *Neopipo* and *Myiobius erythrurus* is hypothesized to be derived.

(11) *Long rictal bristles.* In *Myiobius*, the rictal bristles are as long or longer than the bill (Lanyon 1988a). The rest of the taxa within the ingroup and both outgroups entirely lack rictal bristles or have very short rictal bristles. The long rictal bristles present in *Myiobius* are hypothesized to be derived.

(12) *Pendant, globular nest with side entrance. Myiobius* construct pendant, globular nests with a side entrance (Lanyon 1988a). *Hirundinea, Pyrrhomyias, Myiophobus,* and most members of the outgroups build a simple cup nest, which is primitive for the group. Several species of the *Ochthoeca* group, recognized by Lanyon (1986) as *Silvicultrix*, construct a pendant, globular nest similar to *Myiobius,* but this type of nest is independently evolved in this lineage (Lanyon 1988a). The nesting behavior of *Neopipo* is unknown, and it has been coded as a question mark. Elsewhere in the tyrannids, woven pendant nests have independently evolved in the flat-billed and

tody-tyrant assemblage (Lanyon 1988c). The pendant, globular nest of *Myiobius* is hypothesized to be derived.

(13) *Cup-shaped nest in niche or crevice.* *Pyrromyias cinnamomea* builds a cup-shaped nest that is placed in a niche or crevice, frequently along road cuts (Ewert 1975, Lanyon 1988a). *Hirundinea ferruginea* also builds a cup-shaped nest that is placed in niches or protected ledges on rocky cliffs, walls, or buildings (Belton 1985, Lanyon 1988a, Sick 1993). This form of nest placement is not known from any other species in the *Myiobius* group, and Lanyon (1988a) hypothesized that it was derived in the common ancestor of these two genera. The nest of *Neopipo* is unknown and has been coded as a question mark.

(14) *Syndactyly.* In *Neopipo* and *Myiobius erythrurus,* the two outer toes (digits III and IV) are fused for most of their length (Ridgway 1907). Partial fusion of the outer toes does not occur in other species of *Myiobius, Hirundinea, Pyrrhomyias, Myiophobus,* or the outgroups. Although Prum (1990) has shown that syndactyly can be highly variable and is not a robust synapomorphy of the piprids, this feature may be derived and phylogenetically informative at lower levels within the tyrannoids. Accordingly, syndactyly in *Neopipo* and *Myiobius erythrurus* is hypothesized to be derived.

RESULTS

The cladistic analysis of 14 morphological characters (Table 1) supports two equal length, maximally parsimonious hypotheses for the phylogenetic relationships of *Neopipo cinnamomea* and the rest of the *Myiophobus* group of tyrannids (Fig. 3). Both phylogenetic trees require 20 evolutionary transitions of the 14 binary characters (Consistency Index = 0.70). The monophyly of the ingroup is supported by the presence of at least one or more double A elements forming a complete and ossified ring around each bronchus (Character 1). In both alternative hypotheses, *Myiophobus* is the sister group to a clade including *Myiobius, Neopipo, Hirundinea* and *Pyrrhomyias,* which is supported by the loss of intrinsic syringeal muscles—Mm. obliquus ventrales (Character 7). This clade is also supported by the derived, concealed crown patch (Character 8), which has been subsequently lost in *Myiobius erythrurus,* and by the derived rufous underparts

TABLE 1.   Distributions of primitive (0), derived (1), and unknown (?) character states for 14 morphological and behavioral characters in the *Myiophobus* group of tyrannids (Lanyon 1988a), including *Neopipo cinnamomea*, and its outgroups.

Taxa	Characters													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Neopipo cinnamomea	1	0	1	1	0	1	1	1	1	1	0	?	?	1
Myiobius species[a]	1	1	0	0	0	0	1	1	0	0	1	1	0	0
Myiobius erythrurus[b]	1	1	0	0	0	0	1	0	1	1	1	1	0	1
Hirundinea ferruginea	1	0	1	0	1	0	1	0	1	0	0	0	1	0
Pyrrhomyias cinnamomea	1	0	1	1	1	0	1	1	1	0	0	0	1	0
Myiophobus species[c]	1	0	0	0	0	0	0	1	0	0	0	0	0	0
Outgroup 1[d]	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Outgroup 2[e]	0	0	0	0	0	0	0	0	0	0	0	0	0	0

[a] *Myiobius* species include *barbatus*, *sulphureipygius*, *villosus*, and *atricaudatus*.
[b] Formerly *Terenotriccus erythrurus*.
[c] *Myiophobus* species include only *fasciatus*, *inornatus*, *flavicans*, and *pulcher*. See text.
[d] Includes *Ochthornis*, *Satrapa*, and the *Empidonax*, *Knipolegus*, and *Muscisaxicola* Groups of Lanyon (1988a).
[e] Includes the *Ochthoeca* Group of Lanyon (1988a).

(Character 10), which have been lost secondarily in *Myiobius* excluding *erythrurus*. In both hypotheses, *Myiobius* is the sister group of the remaining three genera—*Neopipo, Hirundinea,* and *Pyrrhomyias*. The monophyly of the expanded *Myiobius* including *erythrurus* is supported by the presence of two double, complete, ossified, and independent A elements in support of each bronchus, long rictal bristles, and the pendant, globular nest with a side entrance (Characters 2, 11, and 12, respectively). The monophyly of *Neopipo, Hirundinea,* and *Pyrrhomyias* is supported by the medial fusion of the A2 and A3 syringeal supporting elements (Character 3).

The two phylogenetic hypotheses differ in the relationships among *Neopipo, Hirundinea,* and *Pyrrhomyias.* In the first hypothesis (Fig. 3A), *Hirundinea* and *Pyrrhomyias* form a clade with *Neopipo* as their sister group. Here, the monophyly of *Hirundinea* and *Pyrrhomyias* is supported by the presence of narrow accessory cartilages between the ventral ends of B2 and B3 (Character 5) and the cup-shaped nest placed in a niche or crevice (Character 13). In the second hypothesis (Fig. 3B), *Neopipo* and *Pyrrhomyias* form a clade with *Hirundinea* as the sister group. The monophyly of *Neopipo* and *Pyrrhomyias* is supported by the presence of a wide pessulus that is dorsally fused to the first complete tracheal element, A5 or A6 (Character 4). The two hypotheses are equally parsimonious because of the lack of information about the nest of *Neopipo*. Without additional information about the nest of *Neopipo* or other systematic data, the rela-

tionships among *Neopipo, Hirundinea,* and *Pyrrhomyias* cannot be resolved.

DISCUSSION

Despite repeated recognition of its aberrant status among the manakins, the original, erroneous placement of *Neopipo cinnamomea* in the Pipridae has remained unchallenged because of the lack of any detailed characters to support any other alternative. The collection of the first spirit specimens of *Neopipo* near Cerro Neblina, Venezuela (Willard et al. 1991) permitted us to critically evaluate its systematic relationships for the first time since its description in 1868 (Lawrence 1868). Although the details of the phylogeny of the group are not completely resolved by available morphological and behavioral evidence, the results of this phylogenetic analysis strongly support the conclusion that *Neopipo cinnamomea* is a member of the *Myiophobus* group of tyrant flycatchers (Fig. 3). Based on the derived morphological features shared by *Neopipo* and other taxa in the *Myiophobus* group, *Neopipo cinnamomea* should be placed in the Tyrannidae near these genera. Additional data, perhaps drawing on molecular characters and skeletal morphology, may be required to establish a completely resolved and well corroborated hypothesis of the radiation of this group. In particular, observation of the nest architecture and placement of *Neopipo cinnamomea* will enable us to reject either of the two most parsimonious hypotheses of relationship for this species.

Based on these results, we recommend that *Neopipo cinnamomea* be placed in the *Myiophobus* group of Lanyon's (1986) *Empidonax* assemblage within the Tyrannidae. The placement of *Neopipo* with the piprids is not supported by any evidence. Continued classification of *Neopipo* in the Pipridae (Sibley and Monroe 1990, Monroe and Sibley 1993, Ridgely and Tudor 1994) perpetuates a traditional practice that lacks empirical support.

The currently supported hypothesis could be in error if *Neopipo* is not a tyrannid. The loss of Mm. obliquus ventrales that supports the placement of *Neopipo* within the expanded *Myiophobus* group is a reversal in the character which best supports the monophyly of the entire tyrannids (McKitrick 1985, Prum 1990). The absence of this character state in *Neopipo* and the other three genera could be interpreted as evidence that they are not members of the Tyrannidae. However, Lanyon (1986, 1988b) documents that *Myiobius, Pyrrhomyias,* and *Hirundinea* share derived cranial characters that place them within the *Empidonax* assemblage of tyrannids, in which Mm. obliquus ventrales are primitively present. The absence of this pair of intrinsic syringeal muscles within the *Myiophobus* group appears to constitute a derived loss of this feature within the tyrannids. Even though there are no skeletal specimens of *Neopipo* to further corroborate its membership in the *Empidonax* assemblage, the proposed classification remains the only corroborated hypothesis of relationships for *Neopipo*.

The two currently supported phylogenetic hypotheses for the *Myiophobus* group (Fig. 3) do resolve the question of convergence between *Neopipo* and *Myiobius erythrurus*. Both hypotheses indicate that some similarities in plumage between these two species are not convergent. For example, the rufous underparts are a homologous feature that evolved early in the radiation of the *Myiophobus* group. On the other hand, the rufous tail and syndactyly (Characters 10 and 14, respectively) are apparently convergently evolved between the two species. Interestingly, syndactyly was originally used to place *Neopipo* within the piprids, and it appears to be homoplasious even at the lowest levels within this group.

Convergences between closely related taxa are frequently referred to as parallelisms, implying that the convergent or homoplasious traits evolved independently from a common primitive state or genetic background (e.g., Wiley 1981). Given our general ignorance of the genetic details of the evolution of such traits, convergence and parallelisms are difficult to distinguish in practice. However, the notion of parallel evolution may have some validity here, since parallel evolution in plumage between two closely related species may be considered much more likely than a similar convergence among species in separate families.

Unfortunately, little is known of the natural history of *Neopipo cinnamomea* which could be interpreted on the basis of these systematic conclusions. This species is among the many poorly known Neotropical passerines for which molt, vocal behavior, diet and nesting behavior have not been documented.

The traditional English name for *Neopipo cinnamomea* was the Cinnamon Manakin (Hellmayr 1929, Hilty and Brown 1986). With the recognition of its problematic status (Snow 1975, Prum 1990), it has been more recently recognized as the Cinnamon Tyrant-Manakin (Sibley and Monroe 1990, Monroe and Sibley 1993, Ridgely and Tudor 1994). Given that all associations with the manakins are erroneous and misleading, we propose that *Neopipo cinnamomea* be called simply the Cinnamon Tyrant. This will distinguish it from the closely related Cinnamon Flycatcher (*Pyrrhomyias cinnamomea*), and unambiguously underscore its phylogenetic relationships to the tyrant flycatchers.

ACKNOWLEDGMENTS

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APPENDIX

DESCRIPTION OF SYRINGES OF INGROUP TAXA AND LIST OF SYRINGEAL SPECIMENS EXAMINED

Neopipo cinnamomea (Figs. 1A, B)

A1 ossified, double and medially incomplete. The ventral and dorsal tips of A1 cartilaginous. A2 double, medially incomplete, and ventrally fused to A3. A3 ventrally fused. The dorsal ends of A3

continue medioventrad and fuse to the ventral ends of A2 just caudal to the fusion of the pessulus to the ventral side of A3. A3 appears like a double element in dorsal view. A4 single and dorsally incomplete. A5 ossified, single, and complete. A6 and above single, complete, and fully ossified. A wide, ossified pessulus dorsally fused to A5. The pessulus narrows greatly and becomes somewhat "keel-shaped" in the tracheobronchial junction and fused ventrally to A3. Small, ossified, internal accessory elements run caudally from the dorsal tips of each A1 and A2 element in both sides of the medial tympaniform membrane. A triangular, internal, cartilaginous accessory element fused to the ventromedial tips of the A3 elements. All B elements double, cartilaginous and medially incomplete. B1–2 fused to one another at their ventral tips by the cranially curved ventral ends of B2. The dorsal tips of B1 widened and spatulate, unlike the other B elements, and slightly fused to the cartilaginous ventral tips A1. B1 broad, flat, and spatulate. B2 and B3 thinner and curved. B2 and subsequent elements are larger in radius making the syrinx conspicuously widen caudally from B2. M. tracheolateralis restricted to the lateral surfaces of the trachea and inserts on the lateral surfaces of A1. The muscle forms a prominent belly between A6 and A1, but is not differentiated into intrinsic musculature. M. sternotrachealis inserts on the lateral surface of M. tracheolateralis between A7 and A9.

Specimens examined: AMNH 9371, 816769.

Myiobius erythrurus (Figs. 2A, B)

A1 ossified, double, and medially incomplete. The medioventral tips of A1 with small, triangular, cartilaginous extensions that approach but do not fuse with the ventral tips of B1. A2 and A3 double, ossified, and complete. A4 variable. In two specimens, A4 single, ossified, and complete. In three specimens, A4 double, and either complete or incomplete. A5 single, complete, and fully ossified. A6 and above single, complete, and fully ossified. Pessulus dorsally and ventrally fused to single or double A4. Two cartilaginous medial accessory elements basally fused to A2 and pointed caudally. B elements completely cartilaginous, double, and medially incomplete. Dorsal tips of B1 wide and spatulate, becoming thinner and curved caudad at their ventral tips. Dorsal tips of B2 fairly wide and spatulate, ventral tips curved craniad to nearly touch the ven-

tral tips of B1. B3 and below uniform in width. M. tracheolateralis is undifferentiated and restricted to the lateral surfaces of the trachea. It inserts on the lateral surface of A1. M. sternotrachealis inserts on M. tracheolateralis on the lateral surface of the trachea between A9 and A11.

Specimens examined: KU 85117, AMNH uncatalogued, KU65481, AMNH 9389, LSU 108469, AMNH 8261.

Myiobius barbatus, M. sulphureipygius, M. villosus, and *M. atricaudatus* (Figs. 2C, D)

A1 ossified, double, medially incomplete with pointed cartilaginous ventral tips. A2 ossified, double, and medially complete. In two specimens (KU65451, 66933), either one or both A2 medially cartilaginous. A3 ossified, double, and complete (ossification medially incomplete in two specimens; KU 65451, 66933). A4 usually ossified, single, and ventrally incomplete. Pessulus completely ossified, wide, flat and dorsally fused to A4. In one specimen (LSU64809), A4 double and pessulus fused to left half. A5 and above ossified, single, and complete. Cartilaginous medial accessory elements fused medially to A2, and either pointed or forked at caudal tips. B elements double, completely cartilaginous, and medially incomplete. Ventral tips of B2 curved craniad and nearly fused at ventral tips. Musculature as in *Myiobius erythrurus.*

Specimens examined: *Myiobius barbatus*— AMNH 9390, AMNH (RWD 17009); KU 66933, KU 65451, LSU 75470. *Myiobius sulphureipygius*—AMNH 6661. *Myiobius atricaudatus*— LSU 108475. *Myiobius villosus*—LSU 108473.

Hirundinea ferruginea (Figs. 1E, F)

A1 double, medially incomplete, and ossified. A2 double, ossified, and medially incomplete; fused medially and ventrally to A3. A3 is double, complete, and ossified; conspicuously broader near fusion with A2. In one specimen (AMNH 19229), A4 single, ossified, and dorsally incomplete. A5 and subsequent cranial elements are single, ossified, and complete. In a second specimen (LSU 64809), an additional complete bronchial ring on the right side between A3 and A4. A4 single and dorsally incomplete. Pessulus dorsally fused to right side of single A4. A5 is single, ossified, and dorsally incomplete. A6 and above are single, complete, and ossified. Pessulus fused

ventrally to A4 and dorsally free. B elements double, cartilaginous, and medially incomplete. Two cartilaginous accessory elements extend caudally from the dorsal tips of each A2. Two L-shaped, cartilaginous accessory elements extend caudally from the fused A2–3. A pair of thin filamentous medial accessory cartilages lie transverse to the bronchial lumen medial to the ventral tips of B3 in the medial tympaniform membrane. Musculature as in *Myiobius erythrurus* but more robust.

Specimens examined: AMNH 19229, LSU 64809.

Pyrrhomyias cinnamomea (Figs. 1C, D)

A1 double, ossified, medially incomplete. A2 double, ossified, and medially incomplete. Ventral tips of A2 extend mediad and fuse to the medial portions of A3. A3 ossified, double, and complete. A4 ossified and double. Ventral ends of both A4 fused to the pessulus. (In the only specimen, an extra, asymmetrical, and medially incomplete element on the right side between A4 and A5). A5 single, ossified, and dorsally fused to the pessulus. A6 and above single, complete, and ossified. Large, curved cartilaginous accessory elements nearly fused to medial surface of A2–3. Small L-shaped cartilaginous accessory elements fused to ventral tips of A1. B elements double, cartilaginous, and medially incomplete. B2, B3, and B4 narrow and curve cranially at their ventral tips. The dorsal tips of B2 and each subsequent caudal B element extend increasingly into the medial tympaniform membrane. Two very small, filamentous, cartilaginous accessory elements lie transverse to the bronchial lumen, medial to the ventral tips of each B3 element. Musculature as in *Myiobius erythrurus*.

Specimens examined: LSU 107652.

Myiophobus fasciatus (Figs. 2E, F)

A elements are completely ossified. A1 double and medially incomplete. A2 double, complete, and the ventral and ventromedial portions broad and robust. A3 double and medially incomplete. In two specimens (LSU 102584 and LSU 113850), A4 and A5 double, and medially incomplete. A6 and all subsequent cranial elements are single and complete. Pessulus dorsally and ventrally free. In one specimen (AMNH 4321), A4 and A5 double; pessulus dorsally fused

to right A4 element. B elements double, cartilaginous, and medially incomplete. Two pairs accessory cartilages. One large J-shaped pair fused to the medial surfaces of A2, and ossified near their bases. A second, smaller pair fused to the ventral ends of A1. M. tracheolateralis restricted to the lateral surface of the trachea and inserts on the lateral surface of A5–7. M. obliquus ventralis origin on the ventral midline of A3–5 and inserts on the lateral surface of A1.

Specimens examined: AMNH 4321, LSU 102584, LSU 113850.

Myiophobus inornatus.

A elements completely ossified. A1 and A2 double and medially incomplete. A3 double and complete. A4 single, and complete. A5 and above are single and complete. Pessulus fused ventrally to A4 and dorsally unfused. B elements cartilaginous, double, and medially incomplete. A pair of large, narrow, and slightly curved internal accessory cartilages medially fused to A3. Small, triangular, cartilaginous accessory cartilages fused to the ventral tips of A1. Musculature as in *Myiophobus fasciatus*.

Specimens examined: LSU 98045.

Myiophobus flavicans.

A elements are completely ossified. A1 and A2 double and medially incomplete. The dorsal tips of A1 broad and robust. A3 double and incomplete medially. A4 double; left A4 element medially incomplete, and right A4 element complete, forming the pessulus. A5 and subsequent cranial elements are single and complete. B elements cartilaginous, double, and medially incomplete. B1 and B2 project cranially and narrow at the ventral tips. B2 approaches but does not fuse to the ventral tip of B1. B3, B4, and the right portion of B5 also narrow and curve cranially but do not approach or fuse with any other elements. All subsequent caudal B elements are simple in shape. A pair of large, cartilaginous medial accessory elements nearly fused to dorsal tips of A2 and the medial portions of A3. These accessory elements narrow and curve significantly toward the caudal tip. A second pair of cartilaginous accessory medial cartilages fused to the ventral tips of A1. Musculature as in *Myiophobus fasciatus*.

Specimens examined: LSU 107656.