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PHYLOGENY OF THE TYRANT FLYCATCHERS (TYRANNIDAE) BASED ON MORPHOLOGY AND BEHAVIOR

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ABSTRACT.—Previously published morphological and behavioral data for the tyrant flycatchers (Tyrannidae) were reanalyzed using cladistic techniques. Several additional characters, including two putative synapomorphies of the Tyrannidae were incorporated. Nearly all of the ~100 traditional tyrannid genera were included. Results of the analysis of this set of 68 characters support three previously proposed tyrannid assemblages: the kingbird assemblage and slightly restricted *Empidonax* and *Myiarchus* assemblages. Characters of the nasal septum that past workers have considered conservative and phylogenetically informative are supported as synapomorphies of the kingbird and restricted *Empidonax* assemblages. Several small monophyletic groups of genera are supported. The monophyly of neither the *Elaenia* assemblage nor the flatbill and tody-tyrant assemblage is supported in any most-parsimonious tree, but such trees are not significantly better than trees supporting their monophyly. A Tyrannidae exclusive of the Cotingidae and Pipridae is monophyletic in some most-parsimonious trees, but not in others in which flatbills and tody-tyrants are basal to a clade containing Cotingidae, Pipridae, and the remaining tyrannid genera. There is some evidence that characters describing plumage color pattern are more homoplasious than the other character suites I examined. *Received 5 August 2000, accepted 9 February 2002.*

RESUMEN.—Utilizando técnicas cladísticas reanalicé datos morfológicos y conductuales previamente publicados para la familia Tyrannidae. Incorporé varios caracteres adicionales incluyendo dos sinapomorfias putativas. Incluí casi todos los géneros de los aproximadamente 100 géneros tradicionales de la familia Tyrannidae. Los resultados del análisis de un set de 68 caracteres apoyan tres grupos de tiránidos previamente propuestos: el grupo *Tyrannus* y los grupos *Emipidonax* y *Myiarchus*. Los caracteres relacionados con el septum nasal que han sido considerados previamente como conservadores y filogenéticamente informativos, son apoyados como sinapomorfias del grupo *Tyrannus* y del grupo restringido *Empidonax*. Varios pequeños grupos de géneros monofiléticos son apoyados. Ni la monofilia del grupo *Elaenia* ni la de los picochato (e.g. *Plathyrhinchus*) y mosqueritos (e.g. *Todirostrum*, *Hemitriccus*) es apoyada en cualquiera de los árboles más parsimoniosos, pero estos árboles no son significativamente mejores que los que apoyan su monofilia. Un Tyrannidae exclusivo de la familia Cotingidae y Pipridae es monofilético en alguno de los árboles más parsimoniosos, pero no en otros en los que los picochatos y mosqueritos son basales a un clado que contiene a Cotingidae, Pipridae y a los demás géneros de tiránidos. Existe cierta evidencia que los carateres que describen los patrones de coloración del plumaje son más homoplásicos que el set de caracteres que examineé.

THE TYRANT FLYCATCHERS (Tyrannidae) are a large, primarily Neotropical family of suboscine passerine birds in the superfamily Tyrannoidea which also include the cotingas (Cotingidae) and manakins (Pipridae). A great behavioral and ecological diversity within that superfamily presents rich opportunities for comparative tests of evolutionary and ecological hypotheses (e.g. Prum 1990a, 1994, 1997). Because well-supported phylogenies are fundamental to such tests, the evolutionary relationships of these birds have received much recent attention (W. E. Lanyon 1984, 1985, 1986, 1988a, b, c; McKitrick 1985; S. M. Lanyon 1985; Prum and Lanyon 1989; Prum 1990b, 1992; Mobley and Prum 1995; Bostwick 2000). W. E. Lanyon's work in particular has resulted in an extensive comparative morphological and behavioral data set for the Tyrannidae.

The relationships among the 90 to 100 genera of tyrant flycatchers were historically based on

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the shape of the bill, wing and tail, and color and pattern of plumage. Warter's (1965) survey of cranial osteological variation in the Tyrannoidea revealed variation in the nasal capsule and septum, palatine and palatomaxillary bones, interorbital septum, and general shape of the cranium. Warter felt that the nasal region provided useful taxonomic characters and recognized several basic states of the configuration of the nasal septum. Building upon Warter's (1965) work, W. E. Lanyon (1984, 1985, 1986, 1988a, b, c) completed a nearly exhaustive survey of tyrannoid cranial variation and used states of the nasal septum to hypothesize monophyly of five separate tyrannid assemblages that collectively included nearly all traditional tyrannid genera.

Ames (1971) documented great variation in suboscine syringeal musculature and support elements. However, Ames did not use differential stains and so could not readily distinguish between ossified and cartilaginous support elements. Lanyon (1984, 1985, 1986, 1988a, b, c) studied a nearly exhaustive sample of tyrannoid syringes which he stained to distinguish the ossified (primarily tracheal) series of elements from the cartilaginous (primarily bronchial) series. This allowed recognition of homologous elements. Lanyon used syringeal characters to group taxa within his five assemblages and used characters of the cranium, nesting behavior, plumage, and egg coloration wherever necessary to establish relationships within syringeal groups and occasionally at higher levels. That procedure is the equivalent of weighting those syringeal characters more heavily than others, effectively disallowing convergence in them. Nasal septum characters were effectively weighted even more heavily than syringeal characters because Lanyon assumed them to be synapomorphies of his five assemblages and disallowed convergence in them.

Lanyon (1984, 1985, 1986, 1988a, b, c) developed hypotheses of generic relationships based on shared similarities, but because he did not do so within a cladistic framework, some of his groups were supported by plesiomorphies. For example, in the *Elaenia* group Lanyon (1988a) used the poorly ossified condition of the anterior segment of the nasal septum to support a clade composed of *Capsiempis*, *Phaeomyias*, and *Nesotriccus*. He then used the fully ossified condition to support a clade composed of *Serpophaga* and *Anairetes*. Only one of those character states is the derived state and the other is the plesiomorphic, or ancestral, state in that group. Logically, only the derived state may argue for close relationship of the taxa that possess it.

A cladistic reanalysis of Lanyon's (1984, 1985, 1986, 1988a, b, c) data was performed plus any other data that could be found in the literature. I weighted characters equally and analyzed them together in one character matrix containing nearly all tyrannid genera, including several that Lanyon could not place in any of his assemblages. That provided a test of the monophyly of each of the five tyrannid assemblages Lanyon proposed and provided a test of homology of each of the five nasal septum states that supported them. Monophyly of the Tyrannidae has been questioned on the basis of DNA–DNA hybridization analyses that place several ''mionectid'' flycatchers as the sister group to the rest of the tyrannoids (cotingids + piprids + remaining tyrannids) (Sibley and Ahlquist 1985). The present analysis provides a test of the monophyly of the Tyrannidae as traditionally constituted (e.g. American Ornithologists' Union [AOU] 1998).

I compared reliability of morphological, behavioral, and ecological characters to recover tyrannid phylogeny. Although past workers have argued (e.g. Atz 1970) that behavioral and ecological characters lack phylogenetic information, several studies have found such characters to be at least as reliable as morphological and molecular characters (McLennan and Mattern 2001, Paterson et al. 1995, DeQueiroz and Wimberger 1993, but see Lee et al. 1996). Significantly different levels of homoplasy among four suites of tyrannid characters was tested for: cranial, syringeal, plumage, and behavioral and ecological characters.

METHODS

All 95 genera that served as terminal taxa in Lanyon's (1984, 1985, 1986, 1988a, b, c) five assemblages were included and the nomenclature follows his. Lanyon provided character support for monophyly of 64 of those genera. Lanyon (1986, 1988a) split *Mecocerculus* and *Myiophobus* into three groups each and placed them in different parts of his phylogenies yet retaining their generic names until more comparative data are available. Here these taxa are split as Lanyon did. Lanyon (1988b) argued for merging ''*Terenotriccus*'' *erythrurus* into *Myiobius* and his recommendation are followed here, but *Myiobius erythrurus* is kept as a terminal taxon separate from the remaining *Myiobius*. Several traditional tyrannid taxa have a nasal septum morphology that is either unknown or is sufficiently unique that Lanyon (1986, 1988a) refrained from placing them in any of his assemblages, maintaining them *incertae sedis*: *Phyllomyias fasciatus*, *P. griseiceps*, *P. griseocapilla*, and the monotypic genera *Colonia*, *Culicivora*, *Machetornis*, *Muscigralla*, and *Tachuris*. All of these taxa are included in this analysis except for *Phyllomyias griseocapilla* and *Culicivora*. For those two taxa, neither cranial nor syringeal data were available. Also included is the genus *Neopipo*, traditionally placed in the Pipridae, because Mobley and Prum (1995) hypothesized it to belong in the Tyrannidae on the basis of syringeal and plumage data.

Character data were extracted primarily from Lanyon (1984, 1985, 1986, 1988a, b, c). These references include photographs of representative syringes for all terminal taxa and photographs of crania for most. Because Lanyon reported on one assemblage at a time, he often did not explicitly describe, for a given character, the distribution of states across all tyrannid genera and in outgroups. In those cases, family-wide assessments and outgroup comparisons were made using Lanyon's photographs and other literature sources describing tyrannoid crania (Warter 1965) and syringes (Ames 1971; McKitrick 1985; Prum and Lanyon 1989; Prum 1990b, 1992; Mobley and Prum 1995). Lanyon did not make extensive use of syringeal musculature characters so those were extracted from Ames (1971). Because Ames (1971) did not use stains on ossified and cartilaginous syringeal support elements precedence was given to all more-recent information on those elements. Hilty and Brown (1986), Stiles and Skutch (1989), Ridgely and Tudor (1994) and similar guides for plumage characters were consulted. Foraging behavior characters are from Fitzpatrick (1980). For nest and egg characters, an exhaustive literature search was conducted, drawing information from many sources and adding two characters that Lanyon did not use: presence of a visor over the entrance of enclosed nests (character 66) and nests used as a dormitory (character 67). In addition, crania, skins, and Lanyon's cleared-and-stained syringeal specimens were examined at the American Museum of Natural History for any character data that were incomplete or inconclusive in the literature.

Lanyon (1984, 1986, 1988a) hypothesized the Tyrannidae to be monophyletic based on the presence of internal syringeal cartilages. Prum (1990b) questioned the homology of all internal syringeal cartilages and recommended using unique, detailed morphologies of internal cartilages as characters, while refraining from the hypothesis of homology of internal cartilages as broadly defined. Prum (1990b) hypothesized monophyly of the Tyrannidae on the basis of the presence of *Mm. obliqui ventrales*, a pair of intrinsic syringeal muscles. In this analysis ''*Mm. obliqui ventrales*'' is included as a character but not ''internal cartilages,'' except as several characters that describe unique details of some internal cartilages. An additional, heretofore unrecognized, potential synapomorphy of the tyrannids is included: B1 and B2 syringeal support elements which are connected at their ventral tips. That connection is absent in cotingids and piprids (Prum 1992; R. O. Prum pers. comm.).

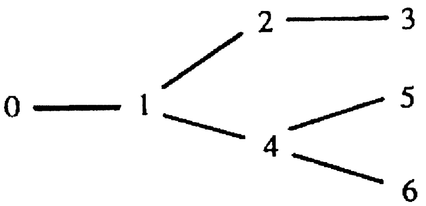

FIG. 1. Character state tree for character 11. Characters and states are described in Appendix 1.

Morphological and behavioral variation were coded as 50 binary characters, 15 unordered multistate characters, and 3 ordered multistate characters (Appendix 1). Characters 6 and 13 were ordered because states shared significant detail but some states had additional details that appeared to be further derived. For character 11 a state tree (Fig. 1) is defined reflecting a trend toward increasing numbers of double, complete syringeal A elements and increasing degree of ossification of those elements. That was justified because such a trend has apparently occurred in piprids (Prum 1992) and in some falconiforms (Griffiths 1994). Also, the ontogenetic development of those elements proceeds from an entirely cartilaginous state to an at least partly ossified state (Ames 1971).

PAUP* 4.0b8 (Swofford 2000) was used to perform heuristic searches for the most-parsimonious trees. To increase the probability of finding globally most-parsimonious trees, I repeated this search using all possible combinations of branch-swapping and stepwise-addition options. For each search I set a maximum of 2,000 trees to be held in memory. I also performed 1,000 replicates with the random addition option and one tree held in memory. Multistate taxa were interpreted as polymorphisms. I gave all characters equal weight. I felt this was justified in the absence of objective criteria for weighting some characters more heavily than others. Equal weighting schemes do, however, carry the assumption of low rates of change in all characters (Felsenstein 1982). I rooted all trees to Furnarioidea and allowed the other potential outgroups, Cotingidae and Pipridae, to ''float'' in the analysis. This allowed a test of the monophyly of the Tyrannidae as traditionally constituted.

I used consensus trees to summarize the resulting set of most-parsimonious trees. I computed a strict consensus tree which identifies groups found in all most-parsimonious trees. I also computed an Adams consensus tree (Adams 1972) which better illustrates patterns and trends among alternative most-parsimonious trees by identifying groups (not necessarily monophyletic) that consistently nest within larger groups in all trees. For example, if a set of nested groups exists in all most-parsimonious trees but in some of them is ''invaded'' by one taxon or a small group of taxa, the Adams consensus preserves the nested structure and places the problematic group outside of it in a polytomous position. The strict consensus simply collapses the entire nested group. Consensus trees should be interpreted with care as they may not be the most parsimonious hypotheses suggested by the data (Swofford 1991).

To evaluate the evidential support for relationships depicted in the strict consensus tree I used Sorenson's (1996) TreeRot program and PAUP* to compute a decay index (Bremer 1988, Källersjö et al. 1992). I ran 10 replicates with TBR branch-swapping, random addition sequence and a maximum of 800 trees held in memory. I also ran 100 replicates with random addition sequence and one tree held in memory. The decay index gives the number of extra steps required to show a node as unsupported. For example, if a node that occurs in all most-parsimonious trees is not present in trees that are one step longer, that node gets a decay index of 1. Higher index values indicate more robust clades.

I used two approaches to evaluate Lanyon's (1984, 1985, 1986, 1988a, b, c) hypothesized assemblages within the context of my data matrix. First, for those assemblages not supported in the strict consensus of most-parsimonious trees, I determined the number of extra steps required to force their monophyly. To do this I conducted heuristic searches constraining monophyly of each assemblage in turn. For each I ran 10 replicates with TBR branch-swapping, random addition, and a maximum of 800 trees held in memory. I also ran 1,000 replicates with one tree held in memory. I used Templeton's test (Templeton 1983) as implemented in PAUP* to determine whether the resulting trees were significantly different from the most-parsimonious trees. Second, I used MACCLADE 3.04 (Maddison and Maddison 1992) to examine evolution of nasal septum characters on the most-parsimonious trees. I evaluated the homology of septum characters that Lanyon (1984, 1985, 1986, 1988a, b, c) used to define his assemblages.

Finally, I used MACCLADE to calculate rescaled consistency indices (RC) for each character and to average them across 2,000 most-parsimonious trees representing all known tree islands. I used a single factor ANOVA to determine if mean RC was significantly different among four suites of characters: cranial (characters 1–10), syringeal (characters 12–45), plumage (characters 46–59), and behavior/ecology (characters 60–67). I did not include character 11 because MacClade does not include characters of user-defined type in these calculations.

RESULTS AND DISCUSSION

Phylogenetic analysis of 68 characters (a total of 101 apomorphies) and 106 taxa (Appendix 2) identified more than 2,000 most-parsimonious trees of length 514 and a consistency index (CI) of 0.44. I found several ''islands'' of most-parsimonious trees using different combinations of PAUP's search options. I found additional tree islands in the course of computing decay indices. The strict consensus of all most-parsimonious trees (Figs. 2–4) indicates support for the monophyly of many small groups of genera and of three assemblages which correspond more or less to Lanyon's (1984, 1985, 1986) kingbird, *Myiarchus*, and *Empidonax* assemblages. The monophyly of neither an *Elaenia* assemblage (Lanyon 1988a) nor a flatbill and tody-tyrant assemblage (Lanyon 1988c) is supported. An Adams consensus tree (Figs. 5 and 6) is better resolved. Each clade depicted in the Adams tree is present in at least some most-parsimonious trees, but the tree as a whole may not be consistent with any single most-parsimonious tree. Despite this, for the purposes of the following discussion it illustrates many results which are not apparent in the strict consensus (Figs. 2–4). Here I discuss my results as compared to each of Lanyon's (1984, 1985, 1986, 1988a, b, c) proposed assemblages and as compared to the traditional concept of the family Tyrannidae. Character numbers refer to characters in the present analysis.

Tyrannidae monophyly.—A traditional Tyrannidae exclusive of Cotingidae and Pipridae is supported in some most-parsimonious trees. However, there are no unambiguous synapomorphies. Neither of the two putative synapomorphies of the Tyrannidae provides unequivocal support for monophyly of the family as traditionally defined. In all most-parsimonious trees, intrinsic syringeal muscles *Mm. obliqui ventrales* that insert ventrally (character 43, state 1) are a synapomorphy of a restricted Tyrannidae whose exact membership varies from tree to tree but never includes the tody-tyrant group or the *Cnipodectes–Onychorhynchus–Myiobius* clade. The ventrally connected B1 and B2 elements (character 19) proved dif-

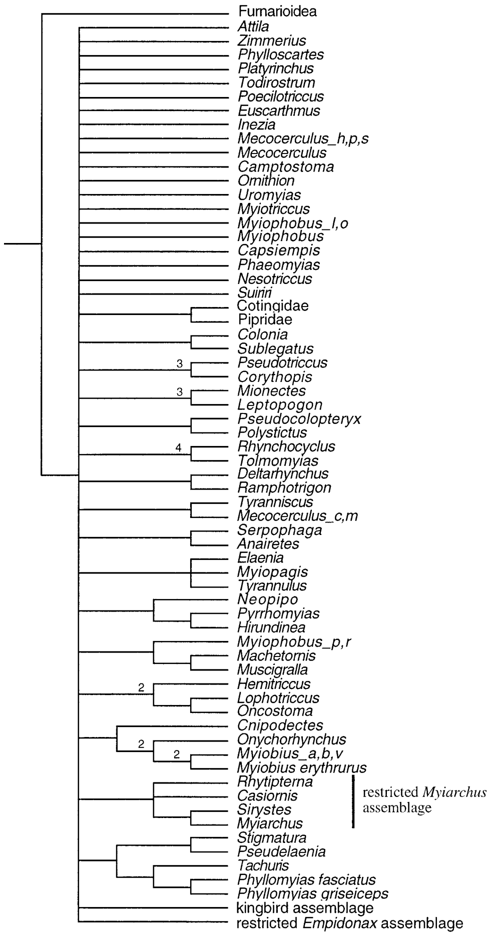

FIG. 2. Strict consensus tree derived from all most-parsimonious trees. Decay indices are shown when greater than 1. The two taxa at the bottom denote the assemblages shown in Figures 3 and 4.

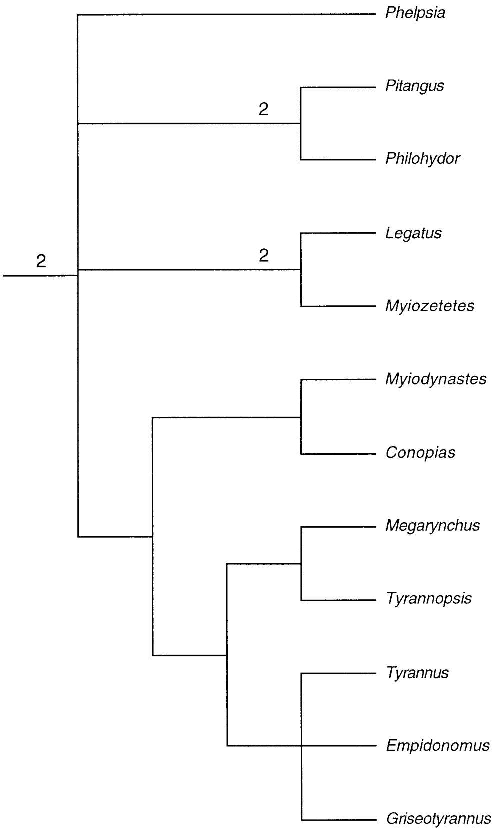

FIG. 3. Strict consensus tree of the kingbird assemblage. Decay indices are shown when greater than 1.

ficult to evaluate as a synapomorphy of the Tyrannidae. The basal or next-to-basal groups in each most-parsimonious tree possess this character, but the outgroup (Furnarioidea) was coded ''?'' (unknown). Therefore character 19 does not provide an unequivocal synapomorphy of the Tyrannidae in any most-parsimonious trees. To assess the level at which it is informative, one would need more information on this trait in the Furnarioidea and Old World suboscines.

Flatbill and tody-tyrant assemblage.—Lanyon (1988c) defined a flatbill and tody-tyrant assemblage based on the possession of: unossified nasal septa (character 1); cranial interorbital septa in which the supraorbital fenestra is reduced (character 9); and enclosed, pendant nests (character 64). This assemblage is not supported in any most-parsimonious trees. Four extra steps are required to force its monophyly, but such trees are not significantly different from most-parsimonious trees ($P > 0.64$; $21 < n < 27$ characters requiring differing numbers of steps on the trees being compared). Within his assemblage, Lanyon (1988c) defined a flatbill group (*Rhynchocyclus*, *Tolmomyias*, *Onychorhynchus*, and *Platyrinchus*) based on the possession of at least one ossified, double, complete syringeal A element (character 11). This state is present in many tyrannids outside the flatbills and tody-tyrants and is not a synapomorphy of these flatbills in any most-parsimonious trees. Lanyon's (1988c) hypothesized sister relationship between *Onychorhynchus* and *Platyrinchus* is not supported in any most-parsimonious trees. Two seemingly unique syringeal characters (23 and 31) shared by *Ony-*

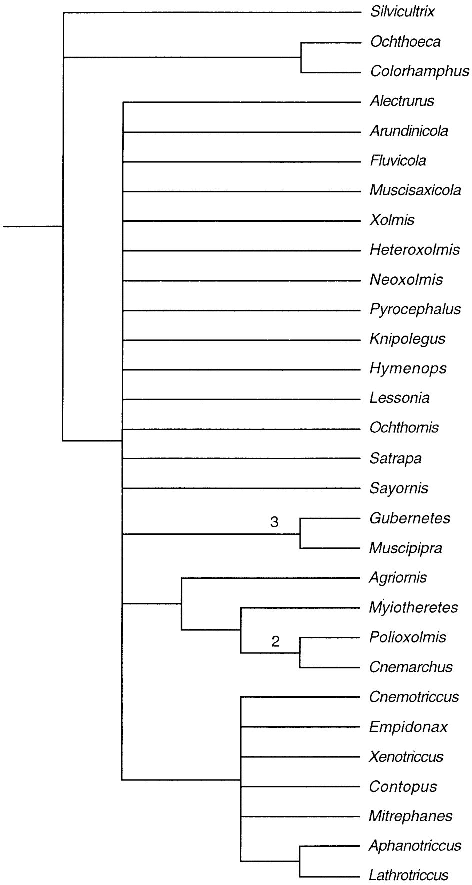

FIG. 4. Strict consensus tree of the restricted *Empidonax* assemblage. Decay indices are shown when greater than 1.

chorhynchus and *Platyrinchus* may be derived independently in these two taxa. A sister relationship between *Rhynchocyclus* and *Tolmomyias* is supported in all most-parsimonious trees by the presence of narrow, linear internal syringeal cartilages (character 29), a retort-shaped pendant nest (character 65) which is used as a dormitory (character 67). In all most-parsimonious trees this relationship is additionally supported by at least two of the following characters: 1, 11, 43, 49, 64.

Lanyon (1988c) could not determine the relationships of *Cnipodectes* within the assemblage, maintaining it in a polytomy with his flatbill clade and tody-tyrant clade. My results suggest that *Cnipodectes* is the sister group to a clade composed of *Onychorhynchus* and *Myiobius* (including *erythrurus*). This relationship is supported in all most-parsimonious trees by the presence of long rictal bristles (character 57) and rufous tails (character 53; lost within *Myiobius*). I discuss the hypothesized sister relationship between *Onychorhynchus* and *Myiobius* below with the *Empidonax* assemblage.

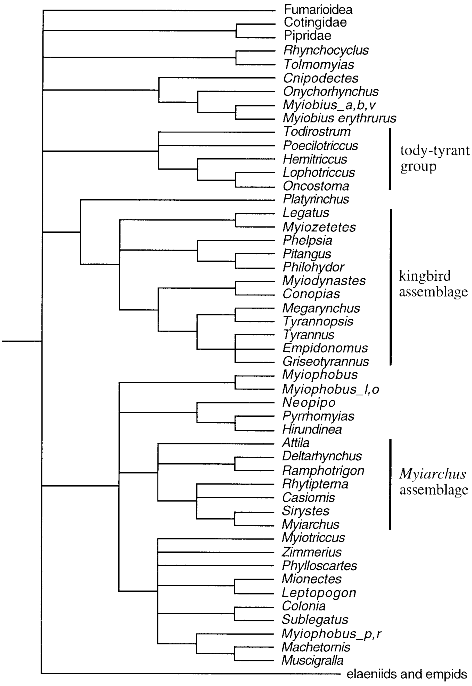

FIG. 5. Adams consensus tree derived from all most-parsimonious trees. The taxon at the bottom denotes the assemblage shown in Figure 6.

Lanyon (1988c) defined a tody-tyrant group (*Todirostrum*, *Poecilotriccus* [including *Taeniotriccus*], *Hemitriccus* [including *Myiornis*], *Lophotriccus* [including *Atalotriccus*], and *Oncostoma*) based on the possession of two characters: 1) a horseshoe-shaped, cartilaginous bronchial plate, and 2) delicate, rod-like internal cartilages located near the caudal ends of the horseshoe. In the present study, I combined these into one character state (character 27, state 1) which supports monophyly of Lanyon's tody-tyrant group in some, but not all most-parsimonious trees. Lanyon (1988c) proposed a clade composed of *Hemitriccus*, *Lophotriccus*, and *Oncostoma* based on the presence of a pessulus that extends anteriorly to divide four or more A elements dorsally (character 16). This clade is supported in all most-parsimonious trees by character 16 and, additionally in some most-parsimonious trees, by characters 43 and

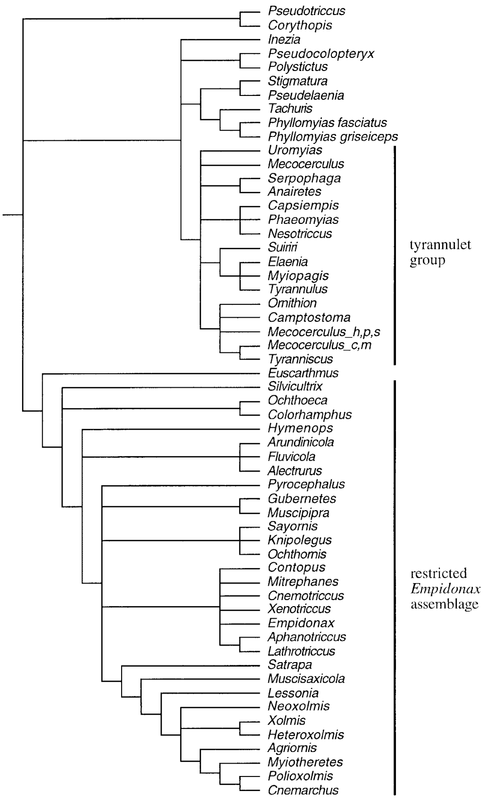

FIG. 6. Adams consensus tree of an ''elaeniid and empid'' clade.

64. *Lophotriccus* and *Oncostoma* are supported as sister groups by a laterally compressed syrinx and trachea (character 26) in all most-parsimonious trees.

There is some support for a basal placement of the flatbills and tody-tyrants within the Tyrannidae and perhaps within the Tyrannoidea. In all most-parsimonious trees the flatbills and tody-tyrants are basal to a large clade containing the majority of tyrannids plus, in some most-parsimonious trees, cotingids and piprids. This large clade is supported by the presence of ossified nasal septa (character 1). This is at least partly congruent with the results of Sibley and Ahlquist's (1985) DNA–DNA hybridization analyses in that the tody-tyrants *Todirostrum* and *Hemitriccus* were among the taxa they placed in their family ''Mionectidae'' as the sister group to the rest of the tyrannoids (cotingids + piprids + remaining tyrannids).

Kingbird assemblage.—Results support a kingbird assemblage completely consistent with that of Lanyon (1984) (Fig. 3). It is supported in all most-parsimonious trees by characters 3, 9, 10, 44, and 55. My hypothesis of relationships within this assemblage is, however, less well resolved than Lanyon's (1984). This is due to the fact that Lanyon (1984) used alternative derived states of the ventral connection of the B1 and B2 syringeal support elements (character 19) to support two major clades within the assemblage: *Phelpsia, Pitangus, Philohydor, Legatus,* and *Myiozetetes* have flattened connections (state 1) whereas the remaining seven genera in the assemblage have rounded connections (state 2). My family-wide analysis indicates that flattened connections, which occur in nearly all tyrannids, are ancestral in the kingbird assemblage and thus do not argue for relationships within it. My results do not support monophyly of Lanyon's clade composed of the five genera named above. However, rounded connections (state 2) appear to be unique to *Myiodynastes, Conopias, Megarynchus, Tyrannopsis, Tyrannus, Empidonomus,* and *Griseotyrannus.* This clade is supported in all most-parsimonious trees by characters 19 and 32. Lanyon's hypothesized relationships among these genera are also supported in all most-parsimonious trees. Character 62 supports a sister-group relationship between *Myiodynastes* and *Conopias.* Characters 20, 42, and 61 support a clade composed of *Megarynchus, Tyrannopsis, Tyrannus, Empidonomus,* and *Griseotyrannus.* Character 32 supports a sister-group relationship between *Megarynchus* and *Tyrannopsis.* Character 59 supports a clade composed of *Tyrannus, Empidonomus,* and *Griseotyrannus.*

Character 11 supports sister-group relationships between *Pitangus* and *Philohydor* (two or more double, complete, ossified A elements) and between *Legatus* and *Myiozetetes* (incomplete A3 elements fused to complete A2). Character 45 (intrinsic syringeal muscles *Mm. obliqui laterales*) supports the *Legatus–Myiozetetes* relationship in some most-parsimonious trees, but in the remainder of trees, this is ambiguous due to uncertainty about the state of this character in *Phelpsia.*

Empidonax assemblage.—A restricted *Empidonax* assemblage (Fig. 4) is supported containing the same genera that Lanyon (1986, 1988b) placed in it except for the four genera that comprise his *Myiophobus* group: *Myiophobus, Pyrrhomyias, Hirundinea,* and *Myiobius.* Seven extra steps are required to force a monophyletic *Empidonax* assemblage including the *Myiophobus* group. However, such trees are not significantly different from most-parsimonious trees ($P > 0.36$; $14 < N < 26$ characters requiring differing numbers of steps on the trees being compared). In all most-parsimonious trees the monophyly of the restricted *Empidonax* assemblage is supported by the presence of a nasal septum with basal trabecular plate and anterior notch (character 4), a wide posterior fork on the trabecular plate (character 7), and ''near-ground generalist'' foraging behavior (character 61). In all most-parsimonious trees, the ''*Myiophobus* group'' genera are distantly related to this restricted *Empidonax* assemblage.

Within the *Empidonax* assemblage, these results support Lanyon's (1986) hypothesis of a basal position of the chat-tyrants *Ochthoeca, Silvicultrix* and *Colorhamphus*. These results do not support the monophyly of Lanyon's (1986) *Ochthoeca* group composed of these three genera plus *Arundinicola, Fluvicola,* and *Alectrurus*. Lanyon (1986) used character 11, state 0 (no A elements completely encircle the bronchi) to support his *Ochthoeca* group, but my family-wide analysis indicates that this state is ancestral in the *Empidonax* assemblage and does not argue for a close relationship of these taxa.

The monophyly of a large clade (*Alectrurus* through *Lathrotriccus* in Fig. 4) composed of all of the restricted *Empidonax* assemblage genera except *Ochthoeca*, *Silvicultrix* and *Colorhamphus* is supported in all most-parsimonious trees by characters 22, 49, or both. Within this large clade, a group (*Cnemotriccus* to *Lathrotriccus* in Fig. 4) similar to Lanyon's (1986) *Empidonax* group is supported in all most-parsimonious trees by character 49, and additionally in some of those trees by characters 13, 22, and 61. *Sayornis*, which possesses the uniquely modified syringeal A2 elements (character 13) of this group is, in some most-parsimonious trees, the basal member of the group. In other most-parsimonious trees, however, *Sayornis* groups with other taxa that lack wing bars (character 49) and are ''near-ground generalist'' foragers (character 61). In all most-parsimonious trees, characters 24, 25, and 52 support *Gubernetes* and *Muscipipra* as sister groups.

Few additional relationships are well resolved in the strict consensus of this assemblage (Fig. 4), but upon examination of the set of most-parsimonious trees and of the Adams consensus (Fig. 6), some patterns are evident. For example, all most-parsimonious trees contain a clade corresponding roughly to Lanyon's (1986) *Muscisaxicola* group containing the ground-tyrants, shrike-tyrants, bush-tyrants and allies. *Hymenops*, which shares some plumage and habitat characters with this group, is, in some most-parsimonious trees, placed within this clade (*Muscisaxicola* through *Cnemarchus* in Fig. 6); hence, a *Muscisaxicola* group is not depicted in the strict consensus (Fig. 4). This group, with or without *Hymenops,* is supported by characters 60 (habitation of open grassland or marsh) and 61 (ground specialist foraging behavior). In agreement with Lanyon's (1986) concept of this group, *Muscisaxicola* always is placed basally, as illustrated in Figure 6. Patterned wings (character 48) and notched or attenuated primaries (character 59) support monophyly of the rest of the group exclusive of *Muscisaxicola*. ''Perch-to-ground'' foraging behavior (character 61) supports a group exclusive of *Muscisaxicola* and *Lessonia*.

A clade composed of *Agriornis, Myiotheretes, Polioxolmis* and *Cnemarchus* is supported in all most-parsimonious trees by the presence of streaked throat plumage (character 50). Lanyon's (1986) hypothesized bush-tyrant clade composed of *Myiotheretes*, *Polioxolmis* and *Cnemarchus* is supported in all most-parsimonious trees by an ossified interorbital septum (character 9) and a transition from open grassland to forest–woodland habitat (character 60). Lanyon (1986) was unable to resolve relationships among these genera, but these results support *Polioxolmis* and *Cnemarchus* as sister groups based on the relatively narrow dorsal ends of their B1 syringeal support elements (character 22, state 0), and the presence of well developed *Mm. obliqui ventrales* (character 44). Lanyon (1988a) used character 44 in the *Elaenia* assemblage but apparently did not recognize it in the *Empidonax* assemblage. Lanyon (1986) hypothesized a clade composed of *Arundinicola, Fluvicola, Alectrurus* supported by characters 8, 56, and 60. In the present study, these characters support such a clade in some most-parsimonious trees. The remainder of most-parsimonious trees hypothesize an (*Arundinicola* (*Fluvicola* (*Alectrurus*, *Hymenops*))) clade. *Hymenops* shares plumage and habitat characters with the other three genera, but Lanyon (1986) placed

Hymenops in his *Knipolegus* group with which it also shares plumage and syringeal characters. *Arundinicola*, *Fluvicola*, and *Alectrurus*, at least, appear to be closely related, as depicted in Figure 6.

The double, complete, ossified syringeal A elements (character 11) and concealed crown patch (character 46) present in Lanyon's (1986, 1988b) *Myiophobus* group are not present in the rest of the *Empidonax* assemblage and argue for the placement of these genera elsewhere. In the set of most-parsimonious trees, *Myiophobus*, *Pyrrhomyias*, and *Hirundinea* are allied with several different groups outside the *Empidonax* assemblage. A sister-group relationship between *Myiobius* (including *erythrurus*) and *Onychorhynchus* is supported by the presence of at least two double, complete, ossified syringeal A elements (character 11) and an ossified interorbital septum (character 9). *Myiobius* also has the long rictal bristles (character 57) and *erythrurus* has the rufous tail (character 53) found in *Onychorhynchus* and *Cnipodectes*. Past workers (Ames 1971, Traylor 1977, Traylor and Fitzpatrick 1982) have hypothesized a close association between *Myiobius* and *Onychorhynchus* based on these syringeal and plumage characters. *Myiobius* builds a pendant, enclosed nest (character 64) as do *Onychorhynchus* and *Cnipodectes*, but in the present analysis this character does not support the relationship of *Myiobius* to these genera because the globular nests (state 1) of *Myiobius* and elongate nests (state 2) of *Onychorhynchus* and *Cnipodectes* were coded as alternative unordered states. Characters 1, 4, 19, and, in some most-parsimonious trees, 64 support *Myiobius* (formerly *Terenotriccus*) *erythrurus* as sister group to the other *Myiobius* species. This is congruent with Lanyon's (1988b) merger of *erythrurus* into *Myiobius*. Characters 40, 48, and, in some most-parsimonious trees, 22 support *Pyrrhomyias* and *Hirundinea* as sister groups in agreement with Lanyon (1986, 1988b). *Neopipo* is supported as their sister group by characters 11, 43, and 54. This agrees with one of Mobley and Prum's (1995) hypotheses. However, cranial data for *Neopipo* are still needed to evaluate this hypothesis.

The nasal septa of ''*Myiophobus*'' (*lintoni*, *ochraceiventris*, *phoenicomitra*, and *roraimae*) have trabecular plates that are elevated above the base of the septum (character 4, state 2) which caused Lanyon (1986, 1988a) to remove them from *Myiophobus* and place them in the *Elaenia* assemblage. He refrained from creating new generic names until more comparative data are available. These results do not give strong support for the removal of *lintoni* and *ochraceiventris*. *Myiophobus*, now including only the species *cryptoxanthus*, *fasciatus*, *flavicans*, *inornatus*, and *pulcher*, is supported as the sister group to ''*Myiophobus*'' *lintoni* and *ochraceiventris* in some most-parsimonious trees by character 49 and, additionally in some trees by 17. However, in no most-parsimonious trees are ''*Myiophobus*'' *phoenicomitra* and *roraimae* closely related to other *Myiophobus*. These results support Lanyon's (1986, 1988a) conclusion that *Myiophobus* as traditionally delimited (Traylor 1979, Sibley and Monroe 1990) is not monophyletic, with at least *phoenicomitra* and *roraimae* belonging elsewhere. In all most-parsimonious trees, ''*Myiophobus*'' *phoenicomitra* and *roraimae* are the sister group of a clade composed of *Machetornis* and *Muscigralla*. The relationship is supported by characters 8, 9, or both. The interorbital septum (character 9) requires further study in these taxa, particularly in *Machetornis* for which I followed Warter (1965) and coded as having two fenestrae open (state 0). The one specimen of *Machetornis* examined (AMNH 6657), however, had the infraorbital fenestra enlarged and supraorbital fenestra reduced (state 1), suggesting some unknown degree of variation.

Myiarchus assemblage.—The monophyly of Lanyon's (1985) *Myiarchus* assemblage is supported in some, but not all, most-parsimonious trees. This clade is supported by the presence of cavity nesting (character 62). A restricted assemblage composed only of *Rhytipterna*, *Casiornis*, *Sirystes*, and *Myiarchus* is supported in all most-parsimonious trees by the presence of internal cartilages that are robust ''J'' or ''L'' shaped (character 32) and are attached to the ventral side of the tracheobronchial junction (character 39). In some most-parsimonious trees it is additionally supported by an ossified interorbital septum (character 9). A *Deltarhynchus–Ramphotrigon* clade is supported in all most-parsimonious trees by characters 37 and 49, and, in some most-parsimonious trees, additionally by character 11. Lanyon (1985) described extreme similarity among the crania and syringes of *Myiarchus*, *Sirystes*, and *Casiornis*. He was unable to develop a hypothesis of their relationships. My results suggest that

Sirystes and *Myiarchus* are sister groups. This relationship is supported by the presence of dorsally divergent B1 and B2 syringeal support elements (character 21), a character that Lanyon (1984) used in the kingbird assemblage but apparently did not recognize in the myiarchines.

Elaenia assemblage.—These results do not support monophyly of the *Elaenia* assemblage (Lanyon 1988a). Seven extra steps are required to force its monophyly, but such trees are not significantly different from most-parsimonious trees ($P > 0.19$; $14 < n < 25$ characters requiring differing numbers of steps on the trees being compared). Some most-parsimonious trees include a large clade containing most of the genera of the *Elaenia* assemblage plus the restricted *Empidonax* assemblage (Fig. 6). In the remainder of most-parsimonious trees this clade also includes a group of ten taxa (*Myiotriccus* through *Muscigralla* in Fig. 5), most of which Lanyon (1988a) placed in his *Elaenia* assemblage. In all most-parsimonious trees, the fusion of tracheal A elements into a drum (character 14) supports a ''tyrannulet'' group (Fig. 6) corresponding roughly to Lanyon's (1988a) *Elaenia* group in his *Elaenia* assemblage. Its monophyly is not supported in the strict consensus (Fig. 2) because *Inezia*, *Pseudocolopteryx*, and *Polystictus* are included in the group in some most-parsimonious trees. That group is characterized in all most-parsimonious trees by the apparently homologous presence of well-developed *Mm. obliqui ventrales* (character 44), a superciliary eye stripe (character 55), perch-gleaning foraging behavior (character 61), and unmarked eggs (character 68).

These results support the monophyly of several of Lanyon's (1988a) smaller clades within the *Elaenia* assemblage. A clade composed of *Elaenia*, *Myiopagis*, and *Tyrannulus* is supported by character 14 plus either 46 or 55. Sister-group relationships between *Stigmatura* and *Pseudelaenia* (character 6), between *Pseudotriccus* and *Corythopis* (characters 5, 18, 33), between *Serpophaga* and *Anairetes* (character 14 plus either 7 or 43), and between *Mionectes* and *Leptopogon* (characters 6, 42, 66, and, in some most-parsimonious trees, 68) are supported. *Tyranniscus* is supported as the sister group to ''*Mecocerculus*'' *calopterus* and *minor* by characters 14 and 35 and, in some most-parsimonious trees, character 6. This supports Lanyon's (1988a) grouping of these taxa and his conclusion that the genus *Mecocerculus* as traditionally delimited (Traylor 1979, Sibley and Monroe 1990) is polyphyletic. In some most-parsimonious trees, ''*Mecocerculus*'' (*hellmayri*, *poecilocercus*, and *stictopterus*) is the sister group to the clade composed of *Tyranniscus* and ''*Mecocerculus*'' *calopterus* and *minor* based on the presence of an additional, posterior trabecular plate in the nasal septum (character 6). Lanyon (1988a) left one species (*leucophrys*) in *Mecocerculus*. In no most-parsimonious trees is it closely related to the other species traditionally placed in *Mecocerculus*.

Additional tyrannid genera.—This analysis resulted in hypotheses of relationships for most of the problematic genera that Lanyon (1986, 1988a) maintained *incertae sedis*. A clade composed of *Tachuris*, *Phyllomyias fasciatus* and *P. griseiceps* is supported by the loss of two derived characters: the elevated trabecular plate in the nasal septum (character 4; cranial data for *P. griseiceps* lacking) and a *Myiarchus*-like configuration of the syringeal B1 and B2 elements (character 22). They also share a derived syringeal character with *Stigmatura* and *Pseudelaenia*: a cartilaginous bronchial plate with robust internal cartilages (character 27) which supports a clade composed of these five taxa. Lanyon (1988a) thought the syringes of *Phyllomyias fasciatus* and *P. griseiceps* to be very different from each other and speculated that *Phyllomyias* (composed of *fasciatus*, *griseiceps*, and *griseocapilla*) is polyphyletic. I examined Lanyon's cleared-and-stained syringeal specimens (three of *fasciatus* and one of *griseiceps*) and found them to be quite similar. The syrinx of *griseiceps* gives the impression of being a more ossified version of the *fasciatus* syringes. Their cartilaginous bronchial plates are very similar in detail and the internal cartilages of both species are attached to narrow caudal extensions of the bronchial plates. Besides the degree of ossification, the only conspicuous difference between the syringes of the two species is the shorter internal cartilages of *griseiceps* which lack the large, amorphous ventral and caudal extension present in *fasciatus*. *Phyllomyias fasciatus* and *P. griseiceps* are supported as sister groups in all most-parsimonious trees by character 61 (fruit/upward hover-glean foraging behavior). I suggest that *Phyllomyias fasciatus* and *P. griseiceps* are indeed closely related, possibly sister species (pending examination of crania of *P. griseiceps* and *P. griseocapilla* and syringes of *P. griseocapilla*).

Machetornis and *Muscigralla* are supported as sister groups by three characters: the loss of a *Myiarchus*-like configuration of the syringeal B1 and B2 elements (character 22), habitation of open grassland or marsh (character 60), and ground specialist foraging behavior (character 61). *Colonia* and *Sublegatus* are supported as sister groups by character 55 and, in some most-parsimonious trees, additionally by characters 9, 30, and 46.

Homology of nasal septum characters.—My results provide a test of the homology of each of the states of the nasal septum that Lanyon (1984, 1985, 1986, 1988a, c) used to define his assemblages. Lanyon (1988c) used the unossified nasal septum (character 1) as one of three characters defining his flatbill and tody-tyrant assemblage. When reconstructed on all most-parsimonious trees, the unossified septum is homologous in *Cnipodectes*, *Onychorhynchus*, *Todirostrum*, *Poecilotriccus*, *Hemitriccus*, *Lophotriccus*, and *Oncostoma*, and, in some most-parsimonious trees, *Rhynchocyclus*, *Tolmomyias*, and *Platyrinchus* as well. The unossified septum in *Tachuris*, which Lanyon (1988c) did not include in his flatbill and tody-tyrant assemblage, is convergent in all most-parsimonious trees. The unossified septum is symplesiomorphic in all most-parsimonious trees because, except for the highly ossified nasal capsules of *Dendrocolaptes*, furnarioids have unossified septa. That character, therefore, does not provide a synapomorphy for a flatbill and tody-tyrant assemblage. However, informative characters are potentially existent in the morphology of the cartilaginous parts of the nasal capsules of these birds. At least some of the tody-tyrants probably have cartilaginous trabecular plates within their cartilaginous septa as suggested by the ossification of those structures in occasional specimens (Lanyon 1988c).

Lanyon (1984) defined his kingbird assemblage partly by the presence of an ossified nasal septum that lacks both a trabecular plate and an internal support rod. In all most-parsimonious trees, a reduced internal support rod (character 3) is homologous in all kingbird assemblage taxa. In all most-parsimonious trees, character 3 is convergent in *Attila*, in *Colonia*, and in *Machetornis*. The absence of a trabecular plate (character 4) is symplesiomorphic in all most-parsimonious trees and does not provide a synapomorphy of the kingbird assemblage.

Lanyon (1985) defined his *Myiarchus* assemblage (without *Attila*) partly by the presence of an ossified nasal septum with a conspicuous internal support rod (character 3). Most tyrannids possess this character. My family-wide analysis indicates that it is symplesiomorphic and does not provide a synapomorphy of the *Myiarchus* assemblage. My results indicate that there are no nasal septum characters supporting this group, with or without *Attila*. Lanyon (1985) recognized that these genera (except *Attila*) have ossified nasal capsules (character 8) which surround the septum, but he did not explicitly include this in his list of characters. In all most-parsimonious trees in the present analysis, character 8 is homologous in *Deltarhynchus*, *Ramphotrigon*, *Rhytipterna*, *Sirystes*, *Casiornis*, and *Myiarchus*, though in some most-parsimonious trees it is not a synapomorphy. I examined the same four crania of *Attila spadiceus* and two of *A. cinnamomeus* that Lanyon (1985) did and, contrary to his report, found one (*A. cinnamomeus*, AMNH 11616) with a completely ossified nasal capsule. A larger sample of *Attila* crania may show a significant tendency for nasal capsules to ossify and thus may strengthen the evidence of a relationship between *Attila* and the *Myiarchus* assemblage.

Lanyon (1986) defined his *Empidonax* assemblage solely by the presence of an ossified nasal septum with basal trabecular plate and anterior notch (character 4) and posterior forking (character 7). In all most-parsimonious trees, a basal trabecular plate and anterior notch is homologous in all genera in the restricted *Empidonax* assemblage (Fig. 4). In all most-parsimonious trees, this character is convergent in *Myiobius* and in the *Pyrrhomyias*–*Hirundinea* clade. This type of nasal septum is also present in *Myiophobus* (composed of *cryptoxanthus*, *fasciatus*, *flavicans*, *inornatus* and *pulcher*) and is, in some most-parsimonious trees, hypothesized to be homologous with those in *Pyrrhomyias* and *Hirundinea*. Lanyon (1988a) described the surprising appearance of this type of nasal septum in six species of *Elaenia*, providing further evidence that this seemingly unique character has arisen convergently. In these *Elaenia* species and in *Pyrrhomyias*, *Hirundinea*, and *Myiobius*, the trabecular plate is not conspicuously forked posteriorly (character 7) as it is in the restricted *Empidonax* assemblage and in *Myiophobus*. In all most-parsimonious trees, a wide posterior fork is homologous in all genera in the restricted *Empidonax* assemblage (except lost in *Cnemarchus*). In all most-parsimonious trees it is convergent in *Myiophobus*. Nasal septa with basal trabecular plates and anterior notches (character 4) and wide posterior forking (character 7) appear to be synapomorphies of a restricted *Empidonax* assemblage.

Lanyon (1988a) defined his *Elaenia* assemblage solely by the presence of an ossified nasal septum with a trabecular plate elevated above the ventral edge of the septum (character 4). In all most-parsimonious trees, an elevated trabecular plate is homologous in all genera of ''tyrannulets'' and allies (*Pseudotriccus* through *Tyranniscus* in Fig. 6). It is also homologous within a smaller group (*Myiotriccus* through *Muscigralla* in Fig. 5). In all most-parsimonious trees, the elevated trabecular plate is a synapomorphy of a clade containing some or all *Elaenia* assemblage genera and the restricted *Empidonax* assemblage genera. In all most-parsimonious trees, the basal plates of the restricted *Empidonax* assemblage are hypothesized to have evolved from elevated plates. In all most-parsimonious trees, the narrow, slender posterior forks (character 7) found in several *Elaenia* assemblage genera arise two or three independent times, but are always homologous in *Capsiempis*, *Phaeomyias*, and *Nesotriccus*, and in *Serpophaga* and *Anairetes*, and in *Pseudocolopteryx* and *Polystictus*. Lanyon (1988a) examined one cranium each of *Phyllomyias fasciatus* and *Tachuris* and both lacked trabecular plates (the septum of *Tachuris* was simply unossified). In all most-parsimonious trees, these are reconstructed as a single derived loss of ossified, elevated trabecular plates.

Levels of homoplasy in character suites.—Cranial characters (mean RC = 0.39), syringeal characters (mean RC = 0.47), plumage characters (mean RC = 0.33), and behavioral and ecological characters (mean RC = 0.52) did not differ significantly in levels of homoplasy ($P = 0.57$). The behavioral and ecological characters in this study contained a level of phylogenetic information similar to those that Hughes (1996) used for the Cuculidae. These results are in accord with a growing number of studies that find significant phylogenetic structure in behavioral and ecological characters (e.g. Prum 1990a, Winkler and Sheldon 1993, Paterson et al. 1995, Hughes 1996, McLennan and Mattern 2001). Among the suites of morphological characters, plumage characters exhibited the most homoplasy, though not significantly so. Only one plumage character—long rictal bristles (character 57)—exhibited no homoplasy on any most-parsimonious tree. A pointed crest (character 58) exhibited no homoplasy on some, but not all most-parsimonious trees. The ten plumage characters that describe color patterns tend to be more homoplasious (mean RC = 0.26) than those that describe feather form, but this is still not significantly different from other character suites ($P = 0.36$). Omland and Lanyon (2000) found similarly high levels of homoplasy in plumage characters in orioles and cautioned against heavy use of such characters in phylogenetic analysis. It appears likely that convergence, parallelism, and reversal have been common in the evolution of avian plumage color patterns, perhaps due to evolutionary conservatism of the underlying developmental pathways coupled with lability of the on–off switches of those pathways (Price and Pavelka 1996).

Summary.—I performed a cladistic analysis of all currently available morphological and behavioral data for the Tyrannidae. Most characters were drawn from Lanyon (1984, 1985, 1986, 1988a, b, c). My analysis differs from Lanyon's in five important ways: first, I added several characters. Second, I examined furnarioid outgroups in addition to the tyrannoid outgroups Lanyon considered. Third, I assessed character states across all tyrannid genera and in outgroups, allowing simultaneous analysis of all taxa and tests of monophyly of the Tyrannidae and of each of Lanyon's proposed assemblages. Fourth, I gave characters equal weight, allowing tests of the homology of cranial and syringeal characters that Lanyon used to define groups. Fifth, I worked within a cladistic framework that explicitly roots trees to an outgroup. This ensures plesiomorphies are not used as character support for clades.

My results provide equivocal support for monophyly of the Tyrannidae. An equally parsimonious hypothesis suggests that the flatbill and tody-tyrant genera are more distantly related to other tyrannids than are cotingids and piprids. Results support monophyly of the kingbird assemblage, restricted *Myiarchus* and

Empidonax assemblages, and several lower-level groupings. Monophyly of neither the *Elaenia* nor the flatbill and tody-tyrant assemblage is supported. Nasal septum characters that past workers have considered conservative and phylogenetically informative are supported as synapomorphies of the kingbird assemblage and of a restricted *Empidonax* assemblage. A nasal capsule character provides equivocal support for a *Myiarchus* assemblage without *Attila*. Many nodes have minimal support. Much more data are needed to resolve relationships in the Tyrannidae, especially at higher levels. In accord with previous studies, plumage coloration patterns exhibited relatively high levels of homoplasy.

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APPENDIX 1. Descriptions of characters used in analysis. Characters 6, 11, and 13 are ordered. Character 11 is ordered by a character state tree described in Figure 1. The remaining characters are unordered.

Cranial

Nomenclature follows Baumel (1979) when possible. Otherwise, it follows Lanyon (1984, 1985, 1986, 1988a, b, c).

1. *Septum nasale*.—(0) Ossified to varying degrees; (1) unossified in the flatbill and tody-tyrant assemblage (Lanyon 1988c), in *Tachuris* (Lanyon 1988a), and in most furnarioids (pers. obs.). In these taxa there is usually just a shallow dorsal remnant of a septum in cleaned museum specimens.

2. *Anterior segment of septum nasale osseum*.—(0) Well ossified anterior to the internal support rod; (1) poorly ossified anterior to support rod.

3. *Internal support rod*.—(0) Conspicuous internal support rod within the septum nasale osseum; (1) no conspicuous internal support rod. In the kingbird assemblage (Lanyon 1984) and in the genera *Attila*, *Colonia*, and *Machetornis* (J. S. Birdsley pers. obs.), there is only a pattern or grain running anterodorsally to posteroventrally on the surface of the septum in the position where the rod is located in the septa of other tyrannoids.

4. *Transverse trabecular plate within septum nasal osseum*.—(0) No transverse trabecular plate; (1) a transverse trabecular plate is at the base (ventral edge) of the septum and there is a distinctive notch in the septum anterior to the trabecular plate; (2) a transverse trabecular plate is elevated above the ventral edge of the septum, so that there appears to be a mid-sagittal ridge on the ventral side of the trabecular plate. There is no anterior notch associated with this type of trabecular plate; (3) a transverse trabecular plate is barely elevated above the ventral edge of the septum and occupies only a very short segment of the anterior part of the septum. It is very broad, truncated posteriorly, and has no anterior notch. Present in *Colonia* and hypothesized by Lanyon (1986) to be unique among tyrannids.

5. *Trabecular plate reduced, anterior*.—(0) The elevated type trabecular plate (if present) is relatively broad and occupies the length of the septum anterior to the internal support rod; (1) the elevated trabecular plate is narrow and occupies only a small part of the most anterior section of the septum.

6. *Trabecular plate divided*.—(0) The trabecular plate (if present) exists only anterior to the internal support rod; (1) the elevated type trabecular plate is divided into a small section posterior to the internal support rod and larger section anterior to the rod. Both sections are relatively slim; (2) the elevated trabecular plate is divided into a bulbous posterior section and a thin anterior section; (3) the elevated trabecular plate is divided into bulbous posterior and bulbous anterior sections.

7. *Trabecular plate forked posteriorly*.—(0) Trabecular plate (if present) is truncate or tapered posteriorly; (1) trabecular plate is widely forked posteriorly (Lanyon 1986, 1988b). (2) trabecular plate is narrowly forked posteriorly, appearing as a slender tuning fork (Lanyon 1988a).

8. *Nasal capsule*.—(0) Unossified; (1) fully ossified including alinasal walls and concha nasalis [turbinals in Lanyon (1985)].

9. *Septum interorbitale*.—(0) Two open fenestrae; (1) infraorbital fenestra enlarged and supraorbital fenestra reduced (Lanyon 1988a, c); (2) both fenestrae reduced or absent; septum ossified.

10. *Medial ridge in frontal region of cranium*.—(0) Absent; (1) present.

Syringeal

Nomenclature of syringeal support elements and cartilages follows Ames (1971) and Lanyon (1984, 1985, 1986, 1988a, b, c). Nomenclature of syringeal musculature follows King (1979) which is also consistent with the above references.

11. *Double, complete A elements*.—(0) None of the (primarily tracheal) ''A'' series of syringeal support rings completely encircle the bronchi; (1) one A element is double (associated with the bronchi rather than the trachea) and complete (completely encircling each bronchus). They are medially cartilaginous; (2) two A elements are double, complete, and medially cartilaginous; (3) two or more A elements are double, complete, and medially ossified; (4) one A element is double, complete, and medially ossified; (5) incomplete A3 elements contribute to support of each bronchus through fusion to the complete A2 elements; (6) incomplete A2 elements contribute to support of each bronchus through fusion to the complete A3 elements.

12. *Cartilaginous dorsal segments of A1 elements*.—(0) A1 elements are nearly fully ossified, sometimes with small, cartilaginous dorsal tips; (1) A1 elements terminate dorsally in large cartilaginous segments.

13. *Medial segments of A2 elements modified*.—(0) Medial segments of A2 elements (when double and complete) are smooth; (1) cartilaginous medial segments of A2 elements are enlarged and bulbous caudally, presumably for the attachment of the internal cartilages (Lanyon 1986); (2) cartilaginous medial segments of A2 elements are enlarged and bulbous as in state (1) but are disconnected from the remaining (ossified) portion of the A2 element.

14. *Tracheal "drum"*.—(0) Tracheal A elements are largely independent of one another; (1) two or more tracheal A elements are fused to form a tracheal drum. The drum is poorly fused and includes A2 and higher elements; (2) the drum is robust and includes A2 and higher elements; (3) the drum is robust and includes A3 and higher elements, but not A2.

15. *Nodule on lateral surface of A1 and A2*.—(0) Lateral surfaces of A1 and A2 are smooth; (1) ossified nodule on the lateral surface of each A1 and A2 element, with cartilaginous connections between them.

16. *Pessulus divides tracheal A elements dorsally*.—(0) Tracheal A elements are complete dorsally; (1) ossified pessulus extends anteriorly on the dorsal side of the trachea to divide four or more A elements.

17. *Pessulus extends from the first single, complete A element*.—(0) Pessulus (when present) is not attached to the first single, dorsally complete A element; (1) pessulus is an ossified caudal extension of the dorsal side of the first single, dorsally complete A element.

18. *Pessulus large, concave*.—(0) Pessulus (when present) is convex dorsally; (1) the ossified pessulus is relatively large and concave dorsally. Its greatest breadth is at the point where the internal cartilages attach.

19. *B1-2 connected ventrally*.—(0) The bronchial, cartilaginous B1 and B2 elements are independent at their ventral tips; (1) B1 and B2 are connected at their ventral tips. The connection is flattened or acute; (2) B1 and B2 are connected at their ventral tips. The connection is symmetrically rounded.

20. *B1-2 connections are close medially*.—(0) The left and right ventral ends of B1 and B2 are relatively far apart; (1) the bronchi are close together in the region of B1 and B2, so that the left and right ventral connections of those elements nearly touch one another medially.

21. *B1-2 diverge dorsally*.—(0) B1 and B2 are nearly parallel dorsally; (1) B1 and B2 diverge dorsally so that their dorsal tips lie relatively far apart.

22. *B1-2 shaped as in* Myiarchus.—(0) B1 is narrow dorsally or B2 is narrow ventrally; (1) B1 and B2 have a distinct configuration as typified by *Myiarchus* (Lanyon 1985): B1 is narrow except for a very broad dorsal end. B2 is narrow except for a broad, triangular ventral end which is barely attached to the ventral end of B1.

23. *B1 breadth*.—(0) Breadth of the lateral region of B1 is less than or equal to the breadth at the ventral and dorsal tips; (1) B1 is broader laterally than at the tips.

24. *B1 bulbous dorsally*.—(0) B1 flat dorsally; (1) B1 bulbous or swollen at dorsal tips.

25. *B2 Y-shaped ventrally*.—(0) Ventral end of B2 is rounded or truncate; (1) ventral end of B2 is forked or shaped like the letter ''Y''.

26. *Syrinx and trachea laterally compressed*.—(0) Trachea and tracheobronchial junction are not both laterally compressed; (1) in *Lophotriccus* and *Oncostoma* (Lanyon 1988c), the entire trachea and tracheobronchial junction are laterally compressed so that they are unusually narrow when viewed dorsally or ventrally, and broad when viewed laterally. Similar morphology occurs in *Machetornis* where the tracheobronchial junction, but not the trachea, is laterally compressed (J. S. Birdsley pers. obs.).

27. *Cartilaginous bronchial plate*.—(0) Dorsal tips of the incomplete bronchial A elements are not connected with one another or with the pessulus; (1) a horseshoe-shaped cartilaginous plate connects the dorsal tips of the incomplete bronchial A elements and the pessulus. It forms the dorsal or craniodorsal margins of the medial tympaniform membranes. The internal cartilages are very small, delicate rods located near the caudal ends of the horseshoe, sometimes attached to it; (2) a cartilaginous plate as in state (1), but the internal cartilages are robust.

28. *Cartilaginous tracheal plate*.—(0) Lower tracheal A elements are ossified dorsally; (1) cartilaginous pessulus extends cranially so that the lower tracheal A elements up to A6 or A8 are cartilaginous dorsally.

29–39. *Internal cartilages*.—The internal tympaniform membranes in the syringes of all tyrannids and some cotingids contain cartilaginous structures which are often attached to A elements. Because there is extreme variation in the shape, position, and attachment of internal cartilages, Prum and Lanyon (1989) hypothesized them to be derived in cotingids independently of those in tyrannids. Prum (1990b) questions their homology even within tyrannids, and recommends using unique, detailed morphologies of internal cartilages as characters, while refraining from the hypothesis of homology of internal cartilages as broadly defined. Here I follow that recommendation and the precedent of Lanyon (1984, 1985, 1986, 1988a, b, c) in coding shared, detailed morphologies of tyrannid internal cartilages as independent, derived characters.

29. *Narrow, linear*.—(0) Absent; (1) cartilages are narrow and basically linear.

30. *Triangular*.—(0) The base (the cranial end) is narrower than or scarcely greater than the width of the rest of the cartilage; (1) the cartilage is triangular, with the base much broader than the rest of the cartilage.

31. *Spatulate*.—(0) Absent; (1) cartilages are broad and shaped like a spatula or child's mitten with a thickened dorsal edge.

32. *"J" or "L" shaped*.—(0) Absent; (1) cartilages are thin and bent in a ''J'' or ''L'' shape; (2) cartilages are robust and bent in a ''J'' or ''L'' shape.

33. *Forked*.—(0) Absent; (1) cartilages are forked caudally.

34. *Ventral extension*.—(0) Absent; (1) cartilages have poorly staining, amorphous ventral extensions from their caudal halves; (2) cartilages have well-formed, squarish ventral extensions from their caudal halves.

35. *Broad, amorphous caudal segments*.—(0) Absent; (1) cartilages are narrow cranially but broaden and become amorphous caudally.

36. *Narrow, curved*.—(0) Absent; (1) cartilages are relatively narrow and curved (medially concave).

37. *Straight, expanded caudally*.—(0) Absent; (1) cartilages are relatively long, straight, and expanded caudally. They are somewhat twisted, with the cranial half flattened at right angles to the internal tympaniform membrane and the caudal half flattened within the plane of the membrane.

38. *Attached to tracheal drum and incomplete A elements*.—(0) Cartilages are attached either to an incomplete A element or to a tracheal drum, but not both; (1) cartilages are attached to the dorsal end of

an incomplete A element (either A1 or A2) as well as to a tracheal drum.

39. *Attached to ventral side of tracheobronchial junction*.—(0) Cartilages are attached to the dorsal side of various structures in the tracheobronchial junction; (1) cartilages are attached to ventral or medioventral segments of A2 or A3.

40. *Narrow strand of cartilage between B2 and B3*.—(0) Absent; (1) in addition to the large internal cartilages, there is a narrow strand of cartilage in the internal tympaniform membrane uniquely placed between the ventral ends of B2 and B3.

41. *Cartilaginous plug of tissue between A2 elements*.—(0) The space just caudal to the tracheobronchial junction is vacant; (1) there is a plug of tissue just caudal to the tracheobronchial junction and between the cartilaginous medial segments of the A2 elements. This plug stains weakly for cartilage.

42. Mm. tracheolaterales.—(0) Cover only the lateral portions of the trachea; (1) right and left Mm. tracheolaterales widen ventrally and meet above A20, sometimes lower, and completely cover the ventral and ventrolateral surface of the trachea from there posteriad, diverging just before their insertion in the region of the syrinx; (2) *Mm. tracheolaterales* cover the ventral and ventrolateral surface of the trachea as in state (1) but do not diverge at their insertion. Instead, they converge to a point and insert midventrally on the lower A elements.

43. Mm. obliqui ventrales.—(0) Intrinsic syringeal muscles (if present) are different from *Mm. obliqui ventrales* in detail of fiber direction and form of insertion (Prum and Lanyon 1989; Prum 1990b, 1992); (1) *Mm. obliqui ventrales* insert on the ventral or lateral side of the syrinx (Ames 1971, McKitrick 1985, Mobley and Prum 1995). (2) *Mm. obliqui ventrales* insert on the dorsal side of the syrinx (Ames 1971).

44. Mm. obliqui ventrales *well developed*.—(0) *Mm. obliqui ventrales* (if present) are relatively undeveloped, appearing flat; (1) *Mm. obliqui ventrales* are well developed, appearing as round, bulging muscle masses. Present in at least some members of the kingbird and *Elaenia* assemblages (Lanyon 1984, 1988a) and in *Hymenops*, *Polioxolmis*, and *Cnemarchus* (pers. obs.).

45. Mm. obliqui laterales.—(0) Absent; (1) syrinx has a pair of laterally-originating and laterally-inserting intrinsic syringeal muscles. In most taxa possessing them, these muscles exist in addition to *Mm. obliqui ventrales*, but apparently in some tody-tyrants, *Mm. obliqui laterales* are the only intrinsic syringeal muscles (Ames 1971).

Plumage

46. *Crown patch*.—(0) Crown plumage is monochromatic; (1) crown plumage contains a patch of white, red, orange, or yellow which is usually concealed or semiconcealed.

47. *Sexually dichromatic plumage*.—(0) Sexes have similar or identical plumage color and patterns; (1) sexes have markedly different plumage color and patterns.

48. *Wing patterned*.—(0) Remiges are similarly colored on their proximal and distal halves; (1) remiges are black or fuscous distally, and buff or cinnamon-rufous proximally; (2) remiges as in state (1) except they are white proximally.

49. *Wing bars*.—(0) Absent; (1) rufous-buff; (2) yellow; (3) white.

50. *Throat plumage*.—(0) Unstreaked; (1) dark streaks against a white background.

51. *Outer rectrix pale*.—(0) Outer rectrices are similarly colored on their inner and outer webs; (1) outer webs of the outer rectrices are pale (white to cinnamon–rufous), contrasting with darker inner webs.

52. *Tail length*.—(0) Short to moderate; (1) elongated, forked.

53. *Tail rufous*.—(0) Tail is various colors but not entirely rufous; (1) entire tail is rufous.

54. *Underparts rufous*.—(0) Underparts various colors but not entirely rufous; (1) underparts entirely rufous.

55. *Superciliary*.—(0) No contrasting stripe over or through the eye; (1) white, yellow, or cinnamon superciliary stripe over or through the eye.

56. *Plumage black and white*.—(0) Plumage has at least some color or is solid black, brown, or white; (1) plumage is black and white or brown and white.

57. *Rictal bristles*.—(0) Short or absent; (1) as long or nearly as long as the bill.

58. *Pointed crest*.—(0) Feathers of the crown form a rounded crest; (1) feathers of the crown form a pointed, prominent crest.

59. *Primaries notched*.—(0) Outer primaries not notched at their tips; (1) outer one, two, or three primaries are notched or attenuated in at least the male of the species.

Behavior and Ecology

60. *Habitat*.—(0) Inhabit forests and woodlands; (1) inhabit open grassland or marsh; (2) inhabit open cliffs, canyons, and roadcuts.

61. *Foraging behavior*.—Fitzpatrick (1980) characterized the foraging behavior of nearly every tyrannid genus and recognized 10 ‘‘foraging mode’’ categories in the family. Here I treat each of these foraging mode categories as alternative unordered derived states of a single character. I consulted Snow (1982), Hilty and Brown (1986), and Marini (1992) for behavior of outgroups.

(0) Fruit/upward hover-glean generalists feed heavily on fruits during most or all of the year but also upward hover-glean and perch-glean insects.

(1) Fruit/hawk generalists combine frugivory with aerial-hawking of flying insects. They

use these capture techniques in roughly equal proportions.

(2) Outward hover-glean generalists often glean insects from foliage surfaces via an outward or downward ''sally'' or capture flight. The bird may slow down and hover while capturing the insect or snap it up while in direct flight, often striking the foliage and continuing to a new perch. Upward hover-gleaning and aerial-hawking are additional significant elements of their foraging repertoires.

(3) Enclosed perch hawk generalists have foraging repertoires composed of roughly equal proportions of aerial-hawking, upward hover-gleaning, and upward-striking.

(4) Near-ground generalists usually hunt from perches near the ground and use a wide variety of capture techniques including perch-to-ground and perch-to-water sallies, upward and outward hover-gleaning and striking, and aerial-hawking.

(5) Perch-glean specialists capture most of their prey while perched, without sallying. Hover-gleaning and frugivory are minor components of their repertoire.

(6) Upward-strike specialists capture most of their prey in an explosively rapid upward sally to the underside of a leaf, snatching or scooping an insect off the under-surface, usually without hovering.

(7) Aerial-hawk specialists capture most of their prey out of the air.

(8) Perch-to-ground specialists hunt from low perches, usually sallying to the ground to catch prey. Aerial-hawking may be a minor component of their repertoire.

(9) Ground specialists stand, walk, or run on the ground and search for their prey which they pick off the ground or low vegetation. Aerial-hawking from the ground may be a minor component of their repertoire.

62. *Cavity nesting*.—(0) Nests are in open situations; (1) nests are located in tree cavities or holes in earthen banks.

63. *Enclosed nest within hanging vegetation*.—(0) Nest, if hanging, is built around a branch and suspended from it; (1) enclosed, globular nest with a side entrance is built within a hanging mass of vegetation.

64. *Enclosed nest pendant*.—(0) Nest is not suspended from a branch; (1) enclosed, globular nest with a side or bottom entrance is suspended from a branch; (2) enclosed, elongate (1 m or more) nest with a side entrance is suspended from a branch.

65. *Enclosed, pendant nest retort-shaped*.—(0) Nest, if hanging, has an entrance hole at or above the bottom of the nest chamber; (1) enclosed, pendant, globular nest shaped like a chemists' retort with a downward-pointing entrance spout.

66. *Enclosed nest with visor over entrance*.—(0) Nest, if enclosed, has an unsheltered entrance hole; (1) enclosed nest has a short roof or visor over the side entrance.

67. *Nest used as dormitory*.—(0) Nests are used only during breeding; (1) adults sleep in their nests at all seasons. Presumed present only in *Rhynchocyclus* and *Tolmomyias* (Skutch 1960).

Eggs

68. *Eggs*.—(0) Marked with dark blotches and streaks; (1) plainly colored, usually some shade of white.

APPENDIX 2. Character-state matrix of 68 characters for 103 tyrannid taxa plus 3 outgroup taxa used in phylogenetic analysis. Asterisks (*) denote character stage polymorphisms of the type "0/1". Other polymorphic combinations are coded with a slash (e.g. "0/2"). Unknown character states are coded "?". See Appendix 1 for descriptions of characters.

	Character																		
					1 2		3		4						5 6				
Taxon	123	4	5678	9	012345678901	2	345678901	2	345678901	2	3	4567	8	9	01234567890	1	23	4	5678
									***Elaenia* assemblage**										
Zimmerius	000	2	0001	0	041000010100	1	000000000	0	000000000	1	0	0000	0	0	00000000000	0	01	0	0000
Phylloscartes	000	2	000*	1	011000010100	1	000000100	0	000000000	1	1/2	?*00	0	0/1/2	00000*00000	6	01	0	000?
Mionectes	000	2	0201	1	040000010100	0	000000000	0	000000000	2	1	0000	0	0	0000*000000	0	00	2	0101
Leptopogon	000	2	0200	0	040000010100	1	000000100	0	*00000000	2	2	0000	0	1	00000000000	0	00	1	0101
Sublegatus	000	2	0001	2	010000010100	1	001000010	0	000000000	1	1	?000	0	3	00000100000	2	00	0	0000
Inezia	000	2	0000	0	010000010100	1	000000000	0	000000000	1	2	?000	0	3	00000100000	5	00	0	0001
Myiophobus l,o	000	2	0000	1	040000000100	1	000000000	0	000000000	?	?	??10	0	1	00000000000	3	??	?	??0?
Myiophobus p,r	000	2	0000	0	040000010100	1	001000010	0	000000000	1	1	0010	0	1	00000000000	3	??	?	??0?
Myiotriccus	000	2	0001	1	040000010000	1	000000010	0	000000000	1	1	0010	0	0	00000000000	3	10	0	000?
Stigmatura	000	2	0300	1	000000000100	1	000021000	0	000000000	1	1	?000	0	0	00000100000	5	00	0	0000
Pseudelaenia	000	2	0300	0	000000010100	1	000020000	0	000000000	?	?	??10	0	3	00000100000	5	00	0	0001
Euscarthmus	000	2	0000	0/2	000000000100	1	000000000	0	000000000	1	1	?010	0	1	00000000000	5	00	0	000*
Pseudotriccus	000	2	1000	1	000000001101	1	000000100	0	100000000	?	?	??00	0	0	000*0000000	6	??	?	??0?
Corythopis	000	2	1000	1	000000001100	1	000000000	0	100000000	1	1	0000	0	0	00000010000	6	00	0	0000
Elaenia	000	2	0100	*	001030000100	1	000000000	0	000000000	*	1	11*0	0	3	00000000000	0	00	0	0000
Myiopagis	000	2	0001	0	001030000100	1	000000000	0	010001000	*	2	1110	0	0/2	00000*00000	5	00	0	0000
Tyrannulus	000	2	0001	0	001030000100	1	000000000	0	010001000	0	1	1010	0	3	00000000000	0	00	0	0001
Tyranniscus	000	2	0100	1	000030000100	1	000000000	0	001000000	1	2	1000	0	2	00000100000	0	00	0	0001
Mecocerculus c,m	000	2	0100	?	000030000100	1	000000000	0	010000000	?	?	1?00	0	1	00000100000	5	??	?	??0?
Ornithion	000	2	0000	1	000020000100	1	000000000	0	010000000	1	2	1000	0	0	00000100000	5	00	0	000?
Camptostoma	000	2	0000	1	000020000100	1	000000000	0	010000000	1	2	1100	0	1	00000100000	5	0*	0	0000
Mecocerculus h,p,s	000	2	0100	?	000020000100	1	000000000	0	020000000	?	?	1?00	0	3	00000100000	5	??	?	??0?
Suiriri	000	2	0001	0	001020000100	0	000000000	0	000000000	0	2	1100	0	3	00000100000	5	00	0	0001
Pseudocolopteryx	000	2	0020	1	000020000?00	1	000000000	0	000000000	1	1	01*0	0	0/3	00000000001	5	00	0	0001
Polystictus	000	2	0020	0	000020000100	1	000000000	0	000000000	1	1	0010	0	1	00000100001	?	00	0	0001
Mecocerculus	000	2	0000	1	000020000100	1	000000000	0	000100000	1	1	0000	0	1/3	00000100000	5	00	0	0001
Uromyias	000	2	0000	?	001020000100	1	000000000	0	000100000	?	?	0?00	0	0	10000100000	5	??	?	??0?
Capsiempis	010	2	0020	1	001020000100	0	000000000	0	000101000	1	1	1000	0	2	00000100000	5	00	0	0001
Phaeomyias	010	2	0020	0	000020000100	1	000000000	0	000101000	0	2	1100	0	1/3	00000100000	0	00	0	0001
Nesotriccus	010	2	0020	0	001020000100	0	000000000	0	000101000	0	2	0000	0	1	00000100000	3	00	0	0001
Serpophaga	000	2	0020	1	001010000100	1	000000000	0	000100000	1	2	0010	0	0/3	00000*00000	5	00	0	0001
Anairetes	000	2	0020	1	000010000100	1	000000000	0	000100000	0	2	0000	0	3	11000*00000	5	00	0	0001
									***Empidonax* assemblage**										
Arundinicola	000	1	0011	0	000000000100	0	000000000	0	000000000	1	1	0000	0	0	00000010011	4	00	0	0101
Fluvicola	000	1	0011	0	000000000000	0	000000000	0	000000000	1	1	0000	0	0	00000010001	9	00	0	0000
Alectrurus	000	1	0011	2	000000000100	0	000000010	0	000000000	1	1	0001	2	0	00100110011	7	00	0	000?
Silvicultrix	000	1	0010	0	000000000100	*	000000000	0	000000000	?	?	??00	0	1	00000100000	4	00	2	0001
Ochthoeca	000	1	0010	0	000020000100	*	000000010	0	000000000	1	1	0100	0	0/1/3	0100*100000	4	00	0	0000
Colorhamphus	000	1	0010	?	000020000100	1	000000010	0	000000000	1	1	?000	0	1	00000000000	4	00	0	0000
Cnemotriccus	000	1	0010	0	020100000100	1	000000000	0	000000001	?	?	??00	0	1	00000100000	3	00	0	0000
Aphanotriccus	000	1	0010	?	020101000100	1	000000000	0	000000001	0	1	0000	0	1	00000000000	3	??	?	??0?
Lathrotriccus	000	1	0011	2	020101000100	1	000000000	0	000000001	?	?	??00	0	1/3	00000000000	3	00	0	0000
Xenotriccus	000	1	0010	0	020100000100	1	000000000	0	000000001	1	1	0000	0	1/3	00000000100	?	00	0	0000
Sayornis	000	1	0010	0	020200000100	0	000000000	0	000000001	1	1	0000	0	0	000000*000*	4	00	0	0001
Contopus	000	1	0010	2	020200000100	1	000000000	0	000000001	1	1	0000	0	0/1/3	00000000100	7	00	0	0000
Mitrephanes	000	1	0010	0	020200000100	0	000000000	0	000000001	1	1	?000	0	1	00000000100	7	00	0	0000
Empidonax	000	1	0010	0	020200000100	1	001000000	0	000000001	1	1	0000	0	1/3	00000000000	3	00	0	000*
Lessonia	000	1	0010	0	010000000100	1	000000000	0	000000001	1	1	0001	1	0	01000000011	9	00	0	0000
Pyrocephalus	000	1	0010	0	010000000000	0	000000000	0	000000001	2	1	0001	0	0	01000000000	4	00	0	0000
Hymenops	000	1	0010	0	020000000100	0	000000010	0	000000001	1	1	1001	2	0	00000010001	9	00	0	0000
Knipolegus	000	1	0010	0	020000000100	0	000000010	0	000000001	1	1	000*	0/2	0/1/3	000000*00*0	7	00	0	000?
Ochthornis	000	1	0010	0	020000000100	0	000000010	0	000000001	?	?	??00	0	0	00000100000	4	00	0	000?
Satrapa	000	1	0010	0	020000000100	1	000000000	0	000000001	1	1	0000	0	3	01000100000	7	00	0	0000

APPENDIX 2. Continued.

	Character																		
					1 2		3		4						5 6				
Taxon	123	4	5678	9	012345678901	2	345678901	2	345678901	2	3	4567	8	9	01234567890	1	23	4	5678
Muscisaxicola	000	1	0010	0	020000000100	1	000000000	0	000000001	1	1	0000	0	0	01000*00001	9	00	0	000*
Agriornis	000	1	0010	0	020000000100	1	000000000	0	000000001	1	1	0000	0	0	11000000011	8	00	0	0000
Xolmis	000	1	0010	0	020000000100	1	000000000	0	000000001	1	1	0000	0/2	0	01000**001*	8	10	0	0000
Heteroxolmis	000	1	0011	0	020000000100	1	000000000	0	000000001	1	1	0000	2	0	00000010011	8	??	?	??0?
Polioxolmis	000	1	0010	2	020000000100	0	000000000	0	000000001	1	1	1000	1	0	11000000010	8	??	?	??0?
Cnemarchus	000	1	0000	?	020000000100	0	000000000	0	000000001	1	1	1000	1	0	11001100000	8	??	?	??0?
Myiotheretes	000	1	0010	2	020000000100	1	000000000	0	000000001	1	1	0000	1	*	1100**000*0	8	??	?	??0?
Neoxolmis	000	1	0010	0	020000000100	0	000000000	2	000000001	1	1	0000	1	0	01000*00011	8	00	0	0000
Gubernetes	000	1	0011	2	010000000100	0	011000000	2	000000001	1	1	0000	1	0	01100100001	7	00	0	000?
Muscipipra	000	1	0010	?	010000000100	0	011000000	0	000000001	1	1	?000	0	0	01100000010	?	??	?	??0?
Myiophobus	000	1	0010	1	040000000*00	1	000000000	0	000000000	0	1	0010	0	1	00000000000	3	00	0	0000
Pyrrhomyias	000	1	0000	1	060000010100	0	000000000	0	000000010	0	0	0010	1	1	00001000000	7	00	0	0000
Hirundinea	000	1	0000	2	060000000000	0	000000000	0	000000010	0	0	0000	1	0	00001000002	7	00	0	0000
Myiobius a,b,v	000	1	0000	2	030000000000	0	000000000	0	000000000	0	0	0010	0	0	00000001000	3	00	1	0000
Myiobius erythrurus	000	1	0000	2	030000000000	0	000000000	0	000000000	0	0	0000	0	0	00011001000	6	00	1	0100
Flatbill and tody-tyrant assemblage																			
Rhynchocyclus	100	0	0000	1	0400000?0100	0	000000100	0	000000000	0	1	?000	0	2	00000000000	6	00	1	1010
Tolmomyias	100	0	0000	1	0400000*0100	0	000000100	0	000000000	0	1	0100	0	2	00000000000	6	00	1	1010
Onychorhynchus	100	0	0000	2	030000000100	0	100000001	0	000000000	0	0	0000	0	0	00010001000	6	00	2	0000
Platyrinchus	100	0	0000	1	040000000100	0	101000001	0	000000000	1	2	0010	0	0	00000000000	6	00	0	0000
Cnipodectes	100	0	0000	1	000000010100	0	000000000	0	100000000	?	?	??00	0	1	00010001000	?	00	2	000?
Todirostrum	100	0	0000	1	000000010100	0	000010000	0	000000000	0	0	0100	0	2	00000000000	6	00	1/2	010*
Poecilotriccus	100	0	0000	1	000000000100	0	000010000	0	000000000	0	0	010*	0	0/1/2	00000000000	6	00	2	0100
Hemitriccus	100	0	0000	1	000000100100	0	000010000	0	000000000	0	2	0100	0	0/2	*0000000000	6	00	1	0000
Lophotriccus	100	0	0000	1	000000100100	0	000110000	0	000000000	*	2	0100	0	0/2	10000000000	6	00	1	0101
Oncostoma	100	0	0000	1	000000100?0?	0	00?110000	0	000000000	0	2	0100	0	2	00000000000	6	00	1	0100
Kingbird assemblage																			
Phelpsia	001	0	0000	?	140000000100	1	000000000	0	000000000	?	?	??00	0	0	00000100000	4	00	0	0000
Pitangus	001	0	0000	2	130000000100	0	000000000	0	000000000	0	2	1010	0	0	00000100000	4	00	0	0000
Philohydor	001	0	0000	2	130000000100	1	000000000	1	000000000	0	2	1010	0	0	00000100000	4	00	0	0000
Legatus	001	0	0000	2	150000000100	1	000000000	2	000000000	0	2	?110	0	0	00000100000	1	00	0	0000
Myiozetetes	001	0	0000	2	150000000101	0	000000000	0	000000000	0	2	1110	0	0	00000*00000	1	00	0	0000
Myiodynastes	001	0	0000	2	140000000200	0	000000000	1	000000000	0	2	1010	0	0	000*0100000	6	10	0	0000
Conopias	001	0	0000	2	140000000200	0	000000000	1	000000000	0	2	10*0	0	0	00000100000	2	10	0	0000
Megarynchus	001	0	0000	2	140000000210	0	000000000	2	000000000	1	2	1010	0	0	00000100000	7	00	0	0000
Tyrannopsis	001	0	0000	2	140000000210	0	000000000	2	000000000	1	2	1010	0	0	00000100000	1	00	0	0000
Tyrannus	001	0	0000	2	140000000210	0	000000000	1	000000000	1	2	1010	0	0	0*10000001*	7	00	0	0000
Empidonomus	001	0	0000	2	140000000210	0	000000000	1	000000000	?	2	1?10	0	0	00000100010	7	00	0	0000
Griseotyrannus	001	0	0000	2	140000000210	0	000000000	1	000000000	1	2	1010	0	0	00000100010	7	00	0	000?
***Myiarchus* assemblage**																			
Attila	001	0	0000	1	010000000100	1	000000000	0	000000000	0	1	0000	0	*	00010000000	2	10	0	0000
Deltarhynchus	000	0	0001	2	040000000100	1	000000000	0	000010000	?	?	??00	0	1	00000000000	?	10	0	0000
Ramphotrigon	000	0	0001	?	040000000100	1	000000000	0	000010000	0	1	?100	0	1	000*0000000	6	10	0	0000
Rhytipterna	000	0	0001	2	010000000100	1	000000000	2	000000100	0	1	0000	0	0/3	0*0**000000	2	10	0	000?
Sirystes	000	0	0001	2	010000000101	1	000000000	2	000000100	0	1	?000	0	0	00000000000	2	10	0	000?
Casiornis	000	0	0001	2	010000000100	1	000000000	2	000000100	1	1	0000	0	0	00010000000	2	10	0	000?
Myiarchus	000	0	0001	2	010000000101	1	000000000	2	000000100	*	1	0000	0	3	0*000000000	2	10	0	0000
Other tyrannids																			
Colonia	001	3	0001	2	050000010100	0	000000010	0	000000000	1	1	0000	0	0	00000110000	7	10	0	0001
Machetornis	001	2	0000	0	130000010100	0	000000010	0	000000000	1	0	0010	0	0	00000000001	9	10	0	0000
Muscigralla	000	2	0000	0	040000010100	0	000000010	0	000000000	1	1	0010	0	3	00000000001	9	??	?	????
Phyllomyias fasciatus	000	0	0000	1	000000000100	0	000021000	0	010000000	1	1	0000	0	3	00000100000	0	??	?	????
Phyllomyias griseiceps	???	?	????	?	?01000000100	0	000020000	0	000000000	1	1	0000	0	0	00000100000	0	00	0	000?
Tachuris	10?	0	0000	1	000000000100	0	000020000	0	000000000	1	1	0010	0	0	00000100001	5	00	0	0001
Neopipo	???	?	????	?	?60000010100	1	000000010	0	000000000	0	0	0010	0	0	00011000000	?	??	?	??0?
Outgroups																			
Cotingidae	000	0/2	000*	1/2	00? 0000*?000	0	000000? ?0	0	????00*00	0/1/2	0	00**	0	0/2/3	0****0*00*0	0	*0	*	0000
Pipridae	000	0	0000	0	00*0?00*0000	0	00000*000	0	000000000	1	0	00*1	0	0	000000*0000	0	00	0	0000
Furnarioidea	100	0	000*	?	00?000000???	?	???0?0000	0	000000000	0	0	000*	*	0/2/3	*00****0*?*	5/9	*0	*	0*0*

Myiophobus, l,o = species *lintoni* and *ochraceiventris*. *Myiophobus p,r* = species *phoenicomitra* and *roraimae*. *Myiophobus* = species *cryptoxanthus, fasciatus, flavicans, inornatus*, and *pulcher*. *Mecocerculus c,m* = species *calopterus* and *minor*. *Mecocerculus h,p,s* = species *hellmayri, poecilocercus*, and *stictopterus*. *Mecocerculus* = species *leucophrys*. *Myiobius a,b,v* = species *atricaudus, barbatus*, and *villosus*.