MONOPHYLY AND PHYLOGENY OF THE
SCHIFFORNIS GROUP (TYRANNOIDEA)[1]

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Abstract. A cladistic analysis of 19 characters was used to investigate the phylogeny of the *Schiffornis* group, a monophyletic assemblage of six genera of suboscine passerines which are currently placed in three different tyrannoid families: *Schiffornis* (Pipridae, manakins), *Laniisoma, Iodopleura* (Cotingidae, cotingas), *Laniocera, Xenopsaris,* and *Pachyramphus* (Tyrannidae, tyrant flycatchers). The character systems analyzed include syringeal and cranial morphology, plumage, and nest architecture. Monophyly of the *Schiffornis* group was supported by two syringeal synapomorphies. Within the group, the phylogenetic relationships of five of the six genera were resolved; *Schiffornis* is the sister group to *Laniisoma* and *Laniocera,* and *Xenopsaris* is the sister group of *Pachyramphus.* The relationship of *Iodopleura* to these two corroborated clades was not resolved. The higher-level relationships of the *Schiffornis* group to other tyrannoids was not resolved. Results of two previous biochemical phylogenies of tyrannoids both corroborate and conflict with this morphological hypothesis. Comparative analysis of the evolution of breeding systems in tyrannoids indicates that polygyny may have developed independently within the group, resulting in the evolution of a novel form a male advertisement behavior without conspicuous sexual dimorphism and a distinct type of spatial dispersion of male territories.

Key words: Phylogenetic systematics; morphology; syrinx; cotingas; manakins; tyrant flycatchers; breeding system evolution; Schiffornis; Pachyramphus.

Resumen. Un análisis cladístico de 19 características se emplea para investigar las relaciónes filogenéticas del grupo *Schiffornis,* un conjunto monofilético de seis géneros, los cuales se ubican ahora en tres familias diferentes en la superfamilia Tyrannoidea: *Schiffornis* (Pipridae), *Laniisoma, Iodopleura* (Cotingidae), *Laniocera, Xenopsaris,* y *Pachyramphus* (Tyrannidae). Las características empleadas incluyen la morfología de la siringe y del craneo, el plumaje, y la estructura del nido. La posición del grupo *Schiffornis* en Tyrannoidea no se ha determinado. Dentro del grupo, las relaciónes de cinco de los seis géneros fueron resueltas por la hipótesis filogenética mas parsimoniosa, es decir, aquella que requiere el menor numero de características derivados. *Schiffornis* es más cercano a un linaje que consiste de *Laniisoma* y *Laniocera;* y *Xenopsaris* es más cercano a *Pachyramphus.* Las relaciónes de *Iodopleura* no eran resolvado. La comparación de estos resultados con dos hipóteses filogenéticas bioquímicas resulta similitudes y conflictos. Un análisis comparativo de la evolución de los comportamientos reproductivos en Tyrannoidea indica que polygínia se ha desarollado independientemente en el grupo *Schiffornis.* También en el groupo *Schiffornis,* se han desarollado nuevos tipos de dispersión territorial y anuncio nupcial de los machos sin dimorfismo sexual.

INTRODUCTION

The New World suboscine superfamily Tyrannoidea (Passeriformes) is a diverse group com-

posed of over 500 species which are placed in the tyrant flycatchers (Tyrannidae), manakins (Pipridae), cotingas (Cotingidae), plantcutters (Phytotomidae), and sharpbills (Oxyruncidae) (Traylor 1979). The phylogenetic interrelationships of the tyrannoids have recently received a great deal of investigation using gel electropho-

resis (Zink and Johnson 1984, S. M. Lanyon 1985, Lanyon and Lanyon 1986, Johnson and Marten 1988), DNA-DNA hybridization (Sibley and Ahlquist 1985, Sibley et al. 1985) and cladistic analysis of a variety of morphological characters (Lanyon 1984a, 1984b, 1985, 1986, 1988a, 1988b, 1988c; McKitrick 1985; Lanyon and Lanyon 1986; Prum, unpubl.). Of particular interest to this investigation, McKitrick (1985) identified a problematic clade of tyrannoids (including *Schiffornis, Pachyramphus,* and *Tityra*) which shares derived morphological characters both with cotingids and piprids and with tyrant flycatchers. In an investigation of the monophyly of the Pipridae and Cotingidae, Prum (unpubl.) has expanded this group to include a number of other tyrannoid genera.

We present here a cladistic analysis using morphological characters of the phylogeny of a previously unrecognized monophyletic assemblage of six genera in this problematic tyrannoid assemblage. These genera are presently placed in three different tyrannoid families: *Schiffornis* (Pipridae), *Laniisoma, Iodopleura* (Cotingidae), *Laniocera, Xenopsaris,* and *Pachyramphus* (Tyrannidae). The systematic relationships of these six genera have remained problematic or enigmatic for over 100 years, resulting in frequent reallocation to different families or placement in isolated positions within them. Reevaluation of their relationships has been made possible by advances in the understanding of the morphological diversification of the tyrannoids (Warter 1965; Ames 1971; Lanyon 1984a, 1984b, 1985, 1986, 1988a, 1988b, 1988c; McKitrick 1985; Prum, unpubl.), and by the recent collection of the first anatomical and skeletal specimens of the genera *Laniisoma* and *Xenopsaris.*

Following a summary of the taxonomic history of these genera, which we refer to collectively as the *Schiffornis* group, we present the morphological characters which support their monophyly and intergeneric relationships. We then discuss the diagnoses of the *Schiffornis* group and its monophyletic subgroups, the alternative hypotheses for the relationships of the *Schiffornis* group genera, and the position of the *Schiffornis* group within the Tyrannoidea. We compare this morphological hypothesis to previous phylogenies of the tyrannoids based on DNA-DNA hybridization (Sibley and Ahlquist 1985) and allozyme electrophoresis (S. M. Lanyon 1985). Lastly, the evolution of various behavioral and natural history traits is discussed in light of this new phylogenetic hypothesis.

REVIEW OF SYSTEMATIC HISTORY OF *SCHIFFORNIS* GROUP GENERA

The genus *Schiffornis* contains three species which range from southern Mexico to southeastern Brazil. The best known species, *Schiffornis turdinus,* is commonly known as the Thrush-like Manakin. The genus was placed in the Pipridae by Sclater (1888), under the names *Schiffornis* and *Heteropelma,* based on the possession of exapsidean tarsal scutellation and extensive fusion of the outer toes (digits III and IV) which he used to define the family. Sclater (1888) placed *Schiffornis* and several other genera, including *Laniisoma* (see below), in the separate subfamily Ptilochlorinae in recognition of their differences from other typical piprids, such as dull, sexually monomorphic plumage and prominently hooked, tyrannid-like bill. Ridgway (1907) and Hellmayr (1929) left *Schiffornis* in the Pipridae but did not recognize the subfamilies of Sclater. Despite suggestions that *Schiffornis* might belong in the Tyrannidae (Ames 1971) or the Cotingidae (Meyer de Schauensee 1966, Wetmore 1972), Snow (1975, 1979) followed previous authors and kept the genus in the Pipridae, citing the lack of substantive evidence supporting a specific taxonomic change. McKitrick (1985) identified *Schiffornis* as a member of a problematic group of genera which possess both a derived form of the femoral artery shared by cotingas and manakins, and derived internal syringeal cartilages which are present elsewhere only in tyrannids. S. M. Lanyon (1985) presented allozyme evidence for the placement of *Schiffornis* as the sister group to the piprids including *Neopelma* and *Tyranneutes.* Based on DNA-DNA hybridization, Sibley and Ahlquist (1985) placed *Schiffornis, Pachyramphus,* and *Tityra* in the subfamily Tityrinae as the sister group to a restricted Tyranninae. The remainder of the tyrannids were placed in the Mionectidae as the sister group to the rest of the Tyrannoidea. Prum (unpubl.) recommended the removal of *Schiffornis* and five other genera of piprid-like tyrannoids (*Neopelma, Tyranneutes, Neopipo, Piprites,* and *Sapayoa*) from the Pipridae based on a cladistic analysis of morphological characters. All six of these genera lack the derived, dorsal fusion of the B1 and B2 syringeal elements which is shared by all other traditional piprid genera (Prum, unpubl.).

Laniisoma elegans, commonly called the Shrike-like Cotinga, is the only species in this little-known genus. It has a disjunct distribution in southeastern Brazil and the eastern slopes of the Andes from Bolivia to Venezuela (Snow 1982). Sclater (1888) placed *Laniisoma* (=*Ptilochloris*) in the piprid subfamily Ptilochlorinae next to *Schiffornis,* but Ridgway (1907) subsequently moved it to the Cotingidae, despite its exaspidean tarsi and fused outer toes. It has remained in the Cotingidae (Hellmayr 1929, Snow 1979), although its placement in this family and its relationships to any other cotingids have been repeatedly questioned (Snow 1973, 1982). Snow (1973, 1982) suggested that within the Cotingidae *Laniisoma* may be most closely related to *Phoenicircus* or *Phibalura* based on general plumage characteristics, toe fusion, and primary feather specializations. Prum (unpubl.) found that *Laniisoma* has internal syringeal cartilages and the derived femoral artery of cotingids and piprids, but that it lacks the derived form of syringeal musculature found in almost all cotingids.

The genus *Laniocera* includes two species, the Cinereous (*L. hypopyrrha*) and Speckled (*L. rufescens*) mourners, which are allopatrically distributed in the tropical lowlands of Central America and Amazonian South America. Originally placed in the Cotingidae by Sclater (1888), *Laniocera* was moved by Ridgway (1907) to the Pipridae and placed near *Schiffornis* based, again, on tarsal scutellation and toe fusion. Hellmayr (1929) replaced it in the Cotingidae, near *Lipaugus, Attila, Casiornis,* and *Rhytipterna.* Ames (1971) described the syrinx of *Laniocera* as very similar in musculature and supporting cartilages to *Attila, Casiornis, Rhytipterna,* and the myiarchine flycatchers, and recommended the placement of these four genera in the Tyrannidae near the myiarchines. This suggestion was followed by Traylor (1979) and by the AOU (1983). W. E. Lanyon (1985) confirmed the close relationships of the latter three genera to the myiarchine flycatchers based on syringeal and osteological synapomorphies, but firmly concluded that *Laniocera* lacks all the derived characters diagnostic of the myiarchine assemblage. Prum (unpubl.) found that *Laniocera* has the derived femoral artery of piprids and most cotingids but lacks the synapomorphies of these two families.

The genus *Pachyramphus* (including *Platypsaris*) contains 15 species, commonly called becards, which range throughout the Neotropics to the southern United States. *Pachyramphus* and *Platypsaris* (originally a separate genus for the *aglaiae* species group) have been consistently placed in the Cotingidae near *Tityra,* on the basis of their possession of emarginate or truncate 9th primaries (Sclater 1888, Ridgway 1907, Hellmayr 1929, Snow 1973). Snow (1973) considered the *aglaiae* species group to be insufficiently distinct to warrant generic status and synonomized *Platypsaris* with *Pachyramphus.* Snow (1979, 1982) and Traylor (1977, 1979) moved *Pachyramphus* and *Tityra* into a separate subfamily, the Tityrinae, in the Tyrannidae, citing the works of Warter (1965) and Ames (1971). The AOU (1983) followed this arrangement. McKitrick (1985) also recognized *Pachyramphus* and *Tityra* as members of the problematic tyrannoid clade which may be related either to the tyrannids or the cotingids and manakins, based on the shared possession of derived femoral arteries and internal cartilages, as in *Schiffornis.* Based on allozyme variation, S. M. Lanyon (1985) placed *Pachyramphus* close to *Tityra* as a basal sister group to, or in an unresolved position near, the piprids. Sibley and Ahlquist (1985) put *Pachyramphus, Tityra,* and *Schiffornis* in a clade as the sister group to a portion of the tyrannids based on DNA-DNA hybridization.

Xenopsaris is a monotypic genus with a disjunct distribution in the reed beds and shrubby riverine habitats of northern Argentina, Paraguay and central Venezuela (Snow 1973, 1979; Traylor 1979). Its natural history is very poorly known. *Xenopsaris albinucha,* commonly called the White-naped Xenopsaris, was first described by Burmeister (1868) as a species in the genus *Pachyramphus.* Subsequently, Ridgway (1891) assigned the single species to the new genus *Xenopsaris* in the Cotingidae. Since that time, the genus has been moved between the Cotingidae, near *Pachyramphus* or *Casiornis,* and the Tyrannidae, near *Serpophaga,* at least six times (Sclater 1893, Ridgway 1907, Hellmayr 1927, Meyer de Schauensee 1966, Smith 1971, Snow 1973). Ridgway (1907) mentioned that a few male *Pachyramphus* specimens have normal ninth primaries and suggested that *Xenopsaris* might properly belong within *Pachyramphus.* Zimmer (unpubl. MS cited in Traylor 1977) placed *Xenopsaris* in a subgenus of *Pachyramphus.* Most recently, *Xenopsaris* was placed incertae sedis at the end of the Tyrannidae by Traylor (1977,

1979). Prum (unpubl.) found that *Xenopsaris* has the derived femoral artery and syringeal cartilages.

Iodopleura is a genus of three species, called purpletufts, which are distributed nonsympatrically in Amazonian and southeastern South America. Although *Iodopleura* has long been placed in the Cotingidae and often been associated with the genus *Calyptura* (Sclater 1888; Ridgway 1907; Hellmayr 1927; Snow 1973, 1979, 1982), its true relationship to other members of the family have remained obscure (Snow 1973, 1982). Ames (1971) concluded that the syrinx of *Iodopleura* was typically tyrannid but did not make any strong recommendations about the placement of the genus in that family. S. M. Lanyon (1985) placed *Iodopleura* within a complex group of other cotingid genera based on allozymes. McKitrick (1985) placed *Iodopleura* with the tyrannids on the basis of its internal cartilages, and on Ames' (1971) description of its intrinsic syringeal musculature as being like the M. obliquus ventralis of tyrannids. Prum (unpubl.) found *Iodopleura* to have the derived, femoral artery, and argued that its intrinsic syringeal musculature is not homologous with the M. obliquus ventralis of tyrannids (see character 4).

METHODS

The morphological characters analyzed were taken from observations of cleared and double stained syringeal specimens, iodine stained syringeal specimens, and skeletal specimens from a number of natural history collections, and from skins housed in the American Museum of Natural History, New York, New York, and the University of Michigan Museum of Zoology, Ann Arbor, Michigan. A list of the 63 syringeal and 46 skeletal specimens of *Schiffornis* group genera observed is presented in the Appendix. The sample of other suboscine material observed included syringes of 140 and skeletons of 137 of the other 145 tyrannoid genera, and syringes of a large sample of furnarioid and Old World suboscine genera. The cleared and double stained syringeal material was prepared by W. E. Lanyon in the manner of Dingerkus and Uhler (1977) and was used primarily for observations of syringeal supporting elements. Uncleared syringeal specimens were treated with reversible iodine stain (Bock and Shear 1972) for observations of syringeal musculature. All syringeal terminology follows Ames (1971:14–16).

The data were analyzed cladistically. Systematic relationships among taxa were defined explicitly in terms of recentness of common ancestry, and shared derived characters (synapomorphies) were hypothesized to be evidence of exclusive common ancestry. Monophyly of the ingroup, the Tyrannoidea, was accepted a priori based on the possession of a derived form of the M. flexor perforatus digiti IV (Raikow 1987: 36), and on DNA-DNA hybridization evidence (Sibley and Ahlquist 1985). Character variation within the tyrannoids was polarized by outgroup comparison (Wiley 1981, Maddison et al. 1984) to the Furnarioidea, the Old World suboscines, and the oscine passerines. Each character analysis begins with a description of the derived character state and its distribution in some portion of the ingroup which is followed by a description of the primitive character state and its distribution in the ingroup and outgroups. Characters were coded separately for the six genera in the *Schiffornis* group, the tyrannids, the cotingids, the piprids, *Tityra, Neopelma, Tyranneutes, Piprites,* the *Lipaugus vociferans* species group, and the outgroups. The data were arranged in a matrix of 19 binary characters (Table 1). Primitive, derived and unknown character states were coded as 0, 1, and ?, respectively. The most parsimonious phylogenies were identified by hand and confirmed using the PAUP computer algorithm (Swofford 1983) with global branch-swapping and mulpars options on the ordered character set.

CHARACTERS

(1) *Internal syringeal cartilages.* All genera in the *Schiffornis* group have complex internal syringeal cartilages which are attached to the A1 or A2 elements or the pessulus, and which project into the internal tympaniform membrane (Fig. 1). Internal syringeal cartilages are also found in all tyrannids (sensu Traylor 1979), *Oxyruncus,* (Oxyruncidae), *Lipaugus vociferans* and *L. unirufus* (Cotingidae), and the piprid-like tyrannoid genera *Tyranneutes, Neopelma, Neopipo, Piprites,* and *Sapayoa* (Lanyon 1984a, 1984b, 1986, 1988a, 1988b, 1988c; McKitrick 1985; Prum, unpubl.). Internal cartilages are absent in all other passerines (with the exception of some analogous structures in *Neodrepanis* and *Acanthisitta;* McKitrick 1985; Prum, unpubl.). Following Lanyon (1984a, 1986, 1988a, 1988b, 1988c) and McKitrick (1985), the presence of internal syringeal cartilages will be hypothesized to be de-

TABLE 1. Distributions of the 19 characters analyzed in the six *Schiffornis* group genera, other tyrannoids, and the outgroup taxa. Outgroups include furnarioids, Old World suboscines, and oscine passerines. Derived, primitive, and unknown character states are coded as 1, 0, and ?, respectively. *Lipaugus* includes *vociferans* and *unirufus* only.

Taxon	Character																		
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Schiffornis	1	1	1	1	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0
Laniisoma	1	1	1	1	1	1	0	0	0	0	1	0	1	1	0	1	0	0	?
Laniocera	1	1	1	1	1	1	0	0	0	0	1	0	1	1	1	0	0	0	?
Pachyramphus	1	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1
Xenopsaris	1	1	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0
Iodopleura	1	1	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0
Tyrannids	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cotingids	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Piprids	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tityra	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lipaugus	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Neopelma	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tyranneutes	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Piprites	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Outgroups	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

rived. However, the homology of internal cartilages as broadly defined has been seriously questioned (see Discussion; Prum, unpubl.).

(2) *Femoral artery enlarged.* In all six *Schiffornis* group genera, *Tityra, Piprites, Neopelma, Tyranneutes,* most cotingas, and all piprids, the main artery supplying the hind limb is the femoral. In all other tyrannoids (including *Oxyruncus, Sapayoa, Neopipo,* and the cotingids *Rupicola, Phoenicircus, Carpornis, Pipreola,* *Ampelioides, Lipaugus cryptolophus* and *L. subalaris*) and in almost all other birds, the main artery of the hind limb is the ischiadic (Garrod 1876; Mitgård 1982; Prum, unpubl.). Following McKitrick (1985) and Prum (unpubl.), the enlarged femoral artery state is here hypothesized to be derived in tyrannoids.

(3) *Constriction of the tracheobronchial junction.* The six genera in the *Schiffornis* group share a unique constriction of the bronchi at the tra-
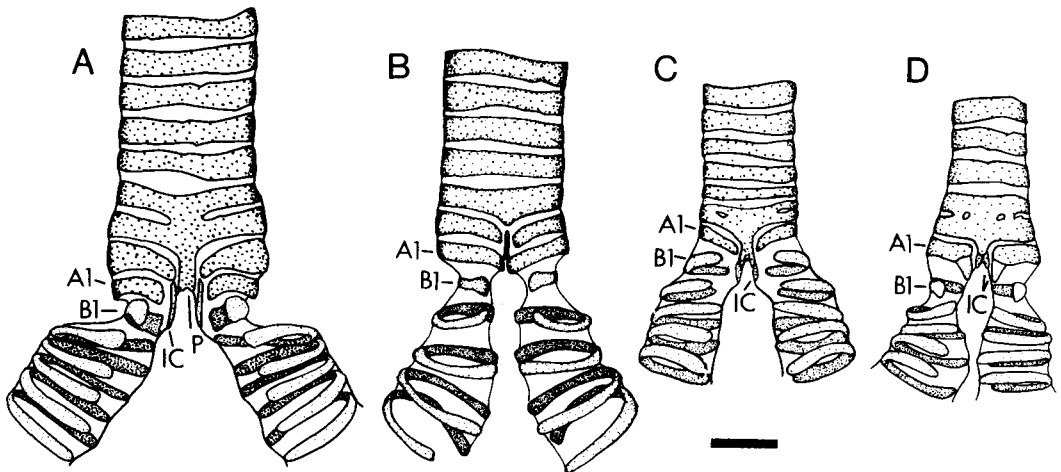

FIGURE 1. Dorsal view of the syringeal supporting elements of: (A) *Schiffornis major* (AMNH 816774), (B) *Laniisoma elegans* (FMNH 322417), (C) *Iodopleura isabellae* (FMNH 322431), and (D) *Xenopsaris albinucha* (AMNH 8389). Scale bar equals 1 mm. Abbreviations: A1—the first A element; B1—the first B element; IC—internal syringeal cartilages; P—pessulus. The internal cartilages of *L. elegans* are not visible. See characters 1, 3, and 8–12.
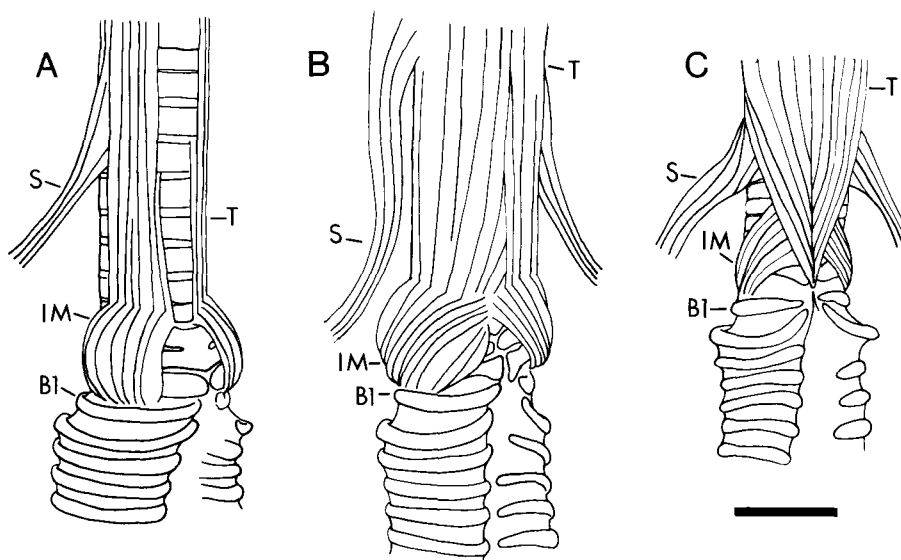
FIGURE 2.   Right ventrolateral views of the syringes of (A) *Schiffornis turdinus* (UMMZ 225044), (B) *Laniocera hypopyrrha* (LSU 79585), and (C) *Pachyramphus rufus* (CM 1275). Scale bar equals 2 mm. Abbreviations: B1—the first B element; IM—intrinsic syringeal musculature; S—M. sternotrachealis; T—M. tracheolateralis. See characters 4 and 7.

cheobronchial junction produced by the shape of the cartilaginous B1 and B2 syringeal elements (Fig. 1). The double, medially incomplete, cartilaginous B1 elements are straight dorsally and only slightly curved ventrally in contrast to all the other syringeal supporting elements, which are completely round or C-shaped. In conjunction with this B1 specialization, the double B2 elements are thinner and curved anteriorly at their ventral ends to meet but not fuse with the ventral ends of the B1 elements. This configuration of the B1 and B2 elements produces a marked constriction in both bronchi as they join the trachea. Ames (1971:37, 42) previously described this condition in *Iodopleura* and *Schiffornis*. This state does not occur in any other tyrannoids, furnarioids, or Old World suboscines examined, and has not been described in any oscine passerines (Ames 1971). The configuration of B1 and B2 elements found in the *Schiffornis* group is here hypothesized to be derived.

(4) *Insertion of intrinsic musculature on A1/ B1 membrane.* All genera in the *Schiffornis* group have a pair of intrinsic syringeal muscles which originate on elements A3–5 and insert on the dorsal half of the A1/B1 external membrane (Fig. 2). In *Schiffornis,* the intrinsic muscles originate on the lateral surfaces of elements A4–5 just pos-

terior to the insertion of M. tracheolateralis (Fig. 2A). In *Laniisoma, Laniocera,* and *Iodopleura,* the intrinsic muscles originate on the ventrolateral surfaces of elements A3–4 immediately posterior to the insertion of M. tracheolateralis (Fig. 2B). In *Pachyrampus* and *Xenopsaris,* the intrinsic muscles originate on the ventral midline on elements A3–5, below and oblique to the fibers of M. tracheolateralis, which converge on the ventral midline and taper posteriorly to insert narrowly on the ventral ends of the A1 elements (see character 7) (Fig. 2C).

The insertion of a pair of intrinsic muscles on the A1/B1 membrane is not found in any cotingids or piprids. With a few interesting exceptions, cotingids entirely lack intrinsic syringeal muscles; the M. tracheolateralis inserts on the middle of the A1/B1 membrane (Prum, unpubl.). According to Ames (1971), the insertion of the intrinsic syringeal muscles of tyrannids (M. obliquus ventralis) on the A1/B1 membrane occurs in only a few species, including *Attila* and a number of genera in Lanyon's (1986) *Empidonax* assemblage. Elsewhere in tyrannoids, this morphology is found only in *Oxyruncus* (Ames 1971; R. O. Prum, pers. observ.). In these genera the insertion is on the ventral or lateral portion of the A1/B1 membrane and not on the dorsal and

lateral portion as in the *Schiffornis* group. Ames (1971:138–141) referred to the intrinsic syringeal muscles of *Laniocera* and *Iodopleura* as M. obliquus ventralis, implying homology with the oblique intrinsic muscles of tyrannids. However, the intrinsic syringeal muscles of the *Schiffornis* group genera are only superficially similar to the M. obliquus ventralis of tyrannids. The variation within the group in fiber direction and the novel form of insertion strongly support an independent origin of this intrinsic musculature from the M. obliquus ventralis of tyrannids (Prum, unpubl.).

The alternative hypotheses for the origination of the intrinsic muscle insertions on the A1/B1 membrane are: (1) it is primitive within the tyrannoids and has been subsequently lost in all but the above groups; (2) it developed independently in the *Schiffornis* group, *Oxyruncus,* and several tyrannid lineages; (3) it evolved in the *Schiffornis* group, independently of tyrannids and *Oxyruncus,* as a novel intrinsic muscle subsequent to the evolution in the cotingids of the derived insertion of M. tracheolateralis on the A1/B1 membrane. The first hypothesis is unparsimonious since it requires the retention and many independent losses of this unusual character state in many widely dispersed taxa. In this analysis, the insertion of the intrinsic musculature on the dorsal portion of the A1/B1 membrane will be hypothesized to be derived independently in the *Schiffornis* group, as in the second and third hypotheses. Evaluation of the third hypothesis, that the syringeal musculature found in the *Schiffornis* group is a terminal state in a character transition series within the cotingids, will require additional data supporting some or all cotingids as the immediate sister group of the *Schiffornis* group (Prum, unpubl.).

(5) *Unique, complex internal syringeal cartilages.* In *Schiffornis, Laniisoma,* and *Laniocera,* the internal syringeal cartilages are large and complex. In *Laniisoma* and *Laniocera,* they are attached to the dorsal and ventral portions of the pessulus, and in *Schiffornis* they are attached both to the dorsal and ventral portions of the pessulus and to the dorsal end of the A2 element. In all three genera, thin threads of tissue extend posteriorly and ventrally from the dorsoposterior corner of the internal cartilages into the internal tympaniform membrane. The distal end of this fibrous tissue runs parallel to the ventral end of the B3 element and is cartilaginous in most spec-

imens. This additional cartilaginous tissue in the internal tympaniform membrane gives the impression of a second, independent pair of internal cartilages. These internal cartilages are unique in shape and character in the tyrannoids and are hypothesized here to be derived.

(6) *Rostral bar on head of lacrimal.* In tyrannoids and Old World suboscines, the lacrimal bone is present and not fused to the ectethmoid, whereas in furnarioids the lacrimal is absent. In most tyrannoids the lacrimal is composed of a broad pneumatized foot which rests on the jugal bar, a thin ascending process which lies adjacent to the ectethmoid, and a larger head which articulates with the frontal and nasal bones lateral to the nasal-frontal hinge. The precise shape and proportions of these components varies throughout the tyrannoids. In *Laniisoma* and *Laniocera,* the caudal margin of the head of the lacrimal articulates with the frontal but the rostral portion consists of a thin arm which extends anteriorly and medially in an arc to articulate with the nasal bone rostral to the nasal-frontal hinge (Figs. 3A, B). The rostral bar creates a gap or foramen between the three bones which is typically covered by thin connective tissue. In *Schiffornis,* the rostral arm of the head of the lacrimal is similar in form but is reduced in length and does not reach the nasal (Fig. 3C).

In *Xenopsaris, Pachyramphus,* and *Iodopleura,* the head of the lacrimal is oval, pneumatized, and articulates closely with the frontal and nasal bones with little or no gap or foramen between them. In all piprids and almost all tyrannids, the lacrimal head also articulates closely to the frontal and nasal (Fig. 3D). In a few scattered tyrannid genera, the head of the lacrimal is loosely articulated and a small gap is formed (e.g., some species of *Elaenia, Terenotriccus, Myiobius,* and *Myiozetetes*), but in none of these cases does the head of the lacrimal have a thin rostral arm or bridge. In most cotingids, the head of the lacrimal is large, round or oval, highly pneumatized, and closely articulated to the frontal and nasal at the facial hinge (e.g., *Pipreola chlorolepidota, Xipholena, Lipaugus vociferans, Carpodectes, Haematoderus, Cephalopterus, Querula, Pyroderus, Perissocephalus, Procnias,* and *Rupicola peruviana*). In *Cotinga,* the head of the lacrimal is large and has a broad rostral portion which forms a small, oval foramen in its articulation to the jugal and nasal. In *Ampelioides* and some *Pipreola,* the head of the lacrimal is large and
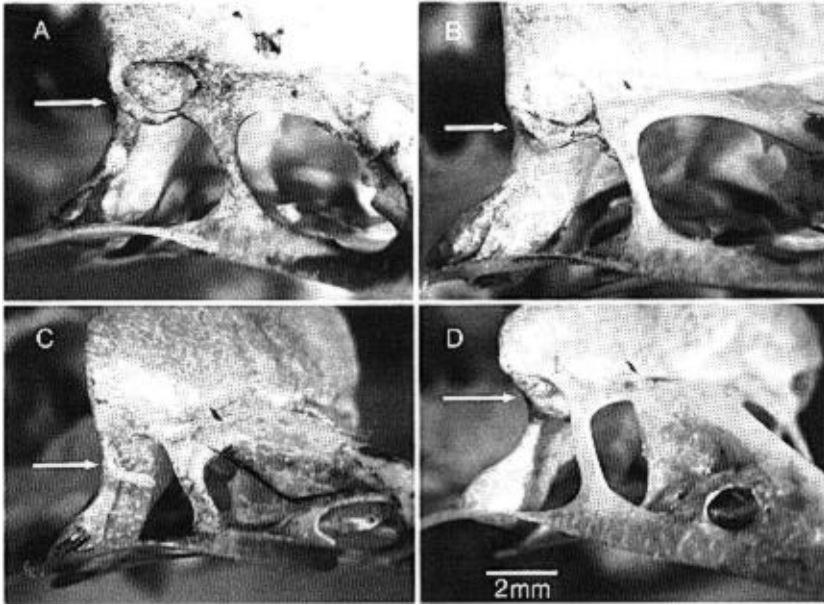
FIGURE 3.   Right dorsolateral views of the crania of (A) *Laniisoma elegans* (FMNH 322419), (B) *Laniocera rufescens* (UMMZ 218410), (C) *Schiffornis virescens* (UMMZ 202192), and (D) *Casiornis rufus* (UMMZ 223838). Arrows indicate the head of the lacrimal. Scale bar equals 2 mm. See character 6.

pneumatized and has a small spike-like rostral projection which does not articulate to the nasal to surround a foramen. In *Gymnoderus* and *Rupicola rupicola,* the head of the lacrimal is large, and highly pneumatized, and has a rostral bar which articulates to the nasal and encloses a foramen, but the lacrimal head is larger, more pneumatized and different in detail from that in *Schiffornis, Laniisoma,* and *Laniocera.* The rostral bar on the head of the lacrimal in *Schiffornis, Laniisoma,* and *Laniocera* is here hypothesized to be derived. Similar structures have apparently developed in a few widely dispersed cotingas, but it is more parsimonious to consider these structures as independently derived.

(7) *Insertion of M. tracheolateralis on ventral ends of A1 elements.* In *Pachyramphus* and *Xenopsaris,* the left and right sides of the M. tracheolateralis converge on the ventral midline of the trachea anterior to the A20 element, and taper narrowly to insert on the ventral ends of the double, medially incomplete A1 elements (Fig. 2C). In *Laniisoma, Laniocera,* and *Iodopleura,* the Mm. tracheolaterales widen ventrally and meet on the ventral midline above A20, covering the entire ventral and ventrolateral surface of the trachea until they divide at the ventral midline immediately before their broad insertion on the

ventrolateral surface of the A3–4 elements (Fig. 2B). In *Schiffornis,* the Mm. tracheolaterales are restricted to the lateral portions of the trachea and do not widen or converge ventrally (Fig. 2A). Cotingids, furnarioids, and Old World suboscines have Mm. tracheolaterales like *Schiffornis,* except that they lack any intrinsic muscles. Most tyrannids and piprids, like *Laniocera,* have Mm. tracheolaterales which converge ventrally to cover the trachea but then diverge before insertion. The condition in *Pachyramphus* and *Xenopsaris* is almost unique within tyrannoids. It is also found in *Pyrocephalus* and *Oxyruncus* (Ames 1971; R. O. Prum, pers. observ.). However, the hypothesis that the character state found in these genera is homologous with that found in *Pachyramphus* and *Xenopsaris* would require numerous convergences or reversals in other characters. The shape and insertion of the M. tracheolateralis in *Pachyramphus* and *Xenopsaris* is hypothesized to be derived independently. It is impossible to determine which of the other two states of the insertion of the M. tracheolateralis present in the *Schiffornis* group is primitive without a corroborated hypothesis for its immediate sister group.

(8) *Additional, triangular internal cartilages.* In *Xenopsaris,* an additional pair of triangular in-

ternal cartilages is attached to the dorsal ends of the ossified, double, medially incomplete A1 elements (Fig. 1D). These structures are unique in position and shape within the tyrannoids, and are here hypothesized to be derived.

(9) *Wide, flat pessulus.* In the genus *Schiffornis,* the pessulus is wide and flat (Fig. 1A). In the other genera in the *Schiffornis* group, the pessulus is narrow (Figs. 1B–D). The pessulus is present and ossified in most tyrannoids and no furnarioids. Among the tyrannoids, the widened flat pessulus observed in *Schiffornis* is nearly unique to that genus. *Rupicola, Phoenicircus,* and *Carpornis* (Cotingidae) have a widened pessulus which is not flat and straight, but wider dorsally than ventrally, slightly concave and fused to different elements. The condition found in *Schiffornis* is hypothesized to be derived.

(10) *Broad B1 elements.* In *Schiffornis,* the B1 element is a broad bar, whereas in the other genera of the *Schiffornis* group and in other tyrannoids generally the B1 element is not especially broad and is of equivalent proportions to the other B elements (Fig. 1). The condition in *Schiffornis* is hypothesized to be derived.

(11) *Dorsally lengthened A1 elements.* In *Laniisoma* and *Laniocera,* the dorsal ends of the paired, incomplete A1 elements are lengthened and broadened, and extend medially toward one another, often obscuring the tracheobronchial junction from view (Fig. 1B). This configuration is unique among tyrannoids and other suboscines, and is here hypothesized to be derived.

(12) *Keel-shaped pessulus.* In *Iodopleura,* the pessulus is attached dorsally and ventrally to the A2 elements in a complex manner which is unique among tyrannoids (Fig. 1C). Posterior to their fusion with the pessulus, the dorsal ends of the A2 elements form two narrow, ossified projections into the internal tympaniform membrane at the dorsoposterior corners of the pessulus. These projections continue ventrally along the posterior edges of the pessulus as ridges, producing an inverted trough or keel-shape to the pessulus. This unique morphology is hypothesized to be derived.

(13) *Black-tipped plumage.* In *Laniisoma,* the unusual juvenal body plumage is composed of rufous or orange-rufous feathers with black tips (Snow 1982, plate 2; R. O. Prum, pers. observ.). The adult plumage of both sexes is characterized by yellow throat, breast, and vent with prominent black barring which is produced by a terminal band of black on each yellow feather. (In some Andean populations, the males have entirely yellow, unbarred underparts; Snow 1982.) In adult *Laniocera rufescens,* the rufous or cinnamon plumage of the head, throat, breast, vent, and lower back is barred terminally with dusky gray. In immature plumages and apparently some adults, a few of the cinnamon feathers are tipped with black and distributed irregularly on the breast. In *Laniocera hypopyrrha,* the immature and adult plumages are almost entirely smoky gray. In immature and apparently some adult birds, a variable number of cinnamon-rufous feathers with black tips are distributed irregularly on the breast, as in *L. rufescens.* The variation in the number of these black-tipped breast feathers in *Laniocera* is thought to be age related (Zimmer 1936, Wetmore 1972), but the molt sequence and timing has yet to be described in detail. Both species of *Laniocera* have yellow or orange-rufous patches on the sides of the chest in some plumages (see character 14), and in some specimens, these feathers are barred lightly with dusky gray. The juvenal plumages of *Laniocera* are undescribed. For illustrations of adult plumages of all three species, see Hilty and Brown (1986).

All three species in both genera are characterized by cinnamon-rufous or orange-rufous feathers tipped with black in some plumage. Furthermore, in all three species, black- or dusky-tipped yellow feathers produce barring on the sides of the breast or underparts. The pattern of pigmentation on these superficially dissimilar feathers from various plumages is strikingly similar and strongly implies a homologous, derived pattern of pigment deposition during feather development. No other species in the *Schiffornis* group has similar barring. Elsewhere in the tyrannoids, some members of the cotingid genera *Pipreola, Ampelioides, Porphyrolaema,* and *Phibalura* are barred with black on the breast in adult plumage, but none of these genera has any black-tipped rufous feathers in any known plumages. The barred pigmentation pattern in *Laniocera* and *Laniisoma* is hypothesized here to be derived independently of other tyrannoids. The alternative hypotheses, (1) that this barring is primitive within tyrannoids or within the *Schiffornis* group, or (2) that *Laniocera* and *Laniisoma* are most closely related to the above cotingid genera, would require more reversals or convergences in other characters and are less parsimonious.

(14) *Orange-rufous wing covert spots.* In *Lan-*

iocera, the upper wing coverts are gray (*hypo-pyrrha*) or dusky brown (*rufescens*), and marked terminally with a spot of bright orange-rufous. In immature plumages of *Laniisoma*, the upper wing coverts are green and marked terminally with orange-rufous (see Snow 1982, plate 2). The position and coloration of the upper wing covert spots in these three species are identical despite the differences in the coloration of the rest of the barbs of these feathers. This plumage pattern is unique among the tyrannoids and quite unusual in the furnarioids, and it is hypothesized here to be derived.

(15) *Yellow or orange-rufous breast patches.* In *Laniocera*, the sides of the breast in immature plumages and some adults have prominent yellow or orange-rufous patches. These patches are not found in other tyrannoids. They are hypothesized to be derived, possibly through the partial retention of the primitive condition of yellow breast pigmentation as found in *Laniisoma*.

(16) *Emarginate 7th primaries.* Male *Laniisoma* have emarginate 7th primaries (Snow 1982: 35, fig. 4). Among tyrannoids, *Phoenicircus* also has a specialized 7th primary which is twisted in a very different manner and combined with a specialization of the 6th primary as well (Snow 1982). The condition in *Laniisoma* is hypothesized to be derived independently.

(17) *Emarginate or truncate 9th primaries.* In adult male *Pachyramphus*, the 9th primaries are approximately half the length of the 10th and abruptly truncate or emarginate at the tip (see Ridgway 1907 for illustration). Specializations of the primary feathers occur in many cotingids and piprids, and a few tyrannids (Ridgway 1907, Snow 1982), but only *Tityra* shows an exclusive specialization of the 9th primary as in *Pachyramphus*. In male *Tityra*, the entire 9th primary is narrow and reduced in size, and sharply emarginate at the tip, instead of merely shortened and truncate as in *Pachyramphus*. The state found in *Pachyramphus* is hypothesized here to be derived. The state in *Tityra* differs significantly in detail and probably had an independent origin.

(18) *Purple breast patches.* In male *Iodopleura*, the sides of the upper breast have prominent purple silky feathers. This plumage is unique among suboscines and is here hypothesized to be derived.

(19) *Globular nest.* Species in the genus *Pachyramphus* construct disheveled, globular nests with a side or bottom entrance, which is made out of miscellaneous vegetation (Skutch 1967, 1969;

Wetmore 1972; Snow 1973; Hilty and Brown 1986). In the *P. aglaiae* species group (formerly *Platypsaris*), the nest is built hanging from a branch, whereas in the other *Pachyramphus* species the nest is placed in the fork of a tree branch (Skutch 1969). Smith (1971) describes the nest of *Xenopsaris* examined in Buenos Aires Museum de Ciencias Naturales as a "compact open cup of fine dry grasses." *Schiffornis* builds a bulky, cup nest of leaves and other vegetation (Skutch 1969, 1981), and *Iodopleura* builds a small, tidy nest of cobwebs and fungus fibers (Snow 1982). The nests of *Laniocera* and *Laniisoma* are unknown. Elsewhere in the Tyrannoidea, globular nests are built by genera or groups of genera in several different assemblages of tyrant flycatchers, and we suggest this behavior is independently derived in these groups (Lanyon 1984a, 1986, 1988a, 1988b, 1988c). Here, the globular nests of *Pachyramphus* are hypothesized to be derived independently.

RESULTS

The characters analyzed support two equally parsimonious alternative hypotheses for the phylogenetic relationships of the *Schiffornis* group and other tyrannoids (Table 1; Figs. 4, 5). Both phylogenies require 20 evolutionary transitions of the 19 binary, morphological, and behavioral characters yielding a consistency index of 0.95. In both phylogenies the monophyly of the *Schiffornis* group is supported, and *Tityra, Piprites, Neopelma, Tyranneutes, Lipaugus vociferans,* and *L. unirufus* are their closest relatives. The two resolutions of the phylogeny differ in whether the *Schiffornis* group and these additional genera are most closely related to the cotingids and piprids, or to the tyrannids. The former hypothesis requires a single evolution of the enlarged femoral artery (character 2) and a convergent development or secondary loss of internal syringeal cartilages (character 1) (Fig. 4A). The latter hypothesis requires a convergent development of secondary loss of the enlarged femoral artery and a single development of internal syringeal cartilages (Fig. 4B).

Within the *Schiffornis* group, the monophyly of each of the genera as traditionally defined was supported by morphological synapomorphies (Fig. 5). The morphological characters also support a single resolution of the phylogenetic interrelationships of *Schiffornis, Laniisoma,* and *Laniocera,* in which *Schiffornis* is the sister group
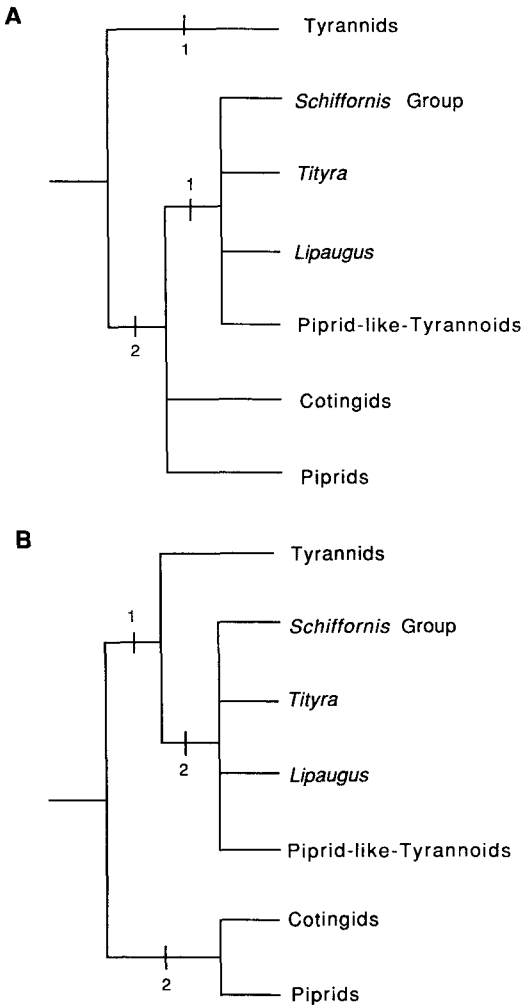
A

B

FIGURE 4. Two equally parsimonious phylogenetic hypotheses for the relationships of the *Schiffornis* group to other tyrannoids. (A) requires a single origin of the enlarged femoral artery (character 2) and two independent developments of internal syringeal cartilages (character 1). (B) requires a single origin of character 1, and two developments of character 2. Convergences in both hypotheses can also be interpreted as an additional secondary loss of the derived character state. *Lipaugus* includes *vociferans* and *unirufus* only. Piprid-like tyrannoids includes the genera *Neopelma, Tyranneutes,* and *Piprites* (this assemblage is not monophyletic; Prum, unpubl.). For character descriptions and distributions, see Table 1 and the text.

to the latter two (Fig. 5). *Pachyramphus* and *Xenopsaris* are sister groups, but the relationship of *Iodopleura* to the two other corroborated clades is unresolved by this data set (Fig. 5).
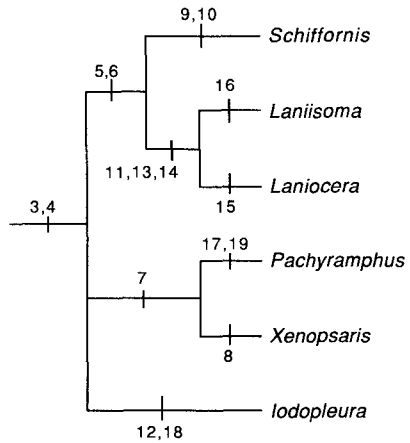

FIGURE 5. Most parsimonious phylogenetic hypothesis for the interrelationships of the *Schiffornis* group genera. The relationships of *Iodopleura* are unresolved. For character descriptions and distributions, see Table 1 and the text.

DISCUSSION

MORPHOLOGICAL EVIDENCE

The monophyly of the *Schiffornis* group, not previously hypothesized, is supported here by two syringeal synapomorphies: the bronchial constriction produced by the unique configuration of the B1 and B2 elements, and the insertion of a pair of intrinsic syringeal muscles on the dorsal portion of the external A1/B1 membrane.

The higher level relationships of the *Schiffornis* group to other tyrannoids are not resolved by this morphological data set (Figs. 4A, B). The conflict between the derived internal syringeal cartilages and enlarged femoral artery has been previously identified and discussed by McKitrick (1985) and Prum (unpubl.). *Tityra, Piprites, Neopelma, Tyranneutes, Lipaugus vociferans,* and *L. unirufus* are also members of this problematic group (Prum, unpubl.) and may be considered tentatively as the most closely related genera to the *Schiffornis* group. A single additional derived morphological character shared by the *Schiffornis* group and either the cotingids and piprids or the tyrannids would favor one of the two alternative hypotheses.

In the absence of additional data, the strength of the two alternative hypotheses can be evaluated in terms of the two conflicting characters which support them: presence of enlarged femoral arteries and internal syringeal cartilages. Both

are certainly derived within the tyrannoids and are almost unique within birds, so there is no justification for weighting one character more heavily than the other on the grounds that one is more commonly evolved generally within birds. However, the homology of the femoral artery of the different taxa is beyond doubt whereas the homology of the various, diverse structures which qualify as internal syringeal cartilages is less certain.

Citing the wide diversity in morphology of structures which are classified as internal cartilages, Prum (unpubl.) questioned the homology of many of these structures and concluded that grouping them together as a single, derived character obscures their complex history. Besides their nonring shape and their general position in the internal tympaniform membrane, the internal cartilages of tyrannoids do not share any detailed similarities in position, shape, attachment, or even composition which strongly supports their homology (Prum, unpubl.). Prum (unpubl.) recommended employing detailed, derived morphologies of internal cartilages as characters, as in Lanyon's work on tyrannid assemblages (Lanyon 1984a, 1986, 1988a, 1988b, 1988c), while reserving judgement on the ultimate homology of all internal cartilages until additional corroborating characters are available. Given these reservations, the femoral artery synapomorphy should be considered as stronger evidence of phylogenetic relationship, and the hypothesis of closer relationship between the *Schiffornis* group and the cotingids and piprids is better supported (Fig. 4A). Additional research on the ontogeny or microstructure of internal syringeal cartilages may identify anatomical details useful in differentiating possibly homologous and analogous internal cartilages in tyrannoids. Ultimately, a hypothesis of homology is supported or refuted by other derived characters with congruent or conflicting distributions (Patterson 1982). Choosing between the two alternative hypotheses for the position of the *Schiffornis* group will require additional data.

Within the *Schiffornis* group, the monophyly of each of the six genera is supported unambiguously (Fig. 5). *Schiffornis* is diagnosed by the widened, flat pessulus (character 9) and the broadened B1 element (character 10). *Laniisoma* is diagnosed by unique primary feather specializations (character 16), and the monophyly of

Laniocera is supported by a derived plumage trait (character 15). *Pachyramphus* is diagnosed by its primary feather specializations and nest architecture (characters 17 and 19), while *Xenopsaris* possesses a unique additional pair of internal syringeal cartilages (character 8). *Iodopleura* is diagnosed by a unique configuration of the pessulus and the A2 elements (character 12) and by purple breast feathers (character 18).

The clade containing *Schiffornis* plus *Laniisoma* and *Laniocera* is supported by a derived rostral bar on the head of the lacrimal and unique internal syringeal cartilages (characters 5 and 6). The monophyly of the group containing *Laniisoma* and *Laniocera* is supported by the dorsally lengthened A1 elements, and two derived plumage traits (characters 11, 13 and 14). Both *Laniisoma* and *Laniocera* have been loosely associated with *Schiffornis* in the past (Sclater 1888, Ridgway 1907), but this is the first evidence that the former two genera are most closely related to one another, and that *Schiffornis* is their sister group.

None of the alternative, traditional hypotheses for the relationships of the *Schiffornis* group genera to other tyrannoids is supported by the morphological characters analyzed. *Schiffornis* is not a member of the Pipridae (Prum, unpubl.), and none of the piprids or other piprid-like tyrannoids is a member of the *Schiffornis* group. The plumage similarities between *Laniisoma* and *Phoenicircus* are certainly convergent. However, the absence of skeletal or syringeal specimens of *Phibalura* make it impossible to assess the putative relationship of this genus to *Laniisoma*. Furthermore, the plumage similarities among *Attila, Casiornis, Rhytipterna, Lipaugus,* and *Laniocera* are not homologous and do not support any close phylogenetic relationship among these taxa. *Attila, Casiornis,* and *Rhytipterna* are members of the *Myiarchus* assemblage (W. E. Lanyon 1985). The genus *Lipaugus* is probably polyphyletic, and its members have yet undetermined relationships outside the *Schiffornis* group (Prum, unpubl.).

The analysis of the first available anatomical specimens of *Xenopsaris* has confirmed the hypothesis that this genus is the sister group to *Pachyramphus* (Ridgway 1891, 1907; Sclater 1893; Meyer de Schauensee 1966) and is not related to the serpophagine flycatchers (Hellmayr 1927, Smith 1971). *Xenopsaris* has the derived

features of the *Schiffornis* group and shares with *Pachyramphus* the derived form of the M. tracheolateralis (character 7). *Pachyramphus* itself has long been placed with *Tityra* based on the specialization of the 9th primary in males (character 17) (Sclater 1888, Ridgway 1907), but this superficial similarity is certainly not substantial enough to support the monophyly of these genera. Warter (1965) grouped *Pachyramphus* and *Tityra* together as aberrant tyrannid-like cotingas, but he did not describe any cranial similarities between the genera which might imply monophyly of the group. Ames (1971) described the syrinx of *Pachyramphus* as tyrannid-like and the syrinx of *Tityra* as typically cotingid. *Tityra* lacks the derived syringeal characters which diagnose either the *Schiffornis* group or the *Pachyramphus-Xenopsaris* clade. The syringeal supporting elements, internal cartilages, and musculature of *Tityra* have some derived similarities to cotingids, *Neopelma, Tyranneutes,* and members of the genus *Lipaugus* (Prum, unpubl.). Based on morphology, *Tityra* cannot be confidently considered a close relative of *Pachyramphus.* Although it is possible that *Tityra* has secondarily lost a number of derived character states, many more detailed synapomorphies of a *Pachyramphus-Tityra* clade would be required to support this hypothesis morphologically.

The available morphological information supports the placement of *Iodopleura* in the *Schiffornis* group but does not provide any additional resolution. The oft stated similarities of *Iodopleura* to the enigmatic and possibly extinct *Calyptura cristata* (Sclater 1888; Ridgway 1907; Snow 1973, 1982) cannot be evaluated at this point.

Some morphological characters that have been cited in traditional classifications and keys including genera in the *Schiffornis* group were not included in this analysis because they are too variable or primitive within tyrannoids. For example, *Schiffornis* group genera have been characterized as having exaspidean (*Schiffornis, Laniisoma, Laniocera*), taxaspidean (*Pachyramphus, Xenopsaris*), or modified holospidean (*Iodopleura*) tarsal scutellation (Sclater 1888, Ridgway 1907). Variation in tarsal scutellation was used heavily by Sclater (1888) and Ridgway (1907) in defining the tyrannoid families. These characters have received repeated criticism (Snow 1973, 1975; Traylor 1977), and have been rejected as useful characters in cladistic analyses of tyrannoid relationships (McKitrick 1985; Prum, un-

publ.). The fusion of the outer two toes (digits III and IV), or syndactyly, has been used traditionally to define the Pipridae. *Schiffornis, Laniisoma,* and *Laniocera* are all syndactyl and have been placed in the Pipridae at various points based on this trait. This character has also been criticized as too variable, subject to convergence, and phylogenetically uninformative (Snow 1973, 1975; Traylor 1977; McKitrick 1985; Prum, unpubl.). Syndactyly appears likely to have been derived many times independently in the tyrannoids. Within the *Schiffornis* group syndactyly is restricted to these three genera and may be independently derived in this clade, but it cannot be confidently used as evidence for their monophyly.

Warter (1965) identified a variety of states of ossification of the nasal septum in tyrannoids, and Lanyon (1984a, 1984b, 1985, 1986, 1988a, 1988b, 1988c) has used them to diagnose a number of large monophyletic assemblages of tyrannid genera. In the *Schiffornis* group, *Laniocera* and *Xenopsaris* have ossified nasal septa with reduced, anterior trabecular plates, and the other four genera have simple, ossified nasal septa. Both of these states are considered primitive within the tyrannoids and do not appear to be phylogenetically informative.

Several other characters have interesting and possibly informative variation within the *Schiffornis* group, but they cannot be polarized confidently without a more specific hypothesis for the sister group of the *Schiffornis* group. For example, the *Schiffornis* group genera differ in degree of dorsal fusion of A elements. However this character varies considerably in other tyrannoids and it would be premature to polarize this character within the *Schiffornis* group without a more reliable sister group. Similarly, the form of the M. tracheolateralis of *Pachyramphus* and *Xenopsaris* is clearly derived (character 7), but the other two forms of this muscle which are found within the group also occur commonly in other tyrannoids.

Interestingly, *Schiffornis* and *Laniisoma* have natal down that is much longer than most passerine birds. Skutch (1969, 1981) describes the natal down on *Schiffornis turdinus* nestlings as copious and approximately 16 mm long. Snow (1982) describes the unusual natal down on *Laniisoma* as approximately 20 mm long on the back and 26 mm long on the head. Natal down from a number of species of North American tyrannids is typically between 5–8 mm long, with a

maximum of 10 mm (Wetherbee 1957). The co-
tingid *Procnias averano* has natal down 10 mm
long (Snow 1970). The down of the other species
of the *Schiffornis* group is undescribed, but ap-
parently unusually long natal down has evolved
somewhere within the group.

In summary, this cladistic analysis provides a
new, almost completely resolved phylogenetic
hypothesis for the interrelationships of six genera
of problematic tyrannoids (Fig. 5). Additional
data are required to resolve the higher level re-
lationships of this assemblage, but the hypothesis
of closer relationship to the cotingids and piprids
is favored at this time.

COMPARISONS WITH
BIOCHEMICAL EVIDENCE

The available biochemical data do not clearly
support the monophyly of the *Schiffornis* group
or favor either of the two alternative phylogenies
for its higher level relationships. In an analysis
of New World suboscine interrelationships based
on DNA-DNA hybridization, Sibley and Ahl-
quist (1985) clustered *Schiffornis* as the sister
group to *Pachyramphus* and *Tityra* in the tyran-
nid subfamily Tityrinae. None of the other *Schif-
fornis* group genera or piprid-like tyrannoids was
included in the study. This result lends some
support to the hypothesized relationship be-
tween *Schiffornis* and *Pachyramphus* but con-
tradicts the conclusion that *Tityra* is not closely
related to the *Schiffornis* group. Sibley and Ahl-
quist (1985) placed the Tityrinae as the sister
group to a large portion of the tyrannids, the
Tyranninae. In the final DNA-DNA hybridiza-
tion phylogeny, however, the branch lengths sep-
arating the Tityrinae and Tyranninae from one
another and from their sister groups including
the cotingids (Cotinginae) and piprids (Piprinae)
were very small (0.2–0.4 T$_{50}$H). Subsequent
analyses by S. M. Lanyon (1985) and Cracraft
(1987) have demonstrated that these branches
are not robust to branch swapping, alternative
tree building or statistical procedures, and are
more accurately represented as a polytomy. Cra-
craft (1987) and Houde (1987) also identified
considerable deviations from metricity in this
data set. Furthermore, many reciprocal hybrid-
izations are missing, causing additional major
difficulties in data analysis (Cracraft 1987). The
limited DNA-DNA hybridization data lend par-
tial support to the morphological hypothesis pre-
sented here, but do not clearly support either of
the two alternative hypotheses for the higher level

relationships of the group. Another investigation
with all relevant taxa and complete data matrices
is required to address the deficiencies in the orig-
inal study.

If one accepts Sibley and Ahlquist's (1985)
placement of *Mionectes, Corythopis,* and the oth-
er genera in the Mionectidae as the sister group
to the rest of the tyrannoids, then the polarity of
the presence of internal syringeal cartilages (char-
acter 1) would reverse within the remainder of
the Tyrannoidea including the *Schiffornis* group
(Lanyon 1988a). By outgroup comparison to the
Mionectidae, the lack of internal cartilages would
be derived in cotingids and piprids, and the sec-
ond hypothesis with the *Schiffornis* group as their
sister group would be favored. At present, there
is no other biochemical or morphological evi-
dence to support the monophyly of the Mionec-
tidae or its placement as the sister group to the
rest of the Tyrannoidea (Prum, unpubl.).

Electrophoretic data analysed by S. M. Lanyon
(1985) do not support the monophyly of the *Schif-
fornis* group. The pertinent genera surveyed
(*Schiffornis, Pachyramphus,* and *Iodopleura*)
came out in very different parts of the tyrannoid
phylogeny (see Systematic Review above). The
close placement of *Pachyramphus* and *Tityra*
based on allozymes again contradicts the most
parsimonious morphological hypothesis that they
are not closely related. The congruence of two
biochemical data sets on the relationships of these
two genera may indicate the weakest point in the
morphological hypothesis presented here.

EVOLUTION OF NATURAL HISTORY AND
BEHAVIOR OF THE *SCHIFFORNIS* GROUP

Unfortunately, little is known of the natural his-
tory and behavior of most of the 27 species in
the *Schiffornis* group, but the recognition of the
monophyly of the assemblage permits a prelim-
inary examination of the evolutionary diversi-
fication of their behavior since common ances-
try. Without resolution of the immediate sister
group relationships of the *Schiffornis* group, it is
difficult to hypothesize the primitive condition
of some behavioral traits within the group; but
even without this information, it is apparent that
the six genera are behaviorally and ecologically
diverse, and have undergone an impressive ra-
diation in breeding system, parental care, nest
construction, and habitat.

Iodopleura and *Pachyramphus* are both mo-
nogamous, while the breeding behavior of *Xe-
nopsaris* is completely undocumented. In *Iodo-*

pleura, both members of the pair assist in nest construction and feeding of the young (Snow 1982). The nest is a small cup of spider web and tiny fungus fibers. Nonreproductive individuals have been reported associating with nesting pairs and may be acting as helpers at the nest (Snow 1982). Elsewhere in the tyrannoids, helpers at the nest are known only from the cotingid *Querula purpurata* (Snow 1982). *Pachyramphus* species are typically conspicuous in nature and some are well-known behaviorally (Skutch 1967, 1969; Wetmore 1972; Hilty and Brown 1986). The females, and in some species males, construct a large globular nest (character 19), and both males and females feed the young. *Pachyramphus* nests are often built in close association with bee hives. In the *P. aglaiae* species group (formerly *Platypsaris*), the nest is hung from an isolated tree limb whereas in other *Pachyramphus* the nest is placed on a horizontal branch or in the crotch of a tree. It appears that the nest construction of the *aglaiae* species group is further derived from the general pattern in *Pachyramphus,* supporting the monophyly of the formerly recognized genus *Platypsaris* (character 19). Additional characters supporting the monophyly of the restricted genus *Pachyramphus,* excluding "*Platypsaris,*" would be required before the two genera could be justifiably separated.

In *Schiffornis,* males are polygynous; they sing syncopated whistled songs from widely dispersed, individual territories to attract females but they do not perform physical courtship displays (*S. turdinus,* Skutch 1969, 1981; *S. major,* R. O. Prum, unpubl. observ.). Females construct the nest (a large, disheveled cup in the crotch of a tree or in a clump of vegetation against a tree trunk) and raise the young solitarily (Skutch 1969, 1981). Little is known about the breeding systems and nesting behaviors of *Laniisoma* and *Laniocera;* however, male *Laniocera* are known to sing persistently from perches 10–20 m high at traditional sites which may be occupied consistently for 10 years (Willis and Eisenmann 1979, Hilty and Brown 1986). Male *Laniisoma* apparently sing from dispersed, widely separated territories as well (Snow 1982).

The type of male vocal advertisement and dispersed territoriality found in *Schiffornis,* and possibly in *Laniocera* and *Laniisoma* as well, is quite different from the type of lek systems which occur in manakins and the best known cotingids (e.g., Snow 1963, 1982). In these species, males display in spatially aggregated territories, giving stereotyped visual displays which usually employ bright, sexually dimorphic plumage. In *Schiffornis,* and possibly *Laniocera* and *Laniisoma,* males are spatially dispersed outside of hearing range of one another and do not perform visual displays. In all three genera, sexual dimorphism is minimal. Within tyrannoids, the one other group known to exhibit a similar behavior is the *Lipaugus vociferans* species group, in which the sexes are monomorphic, and males perform vocal displays in large, concentrated leks (Snow 1982). Interestingly, morphological evidence indicates that the *Lipaugus vociferans* species group may not be most closely related to other true cotingids (Prum, unpubl.).

Although the precise sister group of the *Schiffornis* group is unknown, it is likely that monogamy is the primitive breeding system within the group. The *Schiffornis* group is probably not most closely related to the exclusively lek-breeding lineages of tyrannoids, i.e., the true piprids, certain genera of cotingids, or certain flat-billed tyrannids (Prum, unpubl.). If it is the sister group to any larger clade of cotingids or tyrannids which would include mostly monogamous species, then monogamy with male parental care would be the most likely ancestral character state.

Formerly, *Schiffornis* was considered a behaviorally aberrant member of the Pipridae (Snow 1975), and its behavior could only be described as an enigmatic result of the piprid radiation. The removal of *Schiffornis* from the Pipridae (Prum, unpubl.) and its placement in a corroborated monophyletic group of other tyrannoid genera, in which the primitive breeding system is monogamy with male parental care, supports an alternative, novel hypothesis for the independent evolution of polygyny, male emancipation from parental care, and male song advertisement in these genera. Phylogenetically independent developments of a life history trait may be used as independent data points in comparative biological analyses of evolutionary process (Felsenstein 1985). Detailed information on the ecology and breeding systems of *Schiffornis, Laniisoma,* and *Laniocera* will permit direct comparisons with the natural history of other lekking tyrannoids which will not be confounded by historical interdependence. In particular, these comparisons will be useful in testing hypotheses about the effect of female choice and ecology on male reproductive strategies, and the evolution of lek

and cooperative displays observed in many tyrannoids.

The *Schiffornis* group species are found in a variety of habitats. *Laniisoma* is apparently restricted to mossy cloud and humid upper tropical forest (Snow 1982). *Iodopleura, Laniocera, Schiffornis turdinus,* and *S. virescens* are found in primary humid tropical forest, but *Schiffornis major* is found exclusively in seasonally flooded varzea forest along major rivers in the Amazon basin (Hilty and Brown 1986; R. O. Prum, pers. observ.). *Pachyramphus* is the most wide-ranging and speciose genus in the group, and is found commonly in second growth and forest edge habitats. *Xenopsaris* is found in reed beds and riverine scrub (Snow 1973, Traylor 1977), a habitat which is unusual among tyrannids and unknown in cotingids and piprids.

COMMON NAMES OF SPECIES IN
THE *SCHIFFORNIS* GROUP

This phylogenetic analysis has not resolved the higher level relationships of the *Schiffornis* group, so we will not present a phylogenetic classification of the genera at this time. However, the presently recognized common names of a number of the genera are obsolete and misleading, and should be changed. For example, *Laniisoma elegans* is called the Shrike-like Cotinga (Meyer de Schauensee 1966, Meyer de Schauensee and Phelps 1978, Snow 1982, Hilty and Brown 1986), though it is not even vaguely shrike-like and may be unrelated to cotingas. *Schiffornis turdinus, S. major,* and *S. virescens* are called Thrush-like, Greater, and Greenish manakin, respectively (Meyer de Schauensee 1966, Meyer de Schauensee and Phelps 1978, AOU 1983, Hilty and Brown 1986), though they are not manakins (Prum, unpubl.). Furthermore, the "Greater" manakin is a misnomer since *S. major* is actually smaller than *S. turdinus* (when *major* was first named, the larger *turdinus* was placed in the genus *Heteropelma*).

The two *Laniocera* species are referred to commonly as mourners. It seems appropriate to apply this common name to the three genera in this clade, especially to the *Schiffornis* species which are well-known for their beautiful, mournful, whistled songs (Skutch 1969, 1981). We recommend that *S. turdinus* and *S. virescens* be called the Thrush-like and Greenish mourners, respectively, and that *S. major* be called the Varzea Mourner or Cinnamon Mourner, in reference to

its distinctive habitat preference or its bright cinnamon plumage, rather than its less appropriate specific name. In addition, *L. elegans* should be called the Elegant Mourner, following its very apt specific name.

Elsewhere in the *Schiffornis* group, *Xenopsaris albinucha* has been uninspiringly called the White-naped Xenopsaris (e.g., Meyer de Schauensee 1966, Meyer de Schauensee and Phelps 1978, Hilty and Brown 1986). We propose to call this species the Reed Becard, referring to both its similarities and differences from the well-known becards.

ACKNOWLEDGMENTS

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APPENDIX

List of anatomical specimens of *Schiffornis* group species examined in this analysis. Specimens are listed under each species according to institution, the type of specimen, and the catalog number. The institution acronyms are: AMNH, American Museum of Natural History; CM, Carnegie Museum of Natural History; FMNH, Field Museum of Natural History; LSUMZ, Louisiana State University Museum of Zoology; USNM, United States National Museum of Natural History; UMMZ, University of Michigan Museum of Zoology; YPM, Yale Peabody Museum of Natural History. The types of anatomical specimens examined are skeletons (sk), unstained alcoholic syringes (us), and cleared and doubled stained syringes (c&s).

Schiffornis turdinus—AMNH: sk, 14147, c&s, 2305, 8082; FMNH: us, 290397; LSUMZ: us, 114487, 114888, 118038; c&s, 102439, 102443, 102449, uncat.; UMMZ: sk, 153226, 153359, 153360; us, 225043, 225044; USNM: us, 515120, 515122.

Schiffornis virescens—AMNH: sk, 6662, c&s, 2448; FMNH: us, 107022; UMMZ: sk, 158756, 158793, 200836, 202192, 202193, 202194, 202195.

Schiffornis major—AMNH: c&s, 9376, 816774; LSUMZ: c&s, 105270.

Laniocera hypopyrrha—AMNH: sk, 11448, c&s, 8087, 15208, 816776; FMNH: us, 290394; LSUMZ: us, 79585, 114498, c&s, 102562, 102564.

Laniocera rufescens—LSUMZ: c&s, 108460, 108461; UMMZ: sk, 218410; YPM: c&s, 986.

Laniisoma elegans—FMNH: sk, 322419, c&s, 322417.

Pachyramphus viridis—UMMZ: sk, 202174, 202175; USNM: us, 227304.

Pachyramphus rufus—AMNH: c&s, 2260; CM: us, 1275, 1306, 1320; UMMZ: sk, 156152, 156888.

Pachyramphus cinnamomeus—UMMZ: sk, 133891, 133892, 133893, 133894, 133895, 153352, c&s, 226364.

Pachyramphus polycopterus—AMNH: sk, 7150, c&s, 2389, 8223; CM: us, 1341; LSUMZ: us, 42868, 64797, 64798, 71469, 91220; UMMZ: sk, 133355, 133896, 133897, 133898, 133900, 153353, 153354, 218966; USNM: us, 227742.

Pachyramphus marginatus—AMNH: c&s, GFB1407; LSUMZ: c&s, 102281, UMMZ: sk, 209424.

Pachyramphus versicolor—LSUMZ: us, 107646.

Pachyramphus major—AMNH: c&s, uncat. WS B-1083.

Pachyramphus aglaiae—AMNH: sk, 7151, 7880, 12758, c&s, 2262, 6657, 7889, 8220, 8221, 8222; UMMZ: sk, 85348, 85349, 130945.

Pachyramphus validus—AMNH: c&s, 7897.

Pachyramphus minor—AMNH: sk, 10172; LSUMZ: c&s, 111083; UMMZ: sk, 155464, 159420.

Xenopsaris albinucha—AMNH: sk, 15000, c&s, 3520, 8389.

Iodopleura isabellae—FMNH: sk, 322433, c&s 322431, 322432; LSUMZ: c&s, TJD 1286.