MONOPHYLY AND PHYLOGENY OF THE SCHIFFFORS GROUP (TYRANNOIDEA)\textsuperscript{1}

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Abstract. A cladistic analysis of 19 characters was used to investigate the phylogeny of the Schifffors group, a monophyletic assemblage of six genera of suboscine passerines which are currently placed in three different tyrannoid families: Schifffors (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 Schifffors group was supported by two syringeal synapomorphies. Within the group, the phylogenetic relationships of five of the six genera were resolved; Schifffors 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 Schifffors 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; Schifffors; Pachyramphus.

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 expasidean 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 Ptichlorinae 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 Tyrannutea. 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, Tyrannutea, 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 Ptilochlorinaceae next to Schizophinornis, 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. rucescens) mourners, which are allopatrally 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 Schizophinornis based, again, on tarsal scutellation and toe fusion. Hellmayr (1929) replaced it in the Cotingidae, near Piprids and most cotingids but lacks the derived femoral artery of cotingids and piprids, although its 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 synonymized Platypsraris with Pachyramphus. Snow (1979, 1982) and Traylor (1977, 1979) moved Pachyramphus and Tityra into a separate subfamily, the Tityriniae, in the Tyrannidae, citing the works of Warter (1965) and Ames (1971). The AOU (1983) followed this arrangement. McKittrick (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 Schizophinornis. 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 Schizophinornis 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 digit 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*, *Tyrannneutes*, *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 *Tyrannneutes*, *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 |
| Laniisoma   |           | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 |
| Laniocera   |           | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 |
| Pachyrhamphus|         | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 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 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 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 |

derived. 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 Ru-picola, Phoenicircus, Carpornis, Pipreola, Ampelioiides, Lipaugus cryptophthalmus and L. subalaris) and in almost all other birds, the main artery of the hind limb is the ischiadic (Garrod 1876; Mitgard 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 2. Right ventrolateral views of the syringes of (A) Schifnornis 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 Schifnornis. This state does not occur in any other tyrannoids, fumarioids, 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 Schifnornis group is here hypothesized to be derived.

(4) Insertion of intrinsic musculature on A1/B1 membrane. All genera in the Schifnornis 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 Schifnornis, the intrinsic muscles originate on the lateral surfaces of elements A4–5 just posterior 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 Pachyramphus 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 Schizornis 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 Schizornis 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 Schizornis group, Oxyruncus, and several tyrannid lineages; (3) it evolved in the Schizornis group, independently of tyrannids and Oxyruncus, as a novel intrinsic muscle subsequent to the evolution in the cotinids 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 Schizornis group, in the second and third hypotheses. Evaluation of the third hypothesis, that the syringeal musculature found in the Schizornis group is a terminal state in a character transition series within the cotinids, will require additional data supporting some or all cotinids as the immediate sister group of the Schizornis group (Prum, unpubl.).

(5) Unique, complex internal syringeal cartilages. In Schizornis, 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 Schizornis 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 specimens. 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 Schizornis, 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 Myioglossus), but in none of these cases does the head of the lacrimal have a thin rostral arm or bridge. In most cotinids, 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, Pyriderus, 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 Ampeliopterys and some Pipreola, the head of the lacrimal is large and
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 Pyrrocephalus 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 Schifcornis, the pessulus is wide and flat (Fig. 1A). In the other genera in the Schifcornis 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 Schifcornis is nearly unique to that genus. Rupicola, Phoenicircus, and Car- pornis (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 Schifcornis is hypothesized to be derived.

(10) Broad B1 elements. In Schifcornis, the B1 element is a broad bar, whereas in the other genera of the Schifcornis 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 Schifcornis is hypothesized to be derived.

(11) Dorsally lengthened A1 elements. In Lani- isoma 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 Schifcornis group has similar barring. Elsewhere in the tyrannoids, some members of the cottingid genera Pipreola, Ampelioiides, Porphyrolaema, and Philalura 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 Lani- ocera 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 Schifcornis group, or (2) that Laniocera and Laniisoma are most closely related to the above cottingid genera, would require more reversals or conver- gences in other characters and are less parsimonious.

(14) Orange-rufous wing covert spots. In Lani-
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 yel-
low or orange-rufous patches. These patches are
not found in other tyrannoids. They are hypothe-
sized 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 Laniiso-
ma 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 hypothe-
sized 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 Pachy-
ramphus. In male Tityra, the entire 9th primary
is narrow and reduced in size, and sharply emar-
ginate at the tip, instead of merely shortened and
truncate as in Pachyramphus. The state found in
Pachyramphus is hypothesized here to be de-
 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 Pachy-
ramphus 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
Platysparris), 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 Lan-
isoma are unknown. Elsewhere in the Tyran-
noidea, globular nests are built by genera or groups
of genera in several different assemblages of ty-
rant 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 hypothe-
sized to be derived independently.

RESULTS

The characters analyzed support two equally par-
simonious alternative hypotheses for the phy-
logenetic 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 Schiff-
ornis group is supported, and Tityra, Piprites,
Neopelma, Tryeanoeues, 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 re-
quires a single evolution of the enlarged femoral
artery (character 2) and a convergent develop-
ment or secondary loss of internal syringeal car-
tilages (character 1) (Fig. 4A). The latter hypoth-
esis requires a convergent development of
secondary loss of the enlarged femoral artery and
a single development of internal syringeal car-
tilages (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 sup-
port a single resolution of the phylogenetic in-
terrelationships of Schiffornis, Laniisoma, and
Laniocera, in which Schiffornis is the sister group
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, 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

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 Schïffornis 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 in- between the two alternative hypotheses for the other derived characters with congruent or composition of the conflicting distributions (Patterson 1982). Choosing otherwise (Fig. 5).

Additional data will require additional data.

Within the Schïffornis group, the monophyly of each of the six genera is supported unambiguously (Fig. 5). Schïffornis 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). Iodo- pleura 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 Schïffornis 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 Schïffornis 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 Schïffornis is their sister group.

None of the alternative, traditional hypotheses for the relationships of the Schïffornis group genera to other tyrannoids is supported by the morphological characters analyzed. Schïffornis is not a member of the Pipridae (Prum, unpubl.), and none of the piprids or other piprid-like tyrannoids is a member of the Schïffornis 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 Schïffornis 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 Schizornis group and shares with Pachyramphus the derived form of the M. tracheolateralis (character 7). Pachyramphus itself has long been placed with Titrya 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 Titrya together as aberrant tyrannid-like cotin-gas, 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 Titrya as typically cotingid. Titrya lacks the derived syringeal characters which diagnose either the Schizornis group or the Pachyramphus-Xenopsaris clade. The syringeal supporting elements, internal cartilages, and musculature of Titrya have some derived similarities to cotingids, Neopelma, Tyrannneutes, and members of the genus Lipaugus (Prum, unpubl.). Based on morphology, Titrya cannot be confidently considered a close relative of Pachyramphus. Although it is possible that Titrya 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 Schizornis group but does not provide any additional resolution. The oft-stated similarities of Iodopuleura to the enigmatic and possibly extinct Calliptura 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 Schizornis group were not included in this analysis because they are too variable or primitive within tyrannoids. For example, Schizornis group genera have been characterized as having exaspidean (Schizornis, 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, unpubl.). The fusion of the outer two toes (digits III and IV), or syndactyly, has been used traditionally to define the Pipridae. Schizornis, 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 Schizornis 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 Schizornis 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 Schizornis group, but they cannot be polarized confidently without a more specific hypothesis for the sister group of the Schizornis group. For example, the Schizornis 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 Schizornis 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, Schizornis and Laniisoma have natal down that is much longer than most passerine birds. Skutch (1969, 1981) describes the natal down on Schizornis 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 cot- 
ingid *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 rela-
tionships of this assemblage, but the hypothesis of closer relationship to the cotinigids and piprds 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-
ornis* 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 sepa-
rating the Tityrinae and Tyranninae from one another and from their sister groups including the cotinigids (Cotinginae) and piprids (Piprinae) were very small (0.2-0.4 TsOH). 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 diffi-
culties in data analysis (Cracraft 1987). The lim-
ited DNA-DNA hybridization data lend partial 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 original 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 cotinigids and piprds, and the second 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-
ornis* group. The pertinent genera surveyed (Schiffornis, Pachyramphus, and *Iodoopera*) 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 prelimi-
ary 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.

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

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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). Pachyrhamphus 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. Pachyrhamphus nests are often built in close association with bee hives. In the P. aglaiae species group (formerly Platyspasaris), the nest is hung from an isolated tree limb whereas in other Pachyrhamphus 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 Pachyrhamphus, supporting the monophyly of the formerly recognized genus Platyspasaris (character 19). Additional characters supporting the monophyly of the restricted genus Pachyrhamphus, excluding “Platyspasaris,” 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 Schiffronis group species are found in a variety of habitats. Lanisoma is apparently restricted to mossy cloud and humid upper tropical forest (Snow 1982). Iodopleura, Laniocea, Schiffronis turdinus, and S. virescens are found in primary humid tropical forest, but Schiffronis 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 riparian scrub (Snow 1973, Traylor 1977), a habitat which is unusual among tyrannids and unknown in cotingids and piprids.

COMMON NAMES OF SPECIES IN THE SCHIFFRONIS GROUP

This phylogenetic analysis has not resolved the higher level relationships of the Schiffronis 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, Lanisoma 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 cotings. Schiffronis 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, unpublish.). 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 Hetropelma).

The two Laniocea 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 Schiffronis 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 Schiffronis 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.

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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 double stained syringes (c&s).

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

Laniuscoma 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, 156688.

Pachyramphus cinnamomeus—UMMZ: sk, 133891, 133892, 133893, 133894, 133895, 133532, c&s, 226364.

Pachyramphus polyceropus—AMNH: sk, 7150, c&s, 2389, 8223; CM: us, 1341; LSUMZ: us, 42868, 64797, 64798, 71469, 91220; UMMZ: sk, 133355, 133896, 133897, 133898, 133900, 135335, 135334, 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; USNM: sk, 85334, 85349, 130945.

Pachyramphus validus—AMNH: c&s, 7897.

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

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

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