NUMBER 723 DECEMBER 20, 1990

OCCASIONAL PAPERS OF THE MUSEUM OF ZOOLOGY
THE UNIVERSITY OF MICHIGAN

ANN ARBOR, MICHIGAN

A TEST OF THE MONOPHYLY OF THE MANAKINS (PIPRIDAE) AND OF THE COTINGAS (COTINGIDAE) BASED ON MORPHOLOGY

BY RICHARD O. PRUM*

ABSTRACT.—*Prum, Richard O. A test of the monophyly of the manakins (Pipridae) and of the cotingas (Cotingidae) based on morphology. Occ. Pap. Mus. Zool., Univ. Michigan, 723:1-44, 6 figs.* A phylogenetic analysis of the Tyrannoidea is performed as a test of the monophyly of the manakins (Pipridae) and of the cotingas (Cotingidae). The 12 morphological characters surveyed include the traditional characters used to define the families and other morphological features taken from observations of tyrannoid syringes and hindlimb arteries. Five traditional characters are phylogenetically uninformative. The remaining seven characters support 25 maximally parsimonious phylogenetic hypotheses of length 10 (CI = 0.70). A strict consensus tree based on these trees has few resolved clades, but indicates that neither the Pipridae nor the Cotingidae as traditionally defined is monophyletic. Six currently recognized genera of Pipridae—*Schiffornis, Sapayoa, Piprites, Neopipo, Neopelma,* and *Tyranneutes*—share derived morphological characters with other, non-piprid tyrannoids. The other eleven piprid genera—*Chloropipo, Xenopipo, Antilophia, Heterocercus, Machaeropterus, Manacus, Corapipo, Ilicura, Masius, Chiroxiphia,* and *Pipra*—form a clade diagnosed by the dorsal fusion of the B1–2 syringeal supporting elements. A large clade including most cotingids is supported by a derived syringeal muscle character and provides evidence of the monophyly of the cotingids, but this character conflicts with other derived morphological features. Additional data are required to resolve many portions of tyrannoid higher-level phylogeny. Relative confidence of the homology of derived states and possible resolutions of character conflicts are discussed. Recognition of a restricted monophyletic Pipridae including only 11 genera is recommended.

*Department of Ornithology, American Museum of Natural History, Central Park West at 79th St., New York, NY 10024.

Key words: *Manakins, cotingas, tyrant flycatchers, Pipridae, Cotingidae, Tyrannidae, monophyly, phylogeny, morphology, syrinx.*

RESUMEN.—Se efectuó un ánalisis filogenético de Tyrannoidea para probar la monofilia de las familias de saltarínes (Pipridae) y de cotingas (Cotingidae). Los doce caracteres morfológicos que se emplearon incluyen características tradicionales y otras características nuevas de los tiranoides encontradas en las siringes y en las arterias de las piernas. Cinco de los caracteres tradicionalmente empleados para definir las dos familias no son informativos filogenéticamente. Los otros siete caracteres nuevos sustentan 25 hipótesis filogenéticas igualmente parsimónicas (longitud del cladogram = 10 cambios; indice de consistencia = 0.70). El árbol de consenso basado en estas hipótesis filogenéticas tiene pocos grupos monofiléticos (clados) resueltos, pero indica que ni Pipridae ni Cotingidae son monofiléticos. Seis géneros tradicionalmente incluídos en Pipridae—*Schiffornis, Sapayoa, Piprites, Neopipo, Neopelma,* y *Tyranneutes*—comparten características morfológicas derivadas con otros tiranoides fuera de la familia. Los otros once géneros de Pipridae—*Chloropipo, Xenopipo, Antilophia, Heterocercus, Machaeropterus, Manacus, Corapipo, Ilicura, Masius, Chiroxiphia,* y *Pipra*—comprenden un clado que está sustentado por la fusión dorsal de los elementos siringeles B1–2. Otro gran clado que incluye la mayoría de las cotingas está sustenado por un caracter muscular en la siringe derivado y que provee evidencia inicial de la monofilia de Cotingidae, pero este caracter está en conflicto con otros caracteres morfológicos derivados. Se requieren datos adicionales para resolver mejor la filogenia en los niveles superiores de Tyranniodea. Se discuten aqui problemas de homologías entre ciertos caracteres derivadas y las posibles resoluciones de la filogenia de la superfamilia. Es recomendable el reconocimiento de una nueva Pipridae monofilética que incluya solamente once géneros.

Palabras claves: *Saltarínes, cotingas, atrapamoscas, Pipridae, Cotingidae, Tyrannidae, monofilia, filogenia, morfologia, siringe.*

INTRODUCTION

The neotropical suboscine families of manakins (Pipridae) and cotingas (Cotingidae) have long been thought to be closely related to one another (Sclater, 1888; Ridgway, 1907; Hellmayr, 1927; Snow, 1973, 1975, 1979). Both are presently placed in the suboscine superfamily Tyrannoidea with the diverse tyrant flycatchers (Tyrannidae), the monotypic sharpbill *Oxyruncus* (Oxyruncidae), and the four species of plantcutters *Phytotoma* (Phytotomidae) (Traylor, 1979; Snow, 1979). Many manakins are known for their striking sexual dimorphism, elaborate courtship displays, and lek breeding systems, but others are not sexually dimorphic (Sick, 1959, 1967; Snow, 1963). Likewise, the cotingas vary considerably in size, plumage, and in breeding system. The Cotingidae includes lekking, cooperatively breeding, and monogamous species (Snow, 1982). Traditional avian systematists all recognized the difficulty in separating piprids, cotingids, and tyrannids from one another (Sclater, 1888; Ridgway, 1907; Hellmayr, 1927; Snow, 1973, 1975). In practice, a few variable external characters were used to diagnose the three families. The internal morphological characters used to support these familial boundaries were known from only a few taxa and were assumed to be present in the rest of each family.

The composition of the Cotingidae has been recently influenced by studies of cranial morphology (Warter, 1965) and syringeal anatomy (Ames, 1971), but in the absence of conclusive new anatomical information, the clearly unsatisfactory limits of the Pipridae have changed little in the past one hundred years. In particular, the placement of six atypical genera—*Schiffornis, Sapayoa, Piprites, Neopipo, Neopelma* and *Tyranneutes*—within the Pipridae has been questioned by recent authors (Meyer de Schauensee, 1966; Wetmore, 1972; Snow, 1975; McKitrick, 1985). The placement of the two aberrant genera *Oxyruncus* and *Phytotoma* in separate families has also persisted because of the lack of conclusive evidence about their relationships to other tyrannoids.

A variety of approaches have been used recently to examine higher-level phylogenetic interrelationships of the tyrannoids, but systematic conclusions have been limited by conflicts among data sets (S. M. Lanyon, 1985; McKitrick, 1985; Sibley and Ahlquist, 1985a). The purpose of this paper is to test the monophyly of the Pipridae and Cotingidae using a cladistic analysis of morphological characters from original observations of syringeal and arterial morphology of the tyrannoids, and from the literature. The results of this analysis are compared to previous phylogenetic hypotheses based on molecular characters.

HISTORICAL REVIEW OF THE CLASSIFICATION OF THE PIPRIDAE AND COTINGIDAE

Müller's (1847, 1878) comparisons of the syringes of a wide variety of passerines permitted the first clear differentiation of the New World suboscines from Old World oscines with similar bill shapes and body types: *e.g.*, piprids from parids, cotingids from corvids, and tyrannids from muscicapids. Based on observations of the attachments of syringeal musculature, Garrod (1876, 1877) divided the passerines into two main subgroups: the suboscines or Mesomyodi, and oscines or Acromyodi. Garrod (1876) also described two variations in the arterial supply to the hindlimb that he used to separate the cotingas and manakins from other suboscines. He observed that in eight species of piprids and cotingids (*Chiroxiphia linearis, Manacus manacus, Schiffornis turdinus, Tityra semifasciata, Pachyramphus aglaiae, Lipaugus* sp., *Ampelioides tschudii,* and *Procnias nudicollis*), the main artery supplying the hindlimb is the femoral, whereas in the seven tyrannid species (*Mionectes oleagineus, Zimmerius vilissimus, Pitangus sulphuratus, Myiozetetes luteiventris, Empidonax minimus, Myiarchus crinitus,* and *Tyrannus melancholicus*), the cotingid *Rupicola,* and most other birds, the main artery supplying the hindlimb is the ischiadic. Garrod generalized from this sample to the rest of the suboscines, and recommended placing the piprids and cotingids in the Heteromeri, and all other suboscines in the Homeomeri.

Sclater (1888) presented the first detailed classification of the tyrannoids. In his key to the group he defined each family by a unique combination of bill shape, toe fusion, and tarsal scutellation type. Sclater defined the Pipridae by the combination of exaspidean tarsi and fused outer toes (syndactyly), and he defined the Cotingidae by the possession of unfused toes, pycnaspidean tarsi and elongate, compressed bill. Within the Pipridae, he recognized 19 genera in two subfamilies: Piprinae and Ptilochlorinae (Table 1). Within the Cotingidae, Sclater arranged 28 genera in six subfamilies: Tityrinae, Lipauginae, Attilinae, Rupicolinae, Cotinginae, and Gymnoderinae (Table 1). Sclater (1888) placed the aberrant genus *Phytotoma,* recognized by its pycnaspidean tarsi and finch-like serrate bill, in the Phytotomidae; he placed another aberrant genus *Oxyrhamphus* (= *Oxyruncus*) in the Oxyrhamphidae (= Oxyruncidae), based on the combination of exaspidean tarsi and straight, pointed bill.

Ridgway (1907) recognized the apparent character conflict between the exaspidean tarsal scutellation, shared by piprids and tyrannids, and the unique femoral artery, shared by piprids and cotingids. He concluded that all three families were closely related and that satisfactory familial borders would only result from further anatomical investigation. In his classification, Ridgway relied on the combination of enlarged femoral artery, exaspidean tarsal scutellation, extensive fusion of the outer two digits (III and IV), and short, wide bill to define the Pipridae, and on the enlarged femoral artery, usually pycnaspidean scutellation, and unfused toes to define the Cotingidae. With a few exceptions, Ridgway (1907) recognized the same familial limits as Sclater (1888) (Table 1). Following Garrod's (1876) observa-

TABLE 1.—Major classifications of the genera of tyrannoids (excluding Tyrannidae). Currently recognized names are given only after the first mention of each obsolete synonym, except when the name is presently applied to a different group of species.

Sclater (1888)	Ridgway (1907)	Hellmayr (1929)	Snow (1979)
Oxyrhamphidae	Pipridae	Oxyruncidae	Pipridae
(=Oxyruncidae)	*Manacus*	*Oxyruncus*	*Schiffornis*
Oxyrhamphus	*Allocotopterus*		*Sapayoa*
(=*Oxyruncus*)	(=*Machaeropterus*	Pipridae	*Piprites*
	deliciosus)	*Piprites*	*Neopipo*
Pipridae	*Machaeropterus*	*Pipra*	*Chloropipo*
Piprinae	*Ilicura*	*Teleonema*	*Xenopipo*
Piprites	*Chiroprion*	*Machaeropterus*	*Antilophia*
Chloropipo	(=*Chiroxiphia*)	*Allocotopterus*	*Tyranneutes*
Xenopipo	*Chiroxiphia*	*Chloropipo*	*Neoplema*
Ceratopipra	*Ceratopipra*	*Ceratopipra*	*Heterocercus*
(=*Pipra*	*Cirrhipipra*	*Xenopipo*	*Machaeropterus*
cornuta)	(=*Pipra*	*Tyranneutes*	*Manacus*
Cirrhopipra	*filicauda*)	*Masius*	*Corapipo*
(=*Pipra*	*Pipra*	*Antilophia*	*Ilicura*
filicauda)	*Corapipo*	*Chiroxiphia*	*Masius*
Metopia	*Chloropipo*	*Ilicura*	*Chiroxiphia*
(=*Antilophia*)	*Tyranneutes*	*Corapipo*	*Pipra*
Metopothrix	*Xenopipo*	*Manacus*	
Pipra (incl.	*Heterocercus*	*Neopipo*	Cotingidae
Corapipo and	*Antilophia*	*Massornis*	*Phoenicircus*
Tyranneutes)	*Masius*	(=*Schiffornis*)	*Laniisoma*
Neopipo	*Neopipo*	*Schiffornis*	*Phibalura*
Machaeropterus	*Scotothorus*	*Sapayoa*	*Tijuca*
Chiroxiphia	(=*Schiffornis*)	*Neopelma*	*Carpornis*
Helicura	*Neopelma*	*Heterocercus*	*Ampelion*
(=*Ilicura*)	*Laniocera*		*Pipreola*
Chiromachaeris	*Piprites*	Cotingidae	*Ampelioides*
(=*Manacus*)		*Phoenicircus*	*Iodopleura*
Ptilochlorinae	Cotingidae	*Laniisoma*	*Calyptura*
Ptilochloris	*Phoenicircus*	*Phibalura*	*Lipaugus*
(=*Laniisoma*)	*Laniisoma*	*Heliochera*	*Chirocylla*
Heteropelma	*Phibalura*	*Doliornis*	*Porphyrolaema*
(=*Schiffornis*)	*Heliochera*	*Tijuca*	*Cotinga*
Schiffornis	(=*Ampelion*)	*Ampelion*	*Xipholena*
Neopelma	*Tijuca*	(=*Carpornis*)	*Carpodectes*
Heterocercus	*Ampelion*	*Porphyrolaema*	*Conioptilon*
	(=*Carpornis*)	*Cotinga*	*Gymnoderus*
Cotingidae	*Porphyrolaema*	*Xipholena*	*Haematoderus*
Tityrinae	*Cotinga*	*Carpodectes*	*Querula*
Tityra	*Xipholena*	*Eucholornis*	*Pyroderus*
Hadrostomus	*Carpodectes*	*Ampelioides*	*Cephalopterus*
(=*Pachyramphus*)	*Eucholornis*	*Iodopleura*	*Perissocephalus*
Pachyramphus	*Carpodectes*	*Calyptura*	*Procnias*
Lipauginae	*Stictornis*	*Attila*	*Rupicola*
Chirocylla	(=*Ampelioides*)	*Casiornis*	
Lathria	*Iodopleura*	*Laniocera*	Oxyruncidae
(=*Lipaugus*)	*Calyptura*	*Rhytipterna*	*Oxyruncus*
Aulia	*Microtriccus*	*Lipaugus*	
(=*Laniocera*)	(=*Ornithion*)	*Chirocylla*	Phytotomidae
Lipaugus	*Ornithion*	*Pachyramphus*	*Phytotoma*

TABLE 1.—Continued

Sclater (1888)	Ridgway (1907)	Hellmayr (1929)	Snow (1979)
(=*Rhytipterna*)	*Tyrannulus*	*Platypsaris*	Transferred from
Attilinae	*Idiotriccus*	*Tityra*	Cotingidae to
Attila	(=*Phyllomyias*)	*Haematoderus*	Tyrannidae
Casiornis	*Elainopsis*	*Querula*	
Rupicolinae	(=*Myiopagis*	*Pyroderus*	Tyranninae
Phoenicocercus	*gaimardii*)	*Cephalopterus*	*Laniocera*
(=*Phoenicircus*)	*Attila*	*Perissocephalus*	*Attila*
Rupicola	*Hylonax*	*Gymnoderus*	*Casiornis*
Cotinginae	(=*Myiarchus*	*Procnias*	*Rhytipterna*
Phibalura	*validus*)		Tityrinae
Tijuca	*Ramphotrigon*	Rupicolidae	*Pachyramphus*
Ampelion	*Sirystes*	*Rupicola*	*Tityra*
(=*Pipreola* and	*Casiornis*		Incertae Sedis
Ampelioides)	*Lipaugus*	Phytotomidae	*Xenopsaris*
Pipreola	(=*Rhytipterna*)	*Phytotoma*	
Cotinga	*Lathria*		
Xipholena	(=*Lipaugus*)	Transferred from	
Carpodectes	*Xenopsaris*	Cotingidae back	
Doliornis	*Pachyramphus*	to Tyrannidae	
(=*Ampelion*)	*Platypsaris*	*Ornithion*	
Iodopleura	(=*Pachyramphus*)	*Tyrannulus*	
Calyptura	*Erator* (=*Tityra*)	*Idiotriccus*	
Gymnoderinae	*Haematoderus*	*Phyllomyias*	
Haematoderus	*Querula*	*Myiarchus validus*	
Querula	*Pyroderus*	*Ramphotrigon*	
Pyroderus	*Cephalopterus*	*Sirystes*	
Heliochera	*Calvifrons*	*Xenopsaris*	
(=*Carpornis*)	(=*Perisso-*		
Cephalopterus	*cephalus*)		
Gymnocephalus	*Gymnoderus*		
(=*Perisso-*	*Tityra*		
cephalus)	*Procnias*		
Gymnoderus			
Chasmorhyncus	Rupicolidae		
(=*Procnias*)	*Rupicola*		
Phytotomidae	Phytotomidae		
Phytotoma	*Phytotoma*		
	Oxyruncidae		
	Oxyruncus		

tions, Ridgway removed *Rupicola* from the Cotingidae and placed it in its own family Rupicolidae. Ridgway also removed *Laniisoma* from the Pipridae and placed it near *Phoenicircus* in the Cotingidae, and he moved *Laniocera* from the Cotingidae to the Pipridae following *Schiffornis.* He characterized the tyrannids *Microtriccus, Ornithion, Tyrannulus, Idiotriccus* (=*Phyllomyias*), *Elainopis* (=*Myiopagis gaimardii*), *Hylonax* (=*Myiarchus validus*), *Sirystes,* and *Ramphotrigon* as pycnaspidean in tarsal scutellation, and transferred these taxa to the Cotingidae. He also placed the newly described genus *Xenopsaris* in the Cotingidae next to *Pachyramphus.* Ridgway did not examine *Metopothrix,* placed by Sclater (1888) in the Pipridae, or *Sapayoa,* described by Hartert (1903) and placed in the Pipridae near *Schiffornis,* and he reserved comment on their systematic relationships.

Hellmayr (1927, 1929) placed less emphasis on tarsal scutellation and toe fusion than Ridgway, leading to the reassignment of *Laniocera* to the Cotingidae near *Lipaugus,* and the return of all the pycnaspidean tyrannids to the Tyrannidae (Table 1). Hellmayr included *Sapayoa* in the Pipridae following the suggestion of Hartert (1903) in the original description of the genus. He disagreed with Ridgway about the relationships of *Xenopsaris* and followed Berlepsch (1907) by placing it in the subfamily Serpophaginae of the Tyrannidae. He also followed Berlepsch's (1903) recommendation, removing *Metopothrix* from the Pipridae and placing it near *Xenerpestes* in the Furnariidae.

Warter (1965) did not identify any osteological characters to define the Pipridae in his work on the cranial osteology of the tyrannoids. He did remark that the distinct shape of the lacrimal of the genus *Sapayoa* is reminiscent of the Old World eurylaimids, and that *Neopelma* has a typically tyrannid skull. Within cotingids, Warter described a number of cranial character variations and proposed several intrafamilial groupings. He concluded that *Tityra* and *Pachyramphus* are similar to tyrannids in their skull morphology but also quite distinct from other tyrannoids. He recommended placing them either in their own family or in a subfamily of the Tyrannidae, but did not describe any characters uniting the two genera.

Ames (1971) described the syringes of 11 species in 7 genera of piprids and 18 species in 16 genera of cotingids in his comprehensive survey of the passerine syrinx. Ames documented extensive variation in the syringeal supporting structures and muscles of piprids. He suggested that *Piprites* and *Ilicura* were more tyrannid-like in their syringeal structure than other piprids, and that *Schiffornis* resembled *Lipaugus unirufus* in syringeal structure. He did not make specific systematic conclusions but suggested that the syringes of the piprids resemble those of certain tyrannids more than they do any particular cotingids. Within the cotingids, Ames (1971) recognized four basic syringeal groups, and recommended moving *Attila, Casiornis, Rhytipterna,* and *Laniocera* to the Tyrannidae near *Myiarchus,* based on their possession of internal syringeal cartilages and an intrinsic syringeal muscle, M. obliquus ventralis. He suggested that *Lipaugus* *unirufus* may also belong with these transferred genera, but his limited material was damaged and he was less certain of this conclusion. Ames considered *Pachyramphus* to be tyrannid-like in syringeal structure, but placed *Tityra* in a core group of cotingids.

Snow (1973, 1975) reviewed the problems of identifying the familial limits of the piprids and cotingids, and the new anatomical information of Ames (1971). In the absence of conclusive anatomical information, Snow (1975, 1979) recognized the same limits to the Pipridae as Hellmayr (1927) (Table 1). Within the family, he lumped the monotypic genera *Teleonema* and *Ceratopipra* into *Pipra,* and *Allocotopterus* into *Machaeropterus.* He rearranged the order of the genera to proceed loosely from the "primitive" and "least advanced" to the most "specialized," with the placement of *Schiffornis, Sapayoa,* and *Piprites* at the beginning indicating significant uncertainty about their relationships.

In agreement with Ames (1971), Snow (1973) transferred *Attila, Casiornis, Laniocera,* and *Rhytipterna* from the Cotingidae to the Tyrannidae (Table 1). He further suggested the placement of *Xenopsaris* in the Tyrannidae, and the inclusion of *Rupicola* in the Cotingidae. After questioning their status as cotingids, he left *Laniisoma, Phoenicircus,* and *Lipaugus* in the family for lack of conclusive evidence.

Traylor (1977, 1979) followed the suggestion of Warter (1965) and transferred *Tityra* and *Pachyramphus* to the Tyrannidae, but he placed them both in a single subfamily, the Tityrinae. In agreement with Snow (1973), Traylor also placed *Xenopsaris* at the end of the Tyrannidae as *incertae sedis.*

Recently, McKitrick (1985) performed a cladistic analysis of morphological characters to test the monophyly of the traditionally defined Tyrannidae. She concluded that a slightly enlarged Tyrannidae including all taxa with derived, internal syringeal cartilages (see character 6) may be monophyletic, and that the monophyly of a slightly restricted group of tyrannids is supported by the presence of the M. obliquus ventralis (see character 11). McKitrick hypothesized that the enlarged femoral artery known in a few cotingas and manakins is derived, and identified a problematic group of tyrannoid genera, including *Schiffornis, Pachyramphus,* and *Tityra,* that share both the derived internal syringeal cartilages with tyrannids and the enlarged femoral artery with the cotingids and piprids.

S. M. Lanyon (1985) analyzed allozyme variation among many piprid and cotingid genera, and a single tyrannid. The results indicated that *Piprites* is not a piprid but that *Schiffornis, Neopelma,* and *Tyranneutes* may be, and that the cotingas consist of five distinct lineages with unknown interrelationships. Sibley and Ahlquist (1985a) produced a phylogenetic hypothesis for the neotropical suboscines based on DNA-DNA hybridization. Their phylogeny of the tyrannoids placed one group of tyrannids as a sister group to the rest of the tyrannoids, and the rest of the tyrannids, including *Schiffornis, Tityra,* and *Pachyramphus,* as the sister group to the typical cotingids and piprids. Both biochemical hypotheses are discussed in detail below.

Concurrent with the present investigation, Prum and Lanyon (1989) analyzed syringeal, cranial, and plumage characters to produce a phylogeny of a tyrannoid clade including six genera, formerly placed in the Pipridae, Cotingidae, and Tyrannidae (Snow, 1979; Traylor, 1979): *Schiffornis, Laniocera, Laniisoma, Pachyramphus, Xenopsaris,* and *Iodopleura.* This clade, referred to as the *Schiffornis* group, shares derived characters with both the cotingids and piprids, and the tyrannids, and its higher-level relationships were unresolved.

Lanyon and Lanyon (1989) analyzed allozyme, syringeal, and osteological characters to investigate the relationships of *Phytotoma* to other tyrannoids. Derived biochemical and morphological characters both indicate that *Phytotoma* is closely related to the cotingid genus *Ampelion,* and possibly most closely to *Ampelion rubrocristatus* and *A. rufaxilla.* They recommended placing *Phytotoma* and *Ampelion* in the Phytotomidae because of lack of evidence supporting the monophyly of the Cotingidae.

METHODS

Characters analyzed were taken from the literature and from original observations of the syringes of tyrannoids and other suboscines. The syringeal specimens examined included 266 individuals of 43 of the 51 species in all 17 genera of currently recognized piprids, and 112 specimens of 39 species in 20 genera of cotingids (Snow, 1979). The syringeal specimens were of two types: cleared and double stained specimens to show bone and cartilage (Dingerkus and Uhler, 1977) prepared by W. E. Lanyon, American Museum of Natural History, New York, and specimens stained with reversible iodine muscle stain (Bock and Shear, 1972) to document variation in syringeal musculature. The syringeal morphology of tyrannids, other suboscines, and the oscine passerines was evaluated from limited observations of the collection of cleared and stained syringes prepared by W. E. Lanyon, and from information published by Lanyon (1984a, 1985, 1986, 1988a, 1988b, 1988c) and Ames (1971). A complete list of piprid and cotingid syringeal specimens observed is presented in Appendix 1.

Observations of the major arteries that branch off the lower aorta and supply the hindlimbs were observed through dissection of 186 tyrannoid spirit specimens, including 30 species of 9 genera of piprids and cotingids, and 29 species in 19 genera representing major clades of tyrannids (Lanyon, 1984a, 1985, 1986, 1988a, 1988b, 1988c) (Appendix 2). Skins and skeletons of various passerines in the collections of the University of Michigan Museum of Zoology were examined to evaluate certain traditional characters described in the literature.

Monophyly of the ingroup, the superfamily Tyrannoidea, was accepted *a priori* based on the possession in the small sample observed to date of a derived form of the M. flexor perforatus digiti IV (Raikow, 1987:36). This assumption is congruent with a phylogeny of the New World suboscines based on DNA-DNA hybridization (Sibley and Ahlquist, 1985a). Character variation within the ingroup was polarized by outgroup comparison to the Furnarioidea (Dendrocolaptidae, Furnariidae, Formicariidae, and Rhinocryptidae), the Old World suboscines, and the oscines. Following the outgroup comparison criterion, the character state that is unique to some portion of the ingroup is hypothesized as derived from the character state that is found in the remainder of the ingroup and the outgroups (Stevens, 1980; Wiley, 1981; Maddison *et al.*, 1984). Traditional characters were included in the analysis to test whether they are phylogenetically informative. The phylogenetically informative characters were analyzed using the PAUP computer program, version 3 (Swofford, 1989), with the global branch-swapping and MULPARS options on the unordered data set. Strict consensus trees were calculated using the consensus option on the PAUP program (Swofford, 1989).

CHARACTER ANALYSIS

Of the 12 morphological characters surveyed, 5 lacked phylogenetically informative variation within the Tyrannoidea. These characters (1–5) are presented first. The remaining 7 characters are hypothesized to be derived in some subset of tyrannoids and are used in the phylogenetic analysis. The distribution of the informative characters (6–12) are summarized in Table 2. For convenience, characters of some morphologically similar genera are listed as single taxa (see table footnotes).

UNINFORMATIVE CHARACTERS

(1) *Tarsal Scutellation.* The tarsal scutellation of piprids and tyrannids is exaspidean (Sclater, 1888; Gadow, 1893; Ridgway, 1907; Snow, 1975; McKitrick, 1985). In the exaspidean state, the scutes on the dorsal surface of the tarsus extend around the lateral and plantar surfaces to meet on the medial surface separated by a narrow groove without distinct scutes (Ridgway, 1907; McKitrick, 1985). All piprids, almost all tyrannids, and a few furnariids have exaspidean tarsi (Ridgway, 1907; McKitrick, 1985). The cotingids have pycnaspidean, holospidean, or taxaspidean, but never exaspidean tarsal scutellation (Ridgway, 1907). In these conditions, the lateral and plantar scutes are separated on the medial surface of the tarsus by a large number of independent scutes (pycnaspidean), a few rows of independent scutes (taxaspidean), or a single row of independent scutes (holospidean) (Ridgway, 1907). Other suboscines and oscines have other distinct forms of scutellation (Ridgway, 1911; Rand, 1959). (Scutellation types are illustrated in Van Tyne and Berger, 1971). Hellmayr (1927), Snow (1973, 1975), and Traylor (1977) criticized the tarsal scutellation characters as uninformative. McKitrick (1985) hypothesized that exaspidean scutellation may be derived in the Tyrannoidea, but was primitive within the Tyrannidae and the Pipridae and could not be used as evidence of monophyly of either family. Although the cotingid forms of scutellation may be derived within the tyrannoids from the exaspidean state, the variations among and within taxa in the detail of the different states make them difficult to distinguish confidently. Ridgway (1907) transferred many tyrannids to the Cotingidae based on obvious convergences in tarsal scutellation (see Historical Review above). Generally, these scutellation characters are quite variable within genera and species, resulting in a continuum of scutellation states that are not reliable indicators of phylogenetic relationship.

(2) *Syndactyly.* Sclater (1888) and Ridgway (1907) used the fusion of most of the phalanges of the outer two digits (III and IV) as a diagnostic feature of the Pipridae. However, they apparently disagreed on the recognition of this character state. Sclater (1888) placed *Laniisoma* in the Pipridae and *Laniocera* in the Cotingidae, and Ridgway (1907) did the opposite, though both genera have syndactyl outer toes. They also made several exceptions. In the cotingid genera *Rupicola* and *Phoenicircus* (Ridgway, 1907; Snow, 1973, 1982; pers. obs.), the outer two digits are fused in the typically "piprid" fashion, but neither genus was included in the Pipridae. Further, in the piprid

TABLE 2.—Distributions of the seven phylogenetically informative characters analyzed (6–12) in piprids, cotingids, other tyrannoids, and outgroups. Derived and primitive character states are coded as 1 and 0, respectively. For convenience, many morphologically similar genera are listed in the table as single taxa.

	Characters						
Taxon	6	7	8	9	10	11	12
Piprids[1]	0	0	0	1	0	0	1
Schiffornis Group[2]	1	0	0	1	0	0	0
Sapayoa	1	0	0	1	1	0	0
Neo]pipo	1	0	0	0	0	0	0
Neopelma and *Tyranneutes*	1	1	1	1	0	0	0
Piprites	1	0	0	1	0	0	0
Cotingids[3]	0	0	0	1	0	1	0
Phytotoma	0	0	0	1	0	1	0
Rupicola Group[4]	0	0	0	0	0	1	0
Pipreola and *Ampelioides*	0	0	0	0	0	0	0
Oxyruncus	1	0	0	0	0	0	0
Tityra	1	0	1	1	0	1	0
Lipaugus[5]	1	0	1	1	0	0	0
Tyrannids	1	0	0	0	1	0	0
Outgroups[6]	0	0	0	0	0	0	0

[1] *Corapipo, Masius, Ilicura, Manacus, Chiroxiphia, Antilophia, Machaeropterus, Chloropipo, Xenopipo,* and *Pipra.*

[2] *Schiffornis, Laniocera, Laniisoma, Pachyramphus, Xenopipo,* and *Iodopleura.*

[3] *Ampelion, Porphyrolaema, Cotinga, Carpodectes, Conioptilon, Gymnoderus, Querula, Pyroderus, Cephalopterus,* and *Perissocephalus.*

[4] *Rupicola, Phoenicircus, Carpornis, Lipaugus subalaris,* and *Lipaugus cryptolophus.*

[5] *Lipaugus vociferans* and *L. unirufus.*

[6] The furnarioids, Old World suboscines, and oscine passerines.

Piprites, the inner two digits (I and II) are partially fused rather than the outer two digits (Sclater, 1888; Ridgway,1907; pers. obs.). Almost all tyrannids have minimally fused digits, with the exception of the extensive fusion of the outer digits in *Terenotriccus* and *Rhynchocyclus* (Ridgway, 1907; pers. obs.). Most furnarioids have only the basal phalanx of digits III and IV fused, but in *Syndactyla, Philydor, Automolus, Sclerurus, Xenops,* and the dendrocolaptids, the first phalanges of digits II, III, and IV are all fused (Ridgway, 1907, 1911; Feduccia 1973; pers. obs.). All eurylaimids except *Pseudocalyptomena* have extensively fused digits III and IV, as in piprids (Raikow, 1987; pers. obs.). Clark (1981) found fusion of both inner and outer digits in a number of oscines and documented significant variation within certain families and genera. Raikow (1985) has remarked on the difficulty of distinguishing the syndactyl and anisodactyl (unfused) conditions given the tendency toward fusion of anterior digits in certain taxa. Because of the variation in forms of syndactyly in both the ingroup and outgroups, this character cannot be confidently employed to support the monophyly of any higher taxon within the

Tyrannoidea. Perhaps variation in digit fusion could be useful at lower levels within supported clades of tyrannoids, especially if additional evidence can be gathered supporting the homology of fused toes in subsets of syndactyl taxa. For example, the state found in *Piprites* is completely distinct from the syndactyly observed in other tyrannoids, and is an apparent synapomorphy of the genus.

(3) *Syringeal Position.* A number of terms ending in "-ophone" have been used to describe and classify the passerine syrinx based on its position relative to the tracheobronchial junction (reviewed by Ames, 1971:130–132; McKitrick, 1985). The tyrannoids, old world suboscines, and oscines have been described as "haploophone," meaning that the syrinx is tracheobronchial or incorporates both tracheal and bronchial elements. This condition is contrasted with the "tracheophone" or completely tracheal syrinx of furnarioids. The haploophone syrinx is primitive within all passerine birds and does not support monophyly of any tyrannoid group (McKitrick, 1985).

(4) *Traditional Descriptions of Syringeal Musculature.* Terms ending in "-myodian" were used to classify the syringes of passerines based on the position of attachment of the extrinsic and intrinsic syringeal muscles (reviewed in Ames, 1971:130–132; McKitrick, 1985). As Ames (1971) remarked, these terms were originally employed as accurate descriptions of specific morphologies, but problems arose when they were used to name higher taxa for which little anatomical information was available. The piprids and cotingids have been described in various works as "oligomyodian," having few or no intrinsic syringeal muscles (Sclater, 1888; Ridgway, 1907; Hellmayr, 1927); "mesomyodian," having syringeal muscles attached to the medial portions of the syringeal rings (Sclater, 1888; Ridgway, 1907; Hellmayr, 1927); and "catacromyodian," having syringeal muscles attached to the dorsal ends of the syringeal rings (Gadow, 1893, 1899; Ridgway, 1907). Some of these terms are clearly contradictory and none was used to distinguish the Pipridae or the Cotingidae exclusively from one another or from other tyrannoids. Observations by Ames (1971) and myself (Prum, 1989, in manuscript; Prum and Lanyon, 1989) indicate that syringeal musculature of the tyrannoids is too variable and complex to be accurately summarized by these simple terms. However, more specific variations in syringeal musculature are phylogenetically informative at many levels within tyrannoids (characters 10, 11).

(5) *Bill Shape.* Sclater (1888) used the "parine" bill shape to define his subfamily Piprinae, which included all his piprid genera but *Schiffornis, Laniisoma, Neopelma,* and *Heterocercus* (Table 1). Ridgway (1907)

cited the short, wide bill of piprids and the elongated compressed bill of cotingids as distinguishing the two groups. Warter (1965) did not identify any characters in the cranial morphology of the piprids that might support the general character of "wide" bill shape with finer anatomical detail. Short, wide bill shape is also found in the small cotingids *Iodopleura* and *Calyptura,* and the flatbilled tyrannids, such as *Rhynchocyclus.* Given the amount of variation in bill shape within piprids, the appearance of similar character states in some cotingids and tyrannids, and the great possibility of convergence in such a gross description of bill morphology, this character cannot be used as evidence of piprid monophyly. The family Phytotomidae was defined by its finch-like, serrate bill. This character state is a synapomorphy of the genus, but does not provide information about the relationship of *Phytotoma* to other tyrannoids. Likewise, the sharp, pointed bill of *Oxyruncus* is an autapomorphy of the genus and does not indicate to which tyrannoids *Oxyruncus* may be related.

INFORMATIVE CHARACTERS

(6) *Internal Syringeal Cartilages.* Miskimen (1963) was the first to apply the name internal syringeal cartilages to the cartilaginous elements in the internal tympaniform membrane attached to various supporting elements in the syringes of tyrant flycatchers. Ames (1971), Lanyon (1984a, 1984b, 1985, 1986, 1988a, 1988b, 1988c), and McKitrick (1985) have reported that internal syringeal cartilages are present in all tyrannids (including *Tityra* and *Pachyramphus*), *Oxyruncus* (Oxyruncidae), *Iodopleura* (Cotingidae), and six genera presently placed in the Pipridae: *Schiffornis, Sapayoa, Piprites, Neopipo, Tyranneutes,* and *Neopelma* (Fig. 1C). Prum and Lanyon (1989) observed that internal cartilages are also present in *Xenopsaris* (Tyrannidae), and in *Laniisoma, Lipaugus vociferans,* and *L. unirufus* (Cotingidae). Internal syringeal cartilages are absent in all other New World suboscines and almost all oscine birds (Fig. 1A). *Neodrepanis* (Philepittidae) and *Acanthisitta* (Acanthisittidae) also possess cartilaginous structures in the internal tympaniform membranes (Ames, 1971; McKitrick, 1985; pers. obs.), but two well corroborated morphological and biochemical hypotheses of phylogeny indicate that these genera are only distantly related to the tyrannoids (Sibley and Ahlquist, 1985b; Raikow, 1987); the hypothesis that these structures are homologous with the internal cartilages of tyrannoids would require a large number of losses of the trait in many passerine lineages. Following Lanyon (1984a, 1985,

1986, 1988a, 1988b, 1988c) and McKitrick (1985), the presence of internal cartilages is here hypothesized to be derived in tyrannoids.

(7) *Internal Cartilages Elongate and S-shaped.* In *Neopelma* and *Tyranneutes* (Pipridae), the internal syringeal cartilages are narrow, elongate, and curved in a subtle S-shape (Fig. 1C). This morphology is unique among tyrannoids and is here hypothesized to be derived. In *Cnemarchus* (Tyrannidae), the shape of the internal cartilages is vaguely similar but not as narrow or curved; *Cnemarchus* is a member of the *Muscisaxicola* group in the *Empidonax* assemblage (Lanyon, 1986).

(8) *Complete Medial Bronchial Cartilaginous Sheet.* In *Tityra* (Tyrannidae), *Lipaugus vociferans* and *L. unirufus* (Cotingidae), and *Neopelma* and *Tyranneutes* (Pipridae), the medial portions of some of the double, complete A elements are cartilaginous and fused to form a continuous sheet of cartilage on the medial side of the bronchi at the cranial margin of the internal tympaniform membrane (Fig. 1C). In all four genera, the internal syringeal cartilages are caudal extensions of the caudodorsal edge of this cartilaginous sheet. Elsewhere in tyrannoids, a complete sheet of cartilage connecting the dorsal and ventral ends of bronchial A elements is found only in *Chiroxiphia* and *Antilophia* (Prum, 1989, in manuscript), but in these two genera it is quite different in detail and probably of independent origin (Prum, 1989, in manuscript). This medial cartilaginous sheet and the associated spikelike internal syringeal cartilages are here hypothesized to be derived.

(9) *Femoral Artery Enlarged and Ischiadic Artery Reduced.* Garrod (1876) discovered that some cotingids and piprids have a distinct pattern of hindlimb circulation (see Historical Review above). In the small sample of cotingids and piprids he observed, the main artery supplying the hind limb was the femoral, whereas in *Rupicola,* other passerines, and most other birds, the main hindlimb artery was ischiadic (Garrod, 1876). Midtgård (1982) observed the hindlimb arteries of 43 species from 16 families of birds including *Chiroxiphia* and *Pipra* (Pipridae), and *Procnias* (Cotingidae). He confirmed Garrod's observations of the enlarged femoral and reduced ischiadic arteries in these taxa but added no new suboscine species to those previously surveyed by Garrod (1876). Elsewhere in birds, Midtgård recorded enlarged femoral and reduced ischiadic arteries in only penguins (*Spheniscus,* Spheniscidae) and the plaintain-eaters (*Musophaga,* Musophagidae). McKitrick (1985) hypothesized that the possession of the enlarged femoral artery is a derived character supporting a clade including the cotingids and piprids.

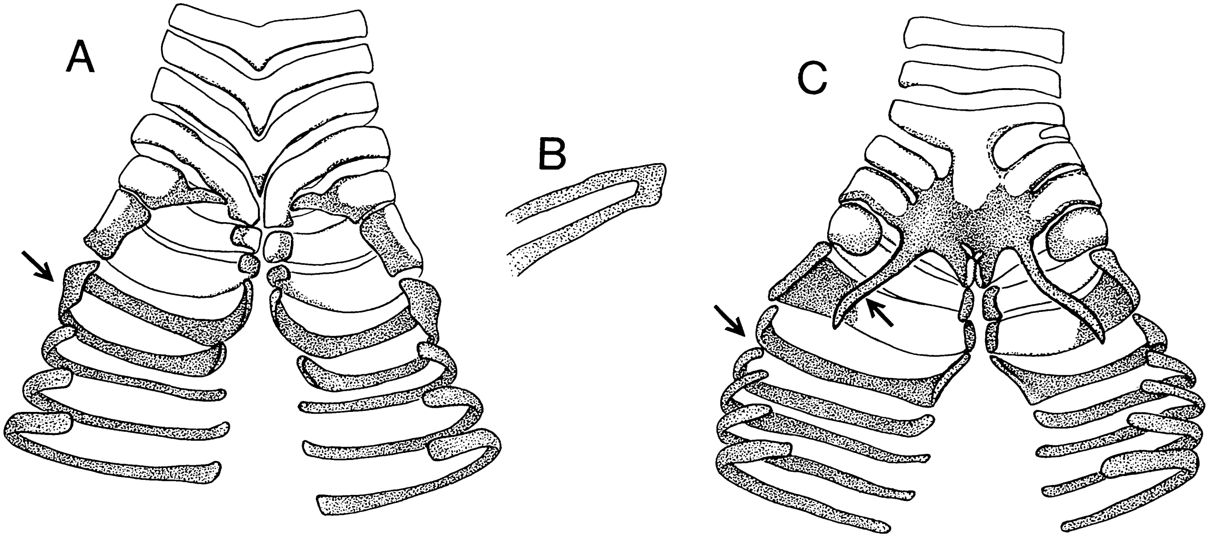

FIG. 1. Illustrations of cleared and double stained syringes. A, *Chloropipo uniformis* (AMNH 7680), dorsal view; arrow indicates fused dorsal ends of B1 and B2 elements. B, *Pipra suavissima* (AMNH 816768), left lateral view of dorsal ends of B1 and B2 elements fused by a short cartilaginous bar. C, *Tyranneutes stolzmanni* (LSUMZ 111082), dorsal view; arrows indicate (left) unfused dorsal ends of the B1 and B2 elements and (center) internal syringeal cartilage. Stippled structures are cartilaginous and unshaded structures are ossified. See characters 6–8 and 12 for descriptions.

I made observations of the major branches of the aorta that supply the gonads, kidneys, and muscles of the hindlimbs in a large sample of tyrannoids, including 30 species of 9 genera of piprids, 29 species of 19 genera of cotingids, 2 of 4 species of *Phytotoma* (Phytotomidae), *Oxyruncus* (Oxyruncidae), and 37 species in 29 genera from each of Lanyon's (1984a, 1985, 1986, 1988a, 1988c) major assemblages of tyrannids (Appendix 2). Latin artery synonyms cited below follow Baumel *et al.* (1979). In the primitive state found generally in most birds, the ischiadic artery (A. ischiadica) is the most well developed of the main branches of the lower aorta; after sending small branches to supply the kidneys, the ischiadic artery passes out of the abdominal cavity through the ilioischiadic foramen to supply the muscles of the hindlimb from the lateral surface (Fig. 2A). In this primitive state, the iliac artery (A. iliaca externa) is narrow and weakly developed, and its two small distal branches—the pubic (A. pubica) and femoral (A. femoralis) arteries—pass into the medial, dorsal muscles of the hindlimb (Fig. 2A; see also Baumel *et al.*, 1979:380, fig. 7; Midtgård, 1982:547, fig. 1). In the derived state, the iliac artery and its distal branch, the femoral artery, are greatly enlarged and supply the major muscles of the hindlimb from the medial side, whereas the ischiadic artery is reduced in length and diameter, supplying only the kidneys and gonads and usually not reaching the ilioischiadic foramen (Fig. 2B; see also Midtgård, 1982:547, fig. 1).

The derived state of the femoral and ischiadic arteries is found in almost all piprids and cotingids (including *Schiffornis, Neopelma, Tyranneutes,* and *Piprites* [Pipridae], and *Lipaugus vociferans* and *L. unirufus* [Cotingidae]); in the problematic genera *Tityra, Pachyramphus,* and *Xenopsaris* (Tyrannidae); in *Phytotoma* (Phytotomidae); and in a few species in the tyrannid genus *Ochthoeca.* The primitive state is found in all other tyrannids observed, and in *Rupicola, Phoenicircus, Carpornis, Pipreola, Ampelioides, Lipaugus cryptolophus,* and *L. subalaris* (Cotingidae); *Sapayoa* and *Neopipo* (Pipridae); and *Oxyruncus* (Oxyruncidae). The cotingid species *Querula purpurata* was variable for both states (n = 2 femoral enlarged; n = 2 femoral reduced; *Querula* coded as present for enlarged arteries). In a single specimen of *Ampelion rubrocristatus,* the femoral artery on one side is enlarged and the other is reduced. Following McKitrick (1985), the enlarged femoral and the reduced ischiadic arteries are hypothesized to be derived. This character is discussed further below.

(10) *M. obliquus ventralis Present.* Ames (1971) described a paired intrinsic syringeal muscle found in most tyrannids that he named M. obliquus ventralis after its oblique fiber direction and position on the

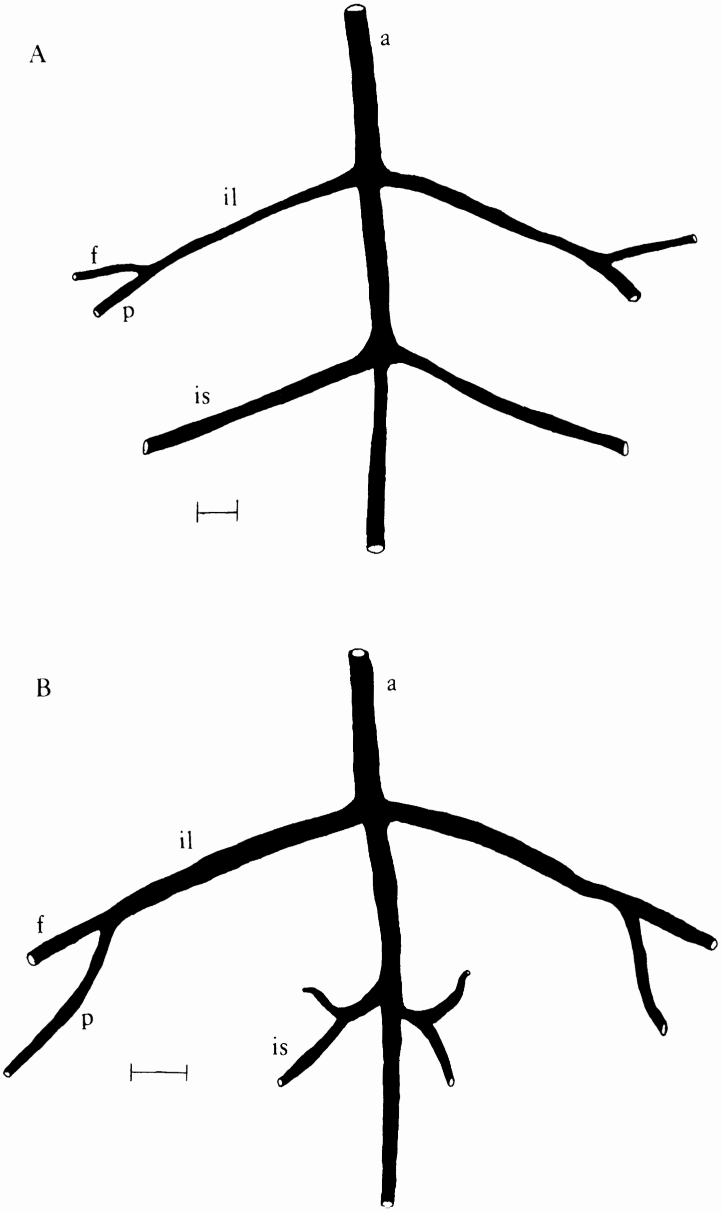

FIG. 2. Dorsal view of the lower branches of the aorta. A, *Tyrannus tyrannus* (UMMZ 226348); B, *Chiroxiphia pareola* (UMMZ 225061). For description see character 9. Scale bars equal one mm. Abbreviations: a, aorta; f, femoral artery; il, iliac artery; is, ischiadic artery; p, pubic artery.

ventrolateral surface of the syrinx. Ames reported that the M. obliquus ventralis is present in all Tyrannidae (*sensu* Traylor, 1979; including *Laniocera*) except *Tityra, Pachyramphus, Terenotriccus, Myiobius, Pyrrhomyias, Onychorhynchus,* and some *Tyranniscus* species. Ames (1971) also considered that the intrinsic musculature of *Oxyruncus* (Oxyruncidae), *Iodopleura* (Cotingidae), and *Ilicura* (Pipridae) might be homologous with M. obliquus ventralis. McKitrick (1985) hypothesized that the presence of M. obliquus ventralis is derived in tyrannoids. The lack of M. obliquus ventralis in the tyrannid genera *Terenotriccus, Myiobius,* and *Pyrrhomyias* has been hypothesized by Lanyon (1986, 1988b) to be a secondary loss, derived within the *Empidonax* assemblage.

My observations include many taxa not available to Ames (1971). Among the problematic piprids, M. obliquus ventralis is present only in *Sapayoa.* In *Sapayoa,* a pair of intrinsic syringeal muscles originates on the ventral midline at the A3–5 elements, and these fibers run caudolateral to insert on the ventral half of the A1–2 external tympaniform membrane. This morphology is similar to the M. obliquus ventralis of many tyrannids (Ames, 1971). M. obliquus ventralis is absent in all other cotingids, plantcutters, and piprids, including the other problematic genera *Neopipo, Neopelma, Tyranneutes,* and *Piprites,* which lack developed intrinsic musculature. Following McKitrick (1985), the presence of M. obliquus ventralis is here hypothesized to be derived.

These observations are largely congruent with those of Ames (1971). However, I differ from Ames (1971) in the characterization of the syringeal muscles of *Laniocera, Iodopleura, Oxyruncus,* and *Ilicura. Laniocera* and *Iodopleura* share derived syringeal characters with *Schiffornis, Laniisoma, Pachyramphus,* and *Xenopsaris* (Prum and Lanyon, 1989). The significant variation in the fiber direction and the derived form of insertion of the intrinsic musculature of these six genera indicate that the oblique intrinsic syringeal muscles of this assemblage evolved independently of those of tyrannids, and are not homologous with M. obliquus ventralis. Likewise, the intrinsic syringeal musculature of *Ilicura* is very different in detail from M. obliquus ventralis of tyrannids; other derived syringeal characters shared by *Ilicura, Corapipo,* and *Masius* strongly indicate that this oblique musculature is independently derived and not homologous with M. obliquus ventralis (Prum, 1989, in manuscript). Lastly, the intrinsic musculature of *Oxyruncus* is quite different from M. obliquus ventralis, and is much more similar to the syringeal musculature of *Pachyramphus*

(Prum and Lanyon, 1989); here, it is hypothesized to be independently evolved.

(11) *M. tracheolateralis Insertion on A1/B1 Membrane.* In *Phytotoma* (Phytotomidae), *Tityra semifasciata* and *T. inquisitor* (Tyrannidae), and *Phoenicircus, Carpornis, Ampelion, Lipaugus subalaris, L. cryptolophus, Porphyrolaema, Cotinga, Xipholena, Carpodectes, Conioptilon, Gymnoderus, Querula, Pyroderus, Cephalopterus, Perissocephalus,* and *Rupicola* (Cotingidae), M. tracheolateralis is a narrow strip of muscle that is restricted to the lateral surface of the trachea and inserts on the external syringeal membrane between the A1 and B1 elements (Fig. 3). In most other tyrannoids, including *Tityra cayana,* almost all piprids, and the cotingids *Pipreola, Ampelioides, Laniisoma, Iodopleura, Lipaugus vociferans,* and *L. unirufus,* the left and right Mm. tracheolaterales widen ventrally to cover the entire ventral surface of the trachea and insert directly on one or more A elements (typically just cranial to the origin of the intrinsic musculature if present). In *Piprites* (Pipridae), M. tracheolateralis is narrow as in the former group of cotingids but it inserts directly on the A1 element. In the cotingid *Procnias,* M. tracheolateralis is also thin and restricted to the lateral surfaces of the trachea, but inserts on the A elements of the syrinx cranial to the origins of a number of complex and unique syringeal muscles (Ames, 1971; pers. obs.). (In cases where I lacked uncleared syringeal specimens of a species, I based my observations on the musculature remaining on incompletely cleared specimens.) The insertion of the M. tracheolateralis on the A1/B1 membrane is not found in any other tyrannoids, furnarioids, or oscines, and it is here hypothesized to be derived.

In a few tyrannid genera, such as *Attila* and *Pyrocephalus* (Ames, 1971), and in the genera *Schiffornis* (Pipridae), *Laniisoma* and *Iodopleura* (Cotingidae), and *Laniocera, Pachyramphus,* and *Xenopsaris* (Tyrannidae), the intrinsic syringeal musculature inserts on the A1/B1 membrane. In the first two genera, this insertion is an independently derived variation of M. obliquus ventralis (Ames, 1971; Prum and Lanyon, 1989), and in the latter six genera, it is hypothesized to be an independent, derived character supporting their monophyly (Prum and Lanyon, 1989). The insertion of the intrinsic muscles on the A1/B1 membrane in these six genera could be homologous with that of cotingids if their intrinsic musculature was secondarily derived from the cotingid state of M. tracheolateralis (Prum and Lanyon, 1989). In this analysis, the six *Schiffornis*-group genera are scored as primitive for this character.

(12) *Dorsal Fusion of B1 and B2 Syringeal Elements.* In the piprid

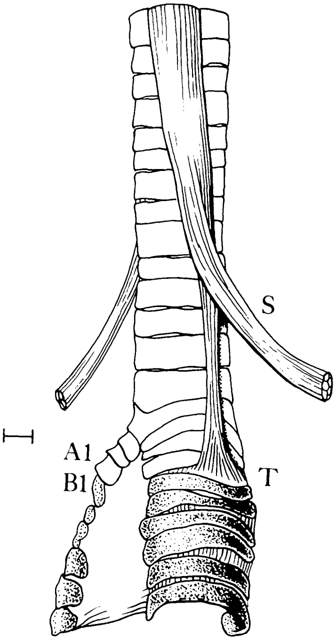

FIG. 3. Dorsolateral view of the syrinx of *Querula purpurata* (LSUMZ 64801). Abbreviations: A1, A1 syringeal element; B1, B1 syringeal element; S, M. sternotrachealis; T, M. tracheolateralis. M. tracheolateralis inserts on the A1/B1 external membrane. Scale bar equals one mm. Stippled structures are cartilaginous and unshaded structures are ossified. See character 11 for details.

genera *Chloropipo, Xenopipo, Antilophia, Heterocercus, Machaeropterus, Manacus, Corapipo, Ilicura, Masius, Chiroxiphia,* and *Pipra,* the B1 and B2 elements are paired, medially incomplete half rings that are fused at their dorsal ends by a short cartilaginous bar (Fig. 1A, B). In the *Pipra aureola* clade, this condition is further derived: the B1 and B2 elements are fused dorsally in an "arrow-head" shape without a distinct cartilaginous bar (Prum, 1989, in manuscript). In *Schiffornis, Piprites, Neopipo, Tyranneutes,* and *Neopelma* (Pipridae), and in all tyrannids, cotingids, other suboscines, and oscines, the B1 and B2 elements are free dorsally and not fused by a short bar (Fig. 1C). In *Sapayoa,* the A1, B1, and B2 elements are oriented at an oblique angle to the trachea, and connected at their dorsal ends by a large, robust cartilaginous bar. Although similar in relative position to the dorsal fusion in some piprids, the *Sapayoa* character state is completely different in form and detail, and it is here hypothesized to be independently evolved. In two individuals of *Cotinga maynana,* the B1 and B2 elements were dorsally fused by slight connections of the widened, paddle-shaped, dorsal ends of these elements and not by a coherent bar. These individuals appear to be anomalies since the rest of the congeners observed (n = 4) showed no such fusion. The dorsal fusion of the B1 and B2 elements found in the 11 piprid genera listed above is here hypothesized as derived.

RESULTS

Characters 1–5 are primitive or highly variable within the Tyrannoidea, and are not phylogenetically informative. These morphological characters have appeared in traditional diagnoses of the Pipridae and Cotingidae, but they provide no evidence for the monophyly of these families or any other major tyrannoid clades.

Phylogenetic analysis of the seven informative morphological characters yields 25 equally parsimonious phylogenetic hypotheses for the interrelationships of the tyrannoid taxa surveyed. Each of these trees requires 10 evolutionary changes (origins or losses) to account for the variation observed in the seven characters (consistency index = 0.70). A strict consensus tree of all the most parsimonious, equal length trees supports a few monophyletic groups but shows little resolution of the higher-level interrelationships of these clades (Fig. 4). The data set is too small and too homoplasious to resolve the higher-level phylogeny of the tyrannoids. Three characters are completely consistent and support the monophyly of three independent groups (characters 7, 10, 12), but the other four characters conflict with one another and produce the numerous equally parsimonious hypotheses of phylogeny for the group. Seven of the eight possible unique combinations of primitive and derived states of the three most conflicting characters (6, 9, 11) are present in the data set. Despite this extensive homoplasy, several coherent results are apparent.

None of the evidence supports the monophyly of the Pipridae or the Cotingidae as traditionally defined (Hellmayr, 1927; Snow, 1973, 1975, 1979) (Table 2). However, two clades that include large portions of the genera traditionally placed within each family are supported. A unique synapomorphy of 11 of the 17 genera of currently recognized piprids was identified. The dorsal fusion of the B1 and B2 elements (12) unambiguously supports a monophyletic group including *Chloropipo, Xenopipo, Antilophia, Heterocercus, Machaeropterus, Manacus, Corapipo, Ilicura, Masius, Chiroxiphia,* and *Pipra.* Five of the

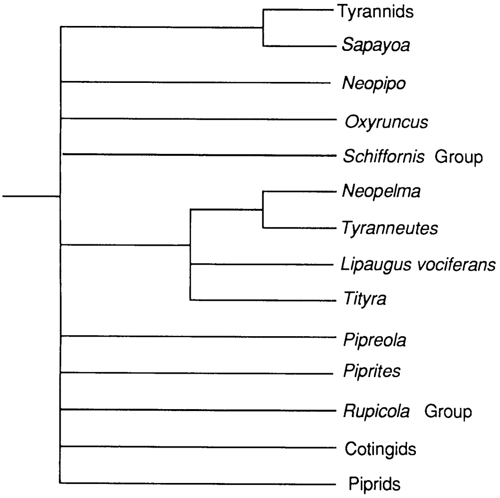

FIG. 4. Consensus hypothesis of phylogeny for the tyrannoids based on 25 maximally parsimonious trees using seven morphological characters (6–12). Each input tree has a length of 10 (consistency index = 0.70). The *Schiffornis* group includes *Laniocera, Laniisoma, Pachyramphus, Xenopsaris,* and *Iodopleura.* The *Rupicola* group includes *Phoenicircus, Carpornis, Lipaugus subalaris,* and *L. cryptolophus. Pipreola* includes *Ampelioides tschudii. Lipaugus vociferans* includes *L. unirufus.* The cotingids include *Phytotoma.*

six problematic genera of piprids completely lack this fusion; *Sapayoa* has a grossly similar but distinctive character state that is unrelated to the derived state in other piprids.

Each of the six genera of problematic piprids shares other derived morphological traits with non-piprid tyrannoids. *Schiffornis, Sapayoa, Neopipo, Piprites, Neopelma,* and *Tyranneutes* all have internal syringeal cartilages, which are derived in tyrannids and absent in other piprids and most cotingids. However, these six genera do not form a clade. *Schiffornis, Piprites, Neopelma,* and *Tyranneutes* possess the derived form of the femoral artery found in most cotingids and piprids, but *Sapayoa* and *Neopipo* lack the derived femoral artery state. *Sapayoa* shares with most tyrannids the derived M. obliquus ventralis (10). *Neopelma* and *Tyranneutes* share a unique form of internal syringeal cartilages indicating that they are sister taxa (7), and these two genera also share with *Lipaugus vociferans, L. unirufus,* and *Tityra* a derived cartilaginous sheet on the medial surfaces of the bronchi (8). However, this evidence conflicts with the presence in two species of *Tityra* of a derived form of syringeal musculature found in a large portion of the cotingids (11).

The derived insertion of the M. tracheolateralis on the A1/B1 membrane (11) supports the monophyly of a large assemblage of cotingids including *Phoenicircus, Carpornis, Ampelion, Lipaugus subalaris, L. cryptolophus, Porphyrolaema, Cotinga, Xipholena, Carpodectes, Conioptilon, Gymnoderus, Querula, Pyroderus, Cephalopterus, Perissocephalus,* and *Rupicola* (Cotingidae), *Tityra semifasciata* and *Tityra inquisitor* (Tyrannidae), and *Phytotoma* (Phytotomidae). This derived state is absent in the traditional cotingids *Laniisoma, Ampelioides, Pipreola, Lipaugus vociferans, L. unirufus, Tityra cayana, Iodopleura,* and *Procnias.* (The syringes of the cotingid genera *Phibalura, Tijuca, Calyptura, Chirocylla,* and *Haematoderus* are unavailable; Wood *et al.,* 1982). The monophyly of the former assemblage of cotingids is contradicted by the absence in *Phoenicircus, Rupicola, Carpornis, Lipaugus subalaris,* and *L. cryptolophus* of the derived form of the femoral artery (9). *Laniisoma, Lipaugus vociferans, L. unirufus,* and *Iodopleura* have the derived form of the femoral artery but lack the derived syringeal musculature. *Pipreola* and *Ampelioides* lack the derived states of all the characters analyzed.

DISCUSSION

This investigation is limited by a number of factors at various levels in the analysis. The sample sizes of available anatomical specimens are small for many manakins and cotingas. Intraspecific variation in morphology may be greater than observed, confounding the phylogenetic analysis. Also, at these higher taxonomic levels, identifying morphological homologies may become more difficult, limiting our ability to recognize synapomorphies or homoplasies. Some homology problems in this analysis are discussed in detail below. Lastly, in a group as large and diverse as the tyrannoids, it is also unreasonable to expect to resolve their phylogeny using only seven characters. All of these problems may be resolved with additional data. However, it is also possible that the radiation of tyrannoids occurred so rapidly that there remains little evidence in present character systems to reconstruct the details of their oldest phylogenetic history.

The main goal of this investigation is to test the monophyly of the Pipridae and the Cotingidae. Although these results are far from providing a complete solution to higher-level tyrannoid phylogeny, they do contribute an initial answer to the monophyly question. The traditional characters used to diagnose the Pipridae and Cotingidae are not synapomorphies, and they do not distinguish monophyletic groups. The morphological characters analyzed do support a revised, limited monophyletic Pipridae and indicate that a large group of cotingid genera is also monophyletic. However, homoplasy in the available morphological characters results in limited resolution in the consensus tree for the group (Fig. 4). Strict consensus trees provide a summary of the monophyletic groups supported unambiguously by all the input trees, but they are unsatisfactory given that our goal is to uncover the single phylogenetic history of the group. Here, I will discuss some of the alternative resolutions of the phylogeny and the interpretation of the data that they require in order to extend the analysis beyond the limitations of consensus trees.

ALTERNATIVE RESOLUTIONS OF TYRANNOID PHYLOGENY

The basic character conflict in the morphological data set is the presence of both the derived internal syringeal cartilages and the enlarged femoral artery in a diverse group of taxa that are presently dispersed among all three major tyrannoid families: *Schiffornis, Piprites, Neopelma,* and *Tyranneutes* (Pipridae); *Laniisoma, Iodopleura, Lipaugus vociferans,* and *L. unirufus* (Cotingidae); and *Laniocera, Tityra, Pachyramphus,* and *Xenopsaris* (Tyrannidae). McKitrick (1985) previously identified this character conflict in *Schiffornis, Tityra,* and *Pachyramphus.* This analysis has expanded the number of taxa known to share these conflicting characters, but it has not resolved the conflict. Recent analysis of additional morphological characters by Prum and Lanyon (1989) supports the placement of six of these problematic genera—*Schiffornis, Laniisoma, Laniocera, Pachyramphus, Xenopsaris,* and *Iodopleura*—in a monophyletic group that is referred to as the *Schiffornis* group.

Any resolution of the tyrannoid phylogeny must hypothesize multiple origins or losses of either or both of these conflicting characters. In some of the alternative resolutions of tyrannoid phylogeny (Fig. 5A), the femoral artery character is hypothesized to have originated once and the internal cartilage character is hypothesized to have originated twice, placing these problematic taxa in a clade with cotingids and a restricted group of piprids. In the other major group of alternative resolutions (Fig. 5B), internal syringeal cartilages are hypothesized to have evolved once and the derived femoral arteries are hypothesized to have developed twice or been lost once, placing the problematic taxa in a clade with the tyrannids.

The other character conflicts in the data set involve derived states within cotingids, and among cotingids and some of the problematic

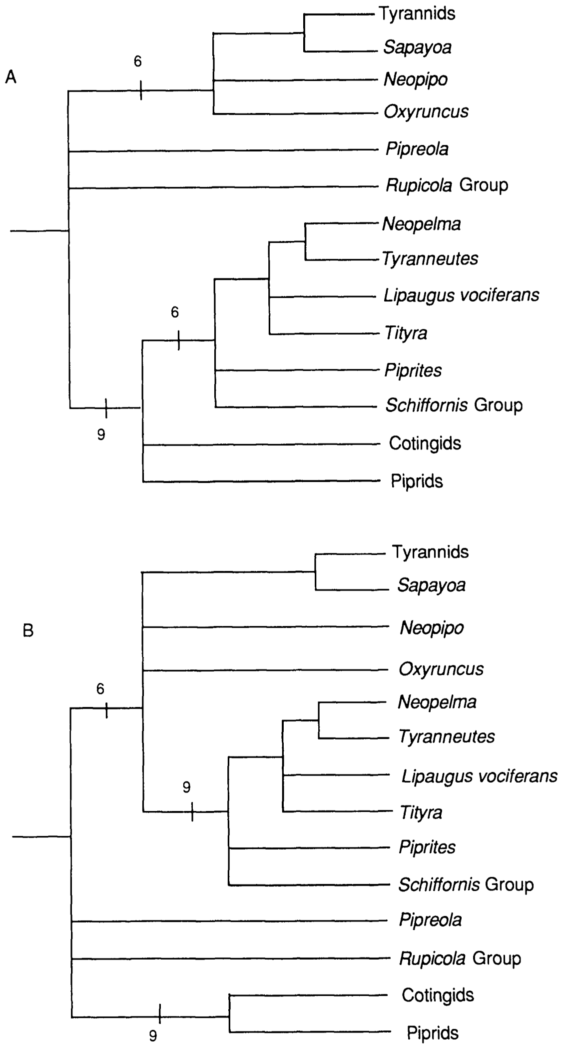

FIG. 5. Two equally parsimonious, partially resolved phylogenies of the superfamily Tyrannoidea based on three derived morphological characters. A, A partial resolution in which (9) presence of enlarged femoral arteries is hypothesized to have evolved a single time, and (6) internal syringeal cartilages are hypothesized to have arisen twice independently. B, A partial resolution in which (6) is hypothesized to have evolved once and (9) is hypothesized to have evolved twice independently. The *Schiffornis* group includes *Laniocera, Laniisoma, Pachyramphus, Xenopsaris,* and *Iodopleura.* The *Rupicola* group includes *Phoenicircus, Carpornis, Lipaugus subalaris,* and *L. cryptolophus. Pipreola* includes *Ampelioides tschudii. Lipaugus vociferans* includes *L. unirufus.* The cotingids include *Phytotoma.*

taxa listed above. The insertion of M. tracheolateralis on the A1/B1 membrane supports the monophyly of a large assemblage of cotingids, but six of these genera lack the enlarged femoral artery derived in the other cotingids, piprids, and the problematic taxa. Furthermore, two of the three *Tityra* species share this derived syringeal musculature feature with those cotingids, but *Tityra* also shares other derived states with *Lipaugus vociferans, L. unirufus, Neopelma,* and *Tyranneutes.* These conflicts require hypothesizing either reversal or independent origins of these characters in any resolution of the phylogeny of the group.

In the absence of additional data on tyrannoid morphology, resolution of the character conflicts in this data set may be furthered by comparing the strength of the hypotheses of homology of the conflicting derived character states of various critical taxa. Most important among these are the homology of the enlarged femoral arteries and the internal syringeal cartilages.

HOMOLOGY OF THE ENLARGED FEMORAL ARTERIES

The general homology of the femoral arteries in the various taxa is not in doubt. The femoral artery is present in all birds and differs little among avian taxa in its relative position. The question is whether the enlargement or reduction of this artery is homologous or analogous in various taxa. Vascular characters are sometimes criticized as being too developmentally malleable to be useful in systematics. Breeding experiments and ontogenetic investigations have demonstrated that aortic arch variants in rabbits are determined by a complex system of quantitative inheritance and differential rates of growth of thoracic and axial skeletal elements (Alberch, 1980). Pattern development in avian circulatory systems may also be subject to similar epigenetic influences that limit the strength of arterial characters as phylogenetic evidence (Glenny, 1955). The variation observed in the femoral and ischiadic arteries of *Querula purpurata* and *Ampelion rubrocristatus* indicates that epigenetic perturbations influence the development of avian hindlimb arterial supply. However, the systematic distribution of the highly unusual, enlarged femoral artery state leaves no doubt that this feature is derived in tyrannoids. Elsewhere in birds, it occurs only in penguins (*Spheniscus,* Spheniscidae) and plantain-eaters (*Musophaga,* Musophagidae) (Midtgård, 1982). The rarity of this trait within birds argues in favor of a single unique origin of the trait within tyrannoids. The evidence of variation within species in the presence of the derived trait may indicate developmental plasticity in the derived condition that could foster rapid or frequent character loss within lineages.

The dissections of the lower aortic branches made in this investigation were the least invasive and least detailed possible. This level of observation was sufficient to characterize the pattern of hindlimb arterial supply for most tyrannoids. Additional dissections of the distal branches of the femoral and ischiadic arteries within the muscles of the hindlimb in problematic tyrannoids may reveal finer morphological details that will further resolve the homology of the enlarged and reduced femoral arteries.

HOMOLOGY OF INTERNAL SYRINGEAL CARTILAGES

The homology of the various structures defined as internal syringeal cartilages is less certain than the homology of the femoral artery. Ames (1971:33) defined internal syringeal cartilages as paired cartilaginous plates lying within the internal tympaniform membrane, and he characterized them as variable in shape, number and attachment to other syringeal elements. Ames (1971) described a number of varieties of internal cartilages in tyrannoids. Lanyon (1984a, 1985, 1986, 1988a, 1988b, 1988c) employed the technique of Dingerkus and Uhler (1977) for clearing and double staining cartilage and bone, and he documented even more variation in the internal syringeal cartilage shape, composition (cartilaginous or partially ossified), and attachment. In the vast majority of tyrannids, the internal cartilages are simple cartilaginous bars, but other extreme morphologies include the minute free-floating internal cartilages in *Todirostrum* and related flat-billed tyrannids, the elongate, racket-shaped internal cartilages in *Mionectes* and *Leptopogon,* the L-shaped internal cartilages of *Tyrannus* and other kingbirds, and the second pair of internal cartilages in *Myiarchus* (Lanyon, 1984a, 1988a, 1988c). Many of these morphologies are derived within tyrannids, and have been hypothesized to be synapomorphies of tyrannid clades (Lanyon, 1984a, 1984b, 1985, 1986, 1988a, 1988b, 1988c). However, there is no single, uniform detail of composition, relative position, or shape that characterizes all internal syringeal cartilages. Any non-ring-like structure in the internal tympaniform membrane qualifies.

According to Patterson's (1982) conjunction test of hypotheses of homology, homologous structures cannot exist in the same animal (*e.g.,* the homology of mammalian ear bones and the primitive quadruped jaw suspension bones would be falsified if an organism were found that possessed both groups of structures). This criterion falsifies the homology between the single pair of internal cartilages present in most tyrannids, and the second pair of internal cartilages found in the *Myiarchus* group (Lanyon, 1985). Outside of the Tyrannoidea, internal syringeal cartilages have also originated twice, once each in *Neodrepanis* and *Acanthisitta* (see character 6). So, internal syringeal cartilages have originated multiple times in the passerines, and additional independent times within tyrannids. These multiple origins in combination with the lack of any special morphological details place the homology of all internal syringeal cartilages within tyrannoids into question.

The morphology of the internal syringeal cartilages in the problematic tyrannoids (those that possess both the derived internal cartilages and enlarged femoral arteries) are quite variable, and distinct from any found in tyrannids. In *Tityra, Lipaugus vociferans, L. unirufus, Neopelma,* and *Tyranneutes,* the internal cartilages are caudal projections from the caudodorsal edge of a sheet of cartilage formed by the fusion of the medial portions of the double, bronchial A elements (8). The shape and position of the internal cartilages in these genera are unlike any found in tyrannids. The association of the internal syringeal cartilages of these taxa with a unique, derived cartilaginous syringeal structure, the stereotyped and uniform position of the internal cartilages relative to other syringeal structures, and the increased development of internal cartilages within these genera support the hypothesis that the internal syringeal cartilages of these four genera are homologous with each other and independently derived within the group.

The internal cartilages of *Piprites, Oxyruncus,* and the *Schiffornis* group are distinct and may have had a unique common origin independent from those of tyrannids and the *Tityra-Lipaugus-Neopelma-Tyranneutes* group. In *Piprites* and *Oxyruncus,* the internal syringeal cartilages are conspicuously U-shaped or horseshoe-shaped. In the *Schiffornis* group, the internal cartilages are variable and complex in shape, but in many species the internal cartilages are similar to the U-shaped internal cartilages in *Piprites* and *Oxyruncus.* In *Xenopsaris* and many *Pachyramphus,* the internal cartilages are a forked pair of short cartilaginous bars. In *Schiffornis, Laniisoma,* and *Laniocera,* the internal cartilages are complex in shape but broad and bifurcating in profile.

Given these problems, the best approach may be to code distinct, derived forms of internal cartilages as independent characters and postpone judgment on the homology of all internal cartilages until additional data either corroborate or refute that hypothesis. Neither absence nor presence of internal cartilages would be considered derived, but specific morphologies of internal cartilages that are distributed exclusively within the ingroup would be hypothesized to be derived. For example, Lanyon (1984a, 1985, 1986, 1988a, 1988b, 1988c) has hypothesized many specific features of internal syringeal cartilages to be derived in various clades of tyrannids.

HEURISTIC RESOLUTION OF THE TYRANNOID PHYLOGENY

The morphological evidence supports the homology of the enlarged femoral artery more strongly than the homology of all internal syringeal cartilages. Here, I present the following resolution of tyrannoid phylogeny based on this assessment as a heuristic prediction (Fig. 6). It is not among the most parsimonious resolutions, but it is presented as a hypothesis to test in future research of both morphological and molecular character systems.

This hypothesis of phylogeny assumes single origins and multiple losses of the enlarged femoral artery (9) and the insertion of M. tracheolateralis on the A1/B1 membrane (11), and multiple origins of internal syringeal cartilages (6). Specifically, the internal syringeal cartilages of *Lipaugus vociferans, L. unirufus, Tityra, Neopelma,* and *Tyranneutes* are hypothesized to be derived independently from the internal cartilages in *Piprites, Oxyruncus,* and the *Schiffornis* group. The enlarged femoral artery is hypothesized to have been lost only twice: in *Oxyruncus,* and in a group including *Rupicola, Phoenicircus, Carpornis, Lipaugus subalaris,* and *L. cryptolophus.* The latter five taxa also share the derived insertion of the M. tracheolateralis with the other cotingids. Additional conflicts between the derived syringeal musculature shared by most cotingids and some *Tityra* species (11) and the derived medial bronchial cartilaginous sheet shared by *Tityra, Lipaugus vociferans, L. unirufus, Neopelma,* and *Tyranneutes* (7) are resolved by hypothesizing secondary loss of the musculature character in *Tityra* and in an hypothesized common ancestor of *Lipaugus, Neopelma,* and *Tyranneutes.*

COMPARISON TO BIOCHEMICAL HYPOTHESES OF TYRANNOID PHYLOGENY

Two hypotheses for phylogeny of the tyrannoids based on biochemical evidence have been presented recently. Using DNA-DNA hybridization, Sibley and Ahlquist (1985a) proposed that the piprids are the sister group to the cotingas, and that *Schiffornis, Pachyramphus,*

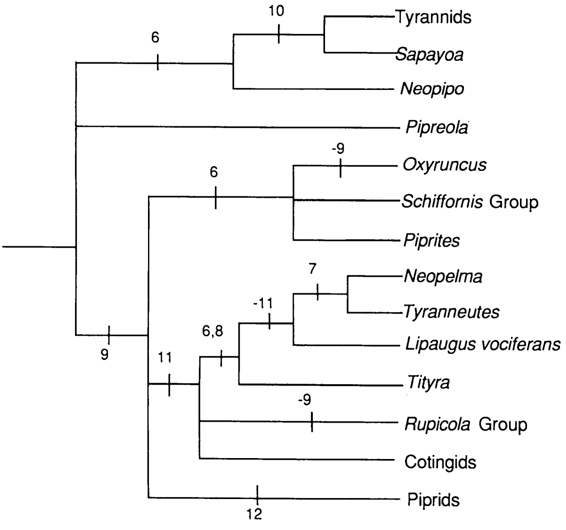

FIG. 6. A heuristic phylogeny of the Tyrannoidea. This partial resolution requires 12 changes of the 7 morphological characters. The phylogenetic hypothesis assumes that (6) internal syringeal cartilages of the tyrannids, of the *Schiffornis* group and *Piprites,* and of *Tityra, Lipaugus vociferans, Neopelma,* and *Tyranneutes* are not homologous, but arose independently in these three groups. The enlarged femoral artery (9) is hypothesized to have evolved once and subsequently been lost in *Oxyruncus,* and in *Rupicola* and related genera. The insertion of M. tracheolateralis on the A1/B1 membrane (11) is hypothesized to have evolved once and then been lost in some *Tityra* species, and in a group including *Lipaugus vociferans, L. unirufus, Neopelma,* and *Tyranneutes.* The *Schiffornis* group includes *Laniocera, Laniisoma, Pachyramphus, Xenopsaris,* and *Iodopleura.* The *Rupicola* group includes *Phoenicircus, Carpornis, Lipaugus subalaris,* and *L. cryptolophus. Pipreola* includes *Ampelioides tschudii. Lipaugus vociferans* includes *L. unirufus.* The cotingids include *Phytotoma.* See text for details.

and *Tityra* are the sister group to most tyrannids; the tyrannid genera *Mionectes, Corythopis,* and *Todirostrum* are the sister group to all other tyrannoids. No other genera of piprid-like tyrannoids were analyzed. Portions of this DNA-DNA hybridization phylogeny are congruent with the morphological hypothesis proposed here. Both the morphological data and the DNA-DNA hypothesis partially support a sister group relationship between the cotingids and piprids (*sensu stricto*) (Fig. 5B). Furthermore, the placement of *Schiffornis* as the sister group to the tityrines indicated by DNA-DNA hybridization is partially congruent with the morphological characters. Because of missing taxa, this DNA-DNA hybridization tree does not comprise a critical test of piprid monophyly but it does address some of the taxa involved in the cotingid monophyly question.

Houde (1987) and Cracraft (1987) have reviewed some of the difficulties of phylogenetic analysis using DNA-DNA hybridization. In particular, DNA-DNA hybridization analyses may be confounded by incomplete matrices, lack of reciprocity and metricity of distances, inconsistencies in average rate of DNA evolution, and inappropriate tree-building algorithms. Cracraft (1987) identified nonmetricities and insignificant branch lengths in Sibley and Ahlquist's (1985a) phylogeny of the New World suboscines. A reanalysis of tyrannoid interrelationships using complete data matrices would greatly increase the confidence in this hypothesis.

If Sibley and Ahlquist (1985a) are correct that *Mionectes, Corythopis, Todirostrum,* and associated tyrannids form a clade that is the sister group to the remaining tyrannoids, then the polarity of a number of morphological characters would be affected. Specifically, the absence of internal syringeal cartilages (6) and the absence of M. obliquus ventralis (11) would become derived. These polarity changes would eliminate the character conflict between the presence of the femoral artery and internal syringeal cartilages, support the monophyly of a clade including most manakins and cotingids, and eliminate all morphological evidence for monophyly of the remainder of the tyrannids. Lanyon (1988a, 1988c) placed the mionectid tyrannids in the *Elaenia* assemblage and the flatbill tyrannid assemblages, and did not encounter any morphological evidence to support the monophyly of the Mionectidae of Sibley and Ahlquist (1985a).

S. M. Lanyon (1985) presented an analysis of allozyme variation in piprids, cotingids, and the tyrannid *Myiarchus crinitus*. He concluded from a variety of distance, cladistic, and jack-knifing procedures that the piprids including *Neopelma, Tyranneutes,* and *Schiffornis* are monophyletic and that they are most closely related to the tyrannids (represented by *Myiarchus crinitus*) and the tityrines (including *Piprites* and *Oxyruncus*). The cotingids were placed as an unresolved polychotomy or as a paraphyletic group of lineages with varying relationship to the clade of piprids, tityrines, and *Myiarchus. Sapayoa* was used as the root for all the distance and cladistic trees.

Portions of the allozyme hypothesis of phylogeny are partially congruent with the hypothesis supported here by morphological characters. *Sapayoa* and *Piprites* were not placed near the other piprids. However, the presence of internal cartilages (7) and M. obliquus ventralis in *Sapayoa* support its placement in the tyrannids, not outside the Tyrannoidea as hypothesized by S. M. Lanyon (1985) and Warter

(1965). In the strict consensus tree based on the two distance trees and in the jack-knifed distance tree, *Neopelma* and *Tyranneutes* were sister groups, as supported by syringeal synapomorphies, and could be the sister group to the genera that comprise the morphological piprid clade. This hypothesis would require independent evolution of the medial bronchial cartilages (8) and the internal cartilages (7) in this clade and other tyrannoids. Although they are apparently not members of the piprid clade, the allozyme evidence suggests that they may be more closely related to the true piprids than the morphological characters indicate.

Some of the results of the allozyme analysis are dependent upon the choice of the outgroup used to root the trees in the analysis. S. M. Lanyon (1985) rooted his Fitch-Margoliash and Wagner distance trees using *Sapayoa,* stating that the distances themselves indicated that *Sapayoa* has no close relatives in the rest of the ingroup. Based on the distance analysis, *Sapayoa* was used as the root or "functional outgroup" in the cladistic analysis. Lanyon relied on this ingroup analysis after concluding that "insufficient knowledge of tyrannoid affinities prevented the designation of an *a priori* outgroup" (S. M. Lanyon, 1985:407).

The lack of any species genetically similar to *Sapayoa* among the taxa analyzed implies that *Sapayoa*'s closest relatives within the ingroup were not included in the analysis. Genetic distances between *Sapayoa* and other taxa analyzed are not more extreme than those among some other taxa in the data set. For example, the calculated Rogers's distances from *Cotinga* and *Schiffornis* to *Pachyramphus* were 0.830 and 0.833, while the distances from these two taxa to *Sapayoa* were 0.818 and 0.823, respectively (S. M. Lanyon, 1985). *Sapayoa* has a unique, potentially autapomorphous, allozyme for the majority of loci examined. For these loci, the most common ingroup allozyme was selected as primitive. The problems with this approach have been discussed (Stevens, 1980; Buth, 1984).

An alternative procedure to ingroup analysis is to root the distance and the cladistic trees using an *a priori* assumption of ingroup and outgroup monophyly supported by an independent data set. For example, these allozyme data could be analyzed assuming the monophyly of the cotingids, piprids, and tityrines based on their possession of a derived femoral artery trait (Fig. 2B; character 6). This approach combined with a large sample of tyrannids to broaden the outgroup sample could yield further insights into tyrannoid interrelationships. However, there may be a limit to the ability of allozyme variation to resolve higher-level tyrannoid interrelationships. Homoplasy can be a significant problem in protein electrophoretic characters at higher levels (Buth, 1984; Mindell and Sites, 1987), and lack of congruence with morphological and DNA-DNA hybridization phylogenies may indicate these problems in available tyrannoid allozyme data.

SYSTEMATIC CONCLUSIONS

The present analysis is an initial effort to test the monophyly of the cotingid and piprid families based on morphology. Although the available data do not yet resolve the higher-level phylogeny of the tyrannoids, they indicate that some changes from the traditional taxonomy are justified. Additional research on both molecular and morphological character systems will be required to corroborate these conclusions and to further resolve character conflicts.

(1) *Piprid Monophyly.* None of the morphological evidence analyzed supports the monophyly of the Pipridae as traditionally defined. Eleven genera of piprids share a unique syringeal synapomorphy. The other six problematic genera previously placed in the family all share derived morphological character states with other non-piprid tyrannoids. *Sapayoa* shares two derived syringeal characters with tyrannids, and *Neopipo* also appears to be most closely related to tyrannids. Additional research on the phylogenetic relationships of these two genera should focus on identifying any derived characters that are shared with tyrannid lineages.

The other four problematic genera—*Schiffornis, Piprites, Neopelma, Tyranneutes*—share derived character states with both the tyrannids and with the cotingids and piprids, but presently available information favors the cotingid-piprid hypothesis. *Schiffornis* is a member of a clade including five other tyrannoid genera that are presently placed in the cotingids and tyrannids (Prum and Lanyon, 1989). *Neopelma* and *Tyranneutes* are sister groups, and may be related to *Lipaugus vociferans, L. unirufus,* and *Tityra.* The relationship of *Piprites* to other tyrannoids is still unresolved.

Based on the present morphological evidence, I recommend the recognition of a restricted Pipridae diagnosed by the possession of the dorsal fusion of the B1-B2 elements and including the genera *Chloropipo, Xenopipo, Antilophia, Heterocercus, Machaeropterus, Manacus, Corapipo, Ilicura, Masius, Chiroxiphia,* and *Pipra.* The monophyly of this restricted group of piprids is partially corroborated by DNA-DNA hybridization. The sister group to the piprids is probably a large assemblage of cotingids, which may include the problematic taxa that have both derived internal syringeal cartilages and enlarged femoral arteries. However, the allozyme characters indicate a closer relationship between *Neopelma, Tyranneutes,* and the true piprids than the morphological evidence indicates.

(2) *Cotingid Monophyly.* None of the morphological characters analyzed supports the monophyly of the cotingids as traditionally defined (Sclater, 1888; Ridgway, 1907; Hellmayr, 1927) or as recently rearranged (Snow, 1979; Traylor, 1979). However, a single derived trait—(11) the insertion of M. tracheolateralis on the A1/B1 membrane—supports the monophyly of a group including all cotingids of Snow (1979) (except *Pipreola, Ampelioides, Laniisoma, Iodopleura, Lipaugus vociferans,* and *L. unirufus*), *Phytotoma* (Phytotomidae), and *Tityra semifasciata* and *T. inquisitor* (Tyrannidae). This derived character is not congruent with all the other data. *Lipaugus vociferans, L. unirufus, Neopelma, Tyranneutes,* and *Tityra* share other derived syringeal characters, and only two species of *Tityra* have the derived 'cotingid' muscle insertion. However, *Laniisoma, Pachyramphus,* and *Iodopleura* lack the derived syringeal muscle character, and are members of the *Schiffornis* group (Prum and Lanyon, 1989). The six cotingid genera that lack the derived form of femoral artery—*Pipreola, Ampelioides, Carpornis, Phoenicircus, Rupicola, Lipaugus subalaris,* and *L. cryptolophus*—may form a clade diagnosed by the loss of the trait.

No morphological evidence was found to support the Tityrinae (Traylor, 1979). Among the problematic genera, *Pachyramphus* and *Tityra* do not share any derived morphological characters, but each shares derived characters with other taxa in this group (see also Prum and Lanyon, 1989). This result conflicts directly with the DNA-DNA hybridization and the allozyme conclusions (Sibley and Ahlquist, 1985a; S. M. Lanyon, 1985), and indicates an area requiring further research.

The derived extrinsic muscle insertion (11) is the first hypothesized morphological synapomorphy of the cotingids. Although the monophyly of the original Cotingidae is falsified, character conflict in the presently available morphological data does not permit unambiguous recognition of a new monophyletic familial taxon. But the monophyly of the cotingids which share this derived syringeal muscle character (11) is proposed for further testing using additional data.

(3) *The status of the Phytotomidae.* Lanyon and Lanyon (1989) document that *Phytotoma* shares both derived biochemical and morphological characters with *Ampelion* (Cotingidae). In the absence of evi-

dence supporting the monophyly of the cotingids, they favored placing *Ampelion* and *Phytotoma* in the Phytotomidae. However, *Phytotoma* also shares with most cotingids the derived femoral artery (9) and syringeal muscle insertion (11). Although these characters are homoplasious in some groups, they do support the monophyly of a large cotingid clade including *Phytotoma* and *Ampelion.* Based on these findings, *Phytotoma* should be placed in the Cotingidae, and the family Phytotomidae should be abandoned.

(4) *The status of the Oxyruncidae.* The morphological evidence on *Oxyruncus* is problematic. Its unique, derived bill shape is phylogenetically uninformative. It shares similarities in syringeal supporting elements with *Piprites,* and similarities in syringeal musculature with *Pachyramphus* and *Xenopsaris,* but it lacks the derived femoral and ischiadic arteries and the syringeal synapomorphies of the *Schiffornis* group (Prum and Lanyon, 1989). DNA-DNA hybridization favors placing *Oxyruncus* within the cotingids (Sibley and Ahlquist, 1985a; Sibley *et al.* 1985), and an allozyme analysis indicates closest relationship with the tyrannids and *Piprites.* Additional investigations of all character systems are required to further resolve the phylogenetic relationships of *Oxyruncus* to other tyrannoids. Until that time, it would be more informative to biologists interested in the evolutionary origins of this distinct genus to place it in the Tyrannoidea as *incertae sedis* than to maintain the monotypic family Oxyruncidae.

(4) *Polyphyly of the genus* Lipaugus. The genus *Lipaugus* Boie (=*Lathria* Swainson; Sclater, 1888; Ridgway 1907) has traditionally included seven species of mostly drab, sexually monomorphic cotingids with prominent rictal bristles. Snow (1973, 1982) questioned the placement of the genus in the Cotingidae but did not question the validity of the limits of the genus. The character analysis performed here has identified two distinct groups within *Lipaugus. Lipaugus vociferans* and *L. unirufus* have the derived enlarged femoral artery (9), internal syringeal cartilages (6), and medial bronchial cartilaginous sheets (8), but lack the derived insertion of M. tracheolateralis (11). *Lipaugus subalaris* and *L. cryptolophus* have the derived insertion of M. tracheolateralis (11) shared with most cotingids, but they lack the derived femoral artery (9), and the medial bronchial cartilage sheets (8) shared by other members of *Lipaugus, Tityra, Neopelma* and *Tyranneutes.* No anatomical specimens of *Lipaugus lanioides, fuscocinereus* or *streptophorus* are available (Wood *et al.,* 1982), so placement of these species is not possible based on syringeal and arterial morphology. However, Snow (1973, 1982) described a number of probably derived

external and behavioral characters that support the placement of these three species with *vociferans* and *unirufus*.

Additional investigations are required before the interrelationships of these taxa are resolved, but the present data strongly indicate that *Lipaugus* as presently composed (Hellmayr, 1929; Snow, 1973, 1979, 1982) is polyphyletic. The genus should be divided into two probably monophyletic genera. The type species of the genus *Lipaugus* Boie is *vociferans* (=*Muscicapa plumbea* Lichtenstein), so *vociferans, unirufus, lanioides, fuscocinereus,* and *streptophorus* should remain in *Lipaugus*. The generic name *Lathria* Swainson was formerly applied to all these species (*e.g.* Sclater, 1888; Ridgway, 1907) and is available for the recognition of a new genus group including *subalaris* and *cryptolophus* only.

ACKNOWLEDGMENTS

This research was conducted as part of my doctoral thesis at the University of Michigan. I would like to thank the members of my doctoral committee, Mary C. McKitrick, Robert B. Payne, William L. Fink, Brian A. Hazlett, and W. H. Wagner, for their helpful comments during the research and on the manuscript. I give special thanks to Wesley E. Lanyon of the American Museum of Natural History for introducing me to suboscine syringes, and for allowing me to study cleared and stained syringeal specimens he prepared as part of his research on tyrannids. George Barrowclough, Ted Cohn, Joel Cracraft, Steve Dobson, Steve Goodman, Anne Heise, Geoff Hill, Rebecca Irwin, Nedra Klein, Arnold Kluge, Michael Nachman, Barry OConnor, Robert Storer, Rob Voss, Mark Wilkinson, Tom Will, and the participants of the University of Michigan Systematics and Biogeography Discussion Group offered helpful advice and stimulating discussion on the research. Margaret Van Bolt prepared Figure 1, and David Rini prepared Figure 3. The manuscript was improved by comments from Richard Zusi and an anonymous reviewer, and by the patient and careful editing of Sara Fink. The Spanish Resumen was rewritten by Patricia Escalante Pliego.

The following curators and museums lent specimens in their collections: J. C. Barlow, Royal Ontario Museum; G. F. Barrowclough, American Museum of Natural History; P. J. K. Burton and G. Cowles, British Museum (Natural History); J. W. Fitzpatrick, S. M. Lanyon, and David Willard, Field Museum of Natural History; N. K. Johnson, Museum of Vertebrate Zoology; R. F. Johnston, University of Kansas Museum of Natural History; M. C. McKitrick, University of Michigan Museum of Zoology; J. V. Remsen, Louisiana State University Museum of Zoology; E. H. Stickney, Yale Peabody Museum of Natural History; D. S. Wood, Carnegie Museum of Natural History; and R. L. Zusi, National Museum of Natural History. The research was funded by a Research Partnership Grant with M. C. McKitrick, a Dissertation Improvement Grant, and One-term Predoctoral Fellowship from the Rackham Graduate School, the University of Michigan; the Department of Biology; the Chapman Memorial Fund of the American Museum of Natural History; the Herbert and Betty Carnes Award of the American Ornithologists' Union; the Sigma Xi Foundation; and a Graduate Student Research in the Collections Grant from the American Museum of Natural History sponsored by Wesley E. Lanyon.

To all these people and institutions, I give my sincere thanks.

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Accepted September 21, 1989

APPENDIX 1

SYRINGEAL SPECIMENS OF PIPRIDS, COTINGIDS, AND PROBLEMATIC TYRANNIDS EXAMINED

Syringeal specimens were cleared and double stained (C&S) for bone and cartilage in the manner of Dingerkus and Uhler (1977), and stained with reversible iodine stain (IS), as described by Bock and Shear (1972). Specimens were borrowed from the American Museum of Natural History (AMNH), British Museum (Natural History) (BM), Carnegie Museum of Natural History (CM), Field Museum of Natural History (FMNH), Louisiana State University Museum of Zoology (LSUMZ), Museum of Vertebrate Zoology (MVZ), Royal Ontario Museum (ROM), United States National Museum of Natural History (USNM), University of Kansas Museum of Natural History (UK), University of Michigan Museum of Zoology (UMMZ), and Yale University Peabody Museum (YPM). Uncatalogued specimens are identified by the original collector's number in parentheses. Taxonomic order follows Snow (1979) and Traylor (1979).

TYRANNIDAE (select species).—*Laniocera hypopyrrha*—C&S: AMNH 8087, 15208, 816776; LSUMZ 102562, 102564. IS: FMNH 290394; LSUMZ 79585, 114498. *Laniocera rufescens*—C&S: LSUMZ 108460, 108461; YPM 986. *Xenopsaris albinucha*—C&S: AMNH 3520, 8389. *Pachyramphus viridis*—C&S: USNM 227304. *Pachyramphus rufus*—C&S: AMNH 2260. IS: CM 1275, 1306, 1320. *Pachyramphus cinnamomeus*—C&S: UMMZ 226364. *Pachyramphus polychopterus*—C&S: AMNH 2389, 8223. IS: CM 1341; LSUMZ 42868, 64797, 64798, 71469, 91220; USNM 227742. *Pachyramphus marginatus*—C&S: AMNH: 15177; LSUMZ 102281. *Pachyramphus versicolor*—IS: LSUMZ 107646. *Pachyramphus major*—C&S: (Uncat., institution unknown) WS B-1083. *Pachyramphus aglaiae*—C&S: AMNH 2262, 6657, 7889, 8220–8222. *Pachyramphus validus*—C&S: AMNH 7897. *Pachyramphus minor*—C&S: LSUMZ 111083. *Tityra cayana*—C&S: AMNH 2390, 7980, 7981, 8224. IS: LSUMZ 120547, 123061. *Tityra semifasciata*—C&S: AMNH 102274. IS: FMNH 291657; LSUMZ 18387, 64799; UMMZ 226615. *Tityra inquisitor*—C&S: AMNH 6659.

PIPRIDAE.—*Schiffornis major*—C&S: AMNH 9376, 816774; LSUMZ 105270. *Schiffornis turdinus*—C&S: AMNH 8082; LSUMZ 102439, 102443, 102444, (uncat.). IS: FMNH 290397; LSUMZ 114487, 114488; UMMZ 225043, 225044; USNM 515120, 515122. *Schiffornis virescens*—C&S: AMNH 2305, 2448. IS: FMNH 107022. *Sapayoa aenigma*—C&S: LSUMZ 108443, 108444, 108918. IS: USNM 431335. *Piprites chloris*—C&S: LSUMZ 102434, 102435, 110625, 115850. IS: FMNH 290398; LSUMZ 103305, 131852. *Neopipo cinnamomea*—C&S: AMNH 9371, 816769. *Chloropipo holochlora*—C&S: LSUMZ 112837; UK 60693, 65552. IS: UMMZ 225045–225051, 226601. *Chloropipo uniformis*—C&S: AMNH 7680. IS: USNM 504508–504510. *Chloropipo unicolor*—C&S: LSUMZ 71544, 89472. IS: LSUMZ 70637, 71541, 71543, 89471, 89474. *Xenopipo atronitens*—C&S: AMNH 8083, 8152. IS: AMNH (PEP2006). *Antilophia galeata*—C&S: BM 1968.66.205. *Tyranneutes stolzmanni*—C&S: AMNH 9375; CM 2096; LSUMZ 111082, 118488. IS: LSUMZ 131851. *Neopelma chrysocephalum*—C&S: AMNH 8078,

8079. *Neopelma aurifrons*—C&S: CM 2092. IS: CM 2091; FMNH 107062, 107063, 107065. *Heterocercus flavivertex*—C&S: AMNH 9840, 15203, 15204; USNM 504517. IS: AMNH 9374. *Heterocercus linteatus*—C&S: FMNH 330655. *Machaeropterus regulus*—C&S: LSUMZ 85980, 85981, 115836; UK 66684. IS: LSUMZ 111081, 114486, 120584; UMMZ 225052. *Machaeropterus pyrocephalus*—C&S: FMNH 289998. IS: FMNH 290401, 322567; LSUMZ 79589, 131842, 131844, 131845. *Machaeropterus deliciosus*—C&S: AMNH 8713. IS: BM 1986–3–1; UMMZ 225054–225057. *Manacus manacus candei*—C&S: AMNH 6654. *Manacus manacus vitellinus*—C&S: AMNH 8084; LSUMZ 108418, 108423. *Manacus manacus manacus*—C&S: AMNH 7707, 7710, 8147. IS: LSUMZ 35355, 112833, 112834, 114482, 114483; ROM 107498, 113119, 127649; USNM 515118, 515119. *Corapipo leucorrhoa*—C&S: LSUMZ 102429, 108441. IS: LSUMZ 104779, 108683; MVZ 4801, 4802, 4804; UMMZ 226607–226610; USNM 510718, 510719. *Corapipo gutturalis*—C&S: AMNH 2256; BM 1968.46.17. *Ilicura militaris*—C&S: FMNH 107023, 107029. IS: FMNH 107028, 107030. *Masius chrysopterus*—C&S: CM 1161; LSUMZ 117121. IS: BM 1968–3–12; LSUMZ 83866, 89470; UMMZ 225059, 226604–226606. *Chiroxiphia linearis*—C&S: AMNH 3671, 3672. IS: USNM 541043–541046, 541048. *Chiroxiphia lanceolata*—C&S: CM 373. *Chiroxiphia pareola*—C&S: AMNH 8080; LSUMZ 95546. IS: LSUMZ 95548, 123335, 131837; UMMZ 225060-225062. *Chiroxiphia caudata*—C&S: AMNH 2447, 2525, 2526. IS: FMNH 107322, 107323, 107334. *Pipra pipra*—C&S: AMNH 2259, 8145, 9358; IS: CM 1395, 1442, 1446; LSUMZ 118022, 118027, 118028, 118030; ROM 107489, 107637, 112440; UMMZ 226614; USNM 515095, 515100, 515101. *Pipra coronata*—C&S: AMNH 2257, 9838, 15194, 15199; LSUMZ 102412, 102419. IS: UMMZ 225063-225066, 226602. *Pipra isidorei*—C&S: LSUMZ 118033. *Pipra coeruleocapilla*—C&S: FMNH 291664. IS: LSUMZ 70636, 71540; USNM 512022, 512071, 512291, 512295. *Pipra nattereri*—IS: FMNH 333842. *Pipra iris*—C&S: AMNH 9892. IS: AMNH 17691. *Pipra serena suavissima*—C&S: AMNH 9366, 9368, 816768. IS: BM 1968–46–19. *Pipra serena serena*—C&S: ROM 127643, 127657. *Pipra aureola*—C&S: CM 1280. IS: AMNH 17689; USNM 515055. *Pipra fasciicauda*—C&S: AMNH 2301. IS: LSUMZ 35361, 72966, 91517, 123381. *Pipra filicauda*—C&S: LSUMZ 83807, 115617; UK 66660. IS: UMMZ 225067–225070, 226603. *Pipra mentalis*—C&S: LSUMZ 95070; UMMZ 226611. IS: USNM 510741, 510743, 510746, 510747; UMMZ 226612. *Pipra erythrocephala*—C&S: AMNH 8081, 9839, 15178; LSUMZ 108388, 108390, 110345, (SWC-1412). IS: BM 1970–34–1; UMMZ 225071, 225073–225075. *Pipra rubrocapilla*—C&S: AMNH 2517, 2520. IS: AMNH 17690; LSUMZ 114472, 131823, 131828, 131830, 131831. *Pipra chloromeros*—C&S: LSUMZ 102394, 102395. IS: FMNH 322838, 322840, 322844; LSUMZ 75568, 79587, 103303, 103304, 107647. *Pipra cornuta*—IS: USNM 504506, 504507. Missing Species: *Piprites griseiceps, Piprites pileatus, Chloropipo flavicapilla, Tyranneutes virescens, Neopelma pallescens, Neopelma sulphureiventer, Heterocercus aurantiivertex, Pipra vilasboasi.*

COTINGIDAE.—*Phoenicircus nigricollis*—C&S: AMNH 9348; LSUMZ 94210, 110267, 118468. *Laniisoma elegans*—C&S: FMNH 322417. *Carpornis cucullatus*—C&S: AMNH 2551. *Ampelion rubrocristatus*—C&S: LSUMZ 75015, 79583, 86219. *Ampelion rufaxilla*—C&S: LSUMZ 107641. IS: MVZ 2896. *Ampelion sclateri*—C&S: LSUMZ 75016, 81150. *Ampelion stresemanni*—C&S: LSUMZ 79584. *Pipreola riefferii*—C&S: LSUMZ 102264, 102266. IS: LSUMZ 71538, 71539, 75018. *Pipreola intermedia*—C&S: CM 402; LSUMZ 75017. IS: LSUMZ 91515, 118009; MVZ 2515. *Pipreola arcuata*—C&S: LSUMZ 75019, 89468, 102269. *Pipreola aureopectus*—C&S: AMNH 8228; LSUMZ 107642. IS: LSUMZ 107643. *Pipreola frontalis*—C&S: FMNH 322425; LSUMZ 2848. *Pipreola chlorolepidota*—C&S: BM 1970.53.2; LSUMZ 117001. IS: BM 1968–3–17. *Pipreola formosa*—C&S: CM 560. *Ampelioides tschudii*—C&S: LSUMZ 90759, 117004. *Iodopleura isabellae*—C&S:

FMNH 322431, 332432; LSUMZ 115613. *Lipaugus subalaris*—C&S: FMNH 290407. *Lipaugus cryptolophus*—C&S: LSUMZ 89469. *Lipaugus vociferans*—C&S: AMNH 2385, 7701; LSUMZ 102270, 102273. IS: CM 1457; LSUMZ 64795, 64796, 71354; USNM 56337. *Lipaugus unirufus*—C&S: AMNH 6655. *Porphyrolaema porphyrolaema*—C&S: LSUMZ 119942. *Cotinga nattererii*—C&S: YPM 7363. *Cotinga maynana*—C&S: LSUMZ 71353, 71468. *Cotinga cayana*—C&S: LSUMZ 102275, 102279. IS: LSUMZ 114467. *Xipholena punicea*—C&S: AMNH 2265, 6653, 7994. IS: AMNH 7995. *Carpodectes hopkei*—C&S: LSUMZ 42915. *Gymnoderus foetidus*—C&S: LSUMZ 64800, 110281, 119972. IS: BM 1975–35–1; LSUMZ 120545. *Conioptilon mcilhennyi*—C&S: LSUMZ 42866, 42870. IS: LSUMZ 64793. *Querula purpurata*—C&S: AMNH 6651, 6652; LSUMZ 108385, 108386, 110282, 115615. IS: CM 1236, LSUMZ 42874, 64801, 64802; UMMZ 226614. *Pyroderus scutatus*—C&S: LSUMZ 107644. *Cephalopterus glabricollis*—C&S: USNM 510877. *Cephalopterus ornatus*—C&S: AMNH 2590. IS: LSUMZ 120546. *Cephalopterus penduliger*—IS: BM 1989–32–1. *Perissocephalus tricolor*—C&S: AMNH 2384; CM 1290. IS: BM 1974–4–69, 1975–4–69. *Procnias tricarunculatus*—C&S: UK 58967. *Procnias alba*—C&S: AMNH 2382; BM 1974.4.71. *Procnias nudicollis*—C&S: AMNH 2264, BM A/OH/89. IS: CM 4516; UMMZ (uncat.). *Rupicola rupicola*—C&S: AMNH 2531, 7682, 7993, 816758. *Rupicola peruviana*—C&S: AMNH 4041. IS: CM 2754; FMNH 106931; LSUMZ 62675, 107645.

Oxyruncidae.—*Oxyruncus cristatus*—C&S: BM (uncat.); LSUMZ 108529, 108530, 108961, 108962. IS: FMNH 107021, 108696.

Phytotomidae.—*Phytotoma raimondii*—C&S: AMNH 2267; LSUMZ 81156. *Phytotoma rara*—C&S: AMNH 4314. *Phytotoma rutila*—C&S: AMNH 4313; LSUMZ 102783, 102784, 102787, 102788. IS: BM 1970–43–64; LSUMZ 91227.

APPENDIX 2

Tyrannoid Specimens Dissected to Observe the Hindlimb Arteries

For abbreviations of institutions see Appendix 1. Taxonomic order follows Snow (1979) and Traylor (1979).

Tyrannidae.—**Elaeniinae.**—*Camptostoma obsoletum*—AMNH 6756. *Elaenia albiceps*—AMNH 2464, 2465. *Euscarthmus melanoryphus*—AMNH 4364. *Mionectes oleaginus*—UMMZ 225028, 225029. *Pseudotriccus pelzelni*—UMMZ 225031. *Lophotriccus vitiosus*—UMMZ 225032. *Todirostrum latirostre*—AMNH 2295. *Todirostrum cinereum*—AMNH 6810. *Rhynchocyclus brevirostris*—UMMZ 225035, 225036. **Fluvicolinae.**—*Terenotriccus erythrurus*—UMMZ 225040. *Myiobius sulphureipygius*—AMNH 6661. *Myiobius villosus*—UMMZ 225041, 225042. *Contopus virens*—AMNH 8379. *Empidonax traillii*—AMNH 6766. *Empidonax minimus*—AMNH 6775. *Sayornis nigricans*—AMNH 4158. *Pyrocephalus rubinus*—AMNH 6727. *Ochthoeca pulchella*—AMNH 3521. *Ochthoeca rufipectoralis*—AMNH 3991. *Ochthoeca fumicolor*—AMNH 4642, 7890. *Ochthoeca leucophrys*—AMNH 6707, 6708. *Xolmis irupero*—AMNH 6822. *Muscisaxicola maculirostris*—AMNH 6670. *Lessonia rufa*—AMNH 6779. *Knipolegus aterrimus*—AMNH 6785. *Knipolegus nigerrimus*—AMNH 6786. *Colonia colonus*—AMNH 6759. *Muscigralla brevicauda*—AMNH 67976. **Tyranninae.**—*Laniocera hypopyrrha*—FMNH 290394. *Myiarchus nuttingi*—AMNH 6685. *Pitangus sulphuratus*—AMNH 7979. *Myiozetetes similis*—AMNH 6715. *Tyrannus tyr-*

annus—UMMZ 226347, 226348. **Incertae Sedis.**—*Xenopsaris albinucha*—AMNH 3520. **Tityrinae.**—*Pachyramphus polycopterus*—LSUMZ 42868, 64797, 64798, 71469, 91220. *Tityra cayana*—LSUMZ 120547, 123061. *Tityra semifasciata*—LSUMZ 18387, 64799.

Pipridae.—*Schiffornis turdinus*—LSUMZ 114487, 114488, 118038; UMMZ 225043. *Schiffornis virescens*—FMNH 107022. *Sapayoa aenigma*—USNM 431335. *Piprites chloris*—FMNH 290398; LSUMZ 103305, 131852. *Neopipo cinnamomea*—AMNH 9372. *Chloropipo holochlora*—UMMZ 225045, 225047–225050, 226601. *Chloropipo uniformis*—USNM 504508–504510. *Chloropipo unicolor*—LSUMZ 70637, 71541, 71543. *Tyranneutes stolzmanni*—LSUMZ 131852. *Neopelma aurifrons*—FMNH 107062, 107063, 107065. *Heterocercus flavivertex*—AMNH 9374; USNM 504518. *Heterocercus linteatus*—FMNH 330655. *Machaeropterus regulus*—LSUMZ 111081, 114486, 120584; UMMZ 225052, 225053. *Machaeropterus pyrocephalus*—LSUMZ 79859, 131842, 131844, 131845. *Manacus manacus*—LSUMZ 35355, 112833, 112834, 114482; ROM 107498, 113119. *Corapipo leucorrhoa*—LSUMZ 104779, 108683; MVZ 4804; UMMZ 226607. *Ilicura militaris*—FMNH 107023, 107028–107030. *Masius chrysopterus*—LSUMZ 83866, 89470; UMMZ 226606. *Chiroxiphia pareola*—LSUMZ 95548, 123335, 131837; UMMZ 225061, 225062. *Pipra pipra*—LSUMZ 118022, 118027, 118028, 118030. *Pipra coronata*—UMMZ 225064, 225066. *Pipra coeruleocapilla*—LSUMZ 70636, 71540. *Pipra nattereri*—FMNH 333842. *Pipra serena suavissima*—AMNH 9366, 9367. *Pipra fasciicauda*—LSUMZ 35361, 72966, 91517, 123381. *Pipra filicauda*—UMMZ 255067. *Pipra erythrocephala*—UMMZ 225072. *Pipra rubrocapilla*—LSUMZ 114472, 131823, 131828, 131830, 131831. *Pipra chloromeros*—LSUMZ 75568, 79587, 103303, 103304, 107647. *Pipra cornuta*—USNM 504506, 504507.

Cotingidae.—*Phoenicircus nigricollis*—LSUMZ 94210. *Laniisoma elegans*—FMNH 322417. *Carpornis cucullatus*—AMNH 2551. *Ampelion sclateri*—LSUMZ 75016, 81150. *Ampelion rufaxilla*—LSUMZ 107641. *Ampelion rubrocristatus*—LSUMZ 75015, 79583, 86219. *Ampelion stresemanni*—LSUMZ 79584. *Pipreola pulchra*—LSUMZ 107642, 107643. *Pipreola riefferii*—LSUMZ 75017, 91515, 118009. *Pipreola intermedia*—LSUMZ 71538, 71539, 75018. *Pipreola frontalis*—FMNH 322425. *Ampelioides tschudii*—LSUMZ 90759. *Iodopleura isabellae*—FMNH 322431. *Lipaugus subalaris*—FMNH 290407. *Lipaugus cryptolophus*—LSUMZ 89469. *Lipaugus vociferans*—LSUMZ 64796, 71354. *Cotinga cayana*—LSUMZ 114467. *Cotinga maynana*—LSUMZ 71353, 71468. *Xipholena punicea*—AMNH 7994. *Carpodectes hopkei*—LSUMZ 42915. *Conioptilon mcilhennyi*—LSUMZ 64793. *Gymnoderus foetidus*—LSUMZ 120545. *Querula purpurata*—LSUMZ 42874, 64801, 64802; UMMZ 226614. *Pyroderus scutatus*—LSUMZ 107644. *Cephalopterus ornatus*—LSUMZ 120546. *Perissocephalus tricolor*—CM 1290. *Procnias nudicollis*—USNM 291981. *Procnias alba*—CM 4516. *Rupicola peruviana*—LSUMZ 62675, 107645.

Oxyruncidae.—*Oxyruncus cristatus*—FMNH 107021; LSUMZ 108696.

Phytotomidae.—*Phytotoma raimondii*—LSUMZ 81156. *Phytotoma rutila*—LSUMZ 91227.