Syringeal Morphology, Phylogeny, and Evolution of the Neotropical Manakins (Aves: Pipridae)

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ABSTRACT

The syringeal morphology of 37 of the 40 species of the monophyletic manakin family (Aves: Pipridae) is described. Observations were made of cleared and double stained, and iodine stained specimens. Twenty-five distinct syringeal morphologies were identified within the family, encompassing variation in supporting elements, membranes, musculature, and innervation. This extensive interspecific variation indicates that the syringeal evolution in the piprids has been dynamic.

A phylogenetic analysis of piprid syringeal morphology is presented. Syringeal variation was coded as 59 characters and polarized by outgroup comparison to cotingas (Cotingidae), tyrant flycatchers (Tyrannidae), and other suboscine passerines. Parsimony analysis using PAUP identified two equal length, maximally parsimonious phylogenetic hypotheses (length = 76; Consistency Index = 0.82). A strict consensus tree based on these output trees includes 23 resolved clades, and is identical to one of the two shortest trees. The monophyly of eight piprid genera and several recently recognized species groups is supported. However, the traditional piprid genera *Chloropipo* and *Pipra* are paraphyletic and polyphyletic, respectively. The monophyly of *Heterocercus* and the *Pipra serena* species group could not be supported by syringeal characters.

The syringeal hypothesis of phylogeny is compared to previous classifications of the piprids and to recent biochemical hypotheses of phylogeny. The relative confidence of the clades in the syringeal hypothesis is discussed.

Intraspecific and interspecific variations in piprid syringeal morphology are reviewed, and possible correlations between syringeal function and structural variation are discussed. Piprids apparently lack independent innervation of the two sides of the syrinx, a hypothetical prerequisite for control of two independent syringeal sound sources. A general model is proposed to explain the differences in the diversity of syringeal morphology in the suboscine and oscine passerines. In oscines, songs are largely learned, whereas in suboscines, available evidence indicates that vocalizations are innate. Natural or sexual selection on innate vocalizations should contribute to correlated morphological differentiation, whereas selection on learned vocalizations should result in cultural evolution without morphological change. The predictions of the model are congruent with the differences in syringeal diversity of these two main clades.

A phylogenetic classification of the manakins that reflects the syringeal hypothesis of phylogeny is presented. Four new tribes are recognized within the family. The four species of the paraphyletic genus *Chloropipo* are combined with *Xenopipo atronitens* in a single monophyletic genus to which the senior genus group name *Xenopipo* is applied. The polyphyletic genus *Pipra* is split into three monophyletic genera: *Pipra* Linnaeus including the *aureola* and *erythrocephala* clades; *Dixiphia* Reichenbach including *pipra*; and *Lepidothrix* Bonaparte including the eight species of the *serena* species group.

RESUMEN

Se describe la morfología de las siringes de 37 de las 40 especies de todos los 11 géneros de la familia de saltarines (Aves: Pipridae). Se observaron ejemplares aclarado y teñidos, y teñidos de yodo. Venticinco morfologías de siringe distintas se identifican en la familia, abarcando variaciones en los elementos de apoyo, las membranas, los músculos, y la innervación. Esta variación interespecifica extensiva indica que la evolución de las siringes en los saltarines ha sido dinámica.

Se presenta un análisis filogenético de la morfología de la siringe de los saltarines. La variación de las siringes fue registrada como 59 caracteres y polarizada por comparaciones con los cotingas (Cotingidae), atrapamoscas (Tyrannidae), y otros suboscinos. Un análisis parsimónico usando PAUP identificó dos hipóteses filogenéticas de igual longitud y de máxima parsimonia (longitud = 76; Indice de consistencia = 0.82). Un árbol de consenso exacto basado en estos árboles incluye 23 clados resueltos y es idéntico a uno de los dos árboles más corto. Se apoyan la monofilia de ocho géneros de piprides y algunos de los grupos de especies reconocidos recientemente. Los dos géneros tradicionales de pipridos, *Chloropipo* y *Pipra,* son parafilético o polifilético, respectivamente. La monofilia de *Heterocercus* y el grupo de especies *Pipra serena* no pueda apoyarse por caracteres de la siringe.

La hipótesis filogenético de la siringe se compara con las clasificaciones previas de los saltarines y con hipóteses filogenéticos de caracteres bioquímicos. Se discute la confianza relativa de los clados de la hipótesis filogenético de las siringes.

Se revisa la variación intraespecífica y interespecífica de la morfología de la siringe de los pipridos, y se discuten las correlaciones posibles entre la función de la siringe y la variación de la estructura. Los pípridos aparentemente carecen de la inervación independiente de los dos lados de la siringe, que es un requisito hipotético para controlar dos orígenes independientes del sonido en la siringe. Se propone un modelo general para explicar las diferencias en la diversidad de la siringe de los paserinos suboscinos y oscinos. En los oscinos, las vocalizaciones son generalmente aprendidas, mientras que en los suboscinos, la evidencia disponible indica que las vocalizaciones son innatas. La selección natural y sexual de las vocalizaciones innatas deben contribuir a la diferenciación correlacionada, mientras que la selección sobre vocalizaciones apprendidas debe producir la evolución cultural sin cambio morfológico. Estas predicciones del modelo son congruentes con las diferencias en la diversidad de la siringe de esto dos clados mayores.

Se propone una clasificación filogenética de la familia de los saltarines, que representa la hipótesis filogenético de la siringe. Se reconocen cuatro tribus nuevas en la familia. Las cuatros especies del género parafilético *Chloropipo* se combinan con *Xenopipo atronitens* en un género monofilético que tiene el nombre mayor *Xenopipo*. El género polifilético de *Pipra* se divide en tres géneros monofiléticos: *Pipra* Linnaeus incluyendo los grupos de especies *aureola* y *erythrocephala*; *Dixiphia* Reichenbach incluyendo *pipra*; and *Lepidothrix* Bonaparte incluyendo las ocho especies del grupo de especies *serena*.

INTRODUCTION

The manakins (Pipridae) are a small family of Neotropical passerine birds. They are members of the suboscine superfamily Tyrannoidea that also includes the cotingas (Cotingidae) and tyrant flycatchers (Tyrannidae) (Snow, 1975, 1979; Prum, 1990b). The manakins are of particular interest because most behaviorally known species breed in polygynous, lek/arena systems. Many species are strikingly sexually dimorphic in plumage and perform acrobatic courtship displays (Snow, 1963; Sick, 1967; Prum, 1990a). Traditional analyses of the evolution of piprid display behavior have been limited by the lack of a corroborated hypothesis of phylogeny for the group (Sick, 1959, 1967; Snow, 1963). This investigation of piprid syringeal morphology was initiated to provide a phylogenetic framework for comparative investigations of the evolution of lek display behavior of the family (Prum, 1990a).

The syrinx—the avian vocal organ—is composed of specialized skeletal supporting elements, membranes, and musculature of the lower respiratory tract. Syringeal morphology of passerines has been traditionally an important character system in the recognition of the major division of passerine birds—the oscines and suboscines (Müller, 1847, 1878; Wunderlich, 1886; Haecker, 1900; Setterwall, 1901; Köditz, 1925). However, the diversity of suboscine syringes was not well

understood until Ames (1971) provided a comprehensive overview of their syringeal morphology. Ames documented an enormous syringeal diversity in the Tyrannoidea, including a small sample of piprids. More recently, syringeal characters have been used in phylogenetic analyses at both higher and lower levels within tyrannoids (Lanyon, 1984a, 1984b, 1985, 1986, 1988a, 1988b, 1988c; McKitrick, 1985; Prum and Lanyon, 1989; Lanyon and Lanyon, 1989; Prum, 1990b).

Traditionally, the Pipridae included 55 species in 17 genera (Hellmayr, 1929; Snow, 1975, 1979). The borders of the three large tyrannoid families have long been regarded as artificial and unsatisfactory. A recent phylogenetic analysis of higher-level relationships in the Tyrannoidea based on morphology indicates that the traditional Pipridae is not monophyletic (Prum, 1990b). Six traditional piprid genera, *Schiffornis, Piprites, Sapayoa, Neopelma, Tyranneutes,* and *Neopipo,* share derived syringeal characters with other nonpiprid tyrannoids (Prum and Lanyon, 1989; Prum, 1990b). However, a unique derived syringeal character supports a clade including 40 species in the other 11 traditional piprid genera, *Pipra, Manacus, Machaeropterus, Chiroxiphia, Antilophia, Chloropipo, Xenopipo, Heterocercus, Corapipo, Ilicura,* and *Masius* (Prum, 1990b). This restricted Pipridae is the subject of this investigation.

In this paper, I report my observations of the syringeal morphology of all available piprid species and perform a phylogenetic analysis of the family based on syringeal characters. I then discuss the implications of these findings for models of syringeal function and evolution, and for the phylogeny and classification of the piprids. I have used these syringeal data and the syringeal hypothesis of phylogeny for the piprids elsewhere in a detailed analysis of the evolution of polygynous display behavior in the family (Prum, 1990a).

The investigation is based on anatomical specimens borrowed from the American Museum of Natural History (AMNH); British Museum (Natural History) (BMNH); Carnegie Museum of Natural History (CMNH); Colección Ornitología Phelps, Caracas, Venezuela (COP); Field Museum of Natural History (FMNH); University of Kansas Museum of Natural History (KU); Louisiana State University Museum of Zoology (LSUMZ); Museu Paraense Emilio Goeldi (MPEG); Museum of Vertebrate Zoology, University of California at Berkeley (MVZ); Museum of Zoology of the University of São Paulo (MZUSP); Royal Ontario Museum (ROM); University of Michigan Museum of Zoology (UMMZ); National Museum of Natural History (USNM); Yale Peabody Museum of Natural History (YPM); and Zoología, Universidade do Brasilia (ZUB). Specimens referred to in the figure captions and the text are identified by the abbreviations given above. A complete list of specimens of piprids examined is given in the Appendix.

HISTORICAL REVIEW OF PIPRID CLASSIFICATION

I have previously reviewed the history of
the familial limits of the Pipridae (Prum,
1990b). Here, I summarize previous classi-
fications with an emphasis on hypotheses of
interrelationship for the members of the 11
genera in the restricted monophyletic Pipri-
dae (Prum, 1990b): *Chloropipo, Xenopipo,
Antilophia, Heterocercus, Machaeropterus,
Manacus, Corapipo, Ilicura, Masius, Chi-
roxiphia,* and *Pipra.*

Sclater (1888) provided the first complete
classification and keys of species and genera
of the Pipridae. He divided the family into
two subfamilies: the Piprinae including the
14 genera *Piprites, Chloropipo, Xenopipo,
Ceratopipra* (= *Pipra cornuta*), *Cirrhipipra* (=
Pipra filicauda), *Metopia* (= *Antilophia*),
Masius, Metopothrix, Pipra (including *Cora-
pipo* and *Tyranneutes*), *Neopipo, Machaerop-
terus, Chiroxiphia, Helicura* (= *Ilicura*), and
Chiromachaeris (= *Manacus*); and the Ptilo-
chlorinae which included the five genera *Ptil-*

ochloris (= *Laniisoma*), *Heteropelma* (=
Schiffornis turdinus), *Schiffornis, Neopelma,*
and *Heterocercus.* Sclater used male plumage
coloration and tail and bill shape to distin-
guish these genera.

In his first revision of *Pipra,* Hellmayr
(1906) defined the genus and species by
plumage traits. He removed *Corapipo* from
Pipra, but left the two species of *Tyranneutes*
in the genus.

Ridgway (1907) removed some species
from larger genera and recognized *Corapipo,
Tyranneutes, Allocotopterus* (to include *Ma-
chaeropterus deliciosus*), and *Chiriprion* (to
include *Chiroxiphia pareola, C. lanceolata,*
and *C. linearis*). He also identified senior syn-
onyms for several genera recognized by Scla-
ter, changing *Metopia* to *Antilophia, Helicura*
to *Ilicura,* and *Chiromachaeris* to *Manacus.*

Hellmayr (1910) provided detailed diag-
noses of the genera of Pipridae, and placed
Chiroprion back in *Chiroxiphia.* He suggest-
ed that *Masius* and *Antilophia,* and *Corapipo*
and *Manacus* might be each other's closest
relatives, based on male plumage similarities.
Later, Hellmayr (1929) presented a formal
classification of all species of piprids in which
he recognized the senior name *Teleonema* for
Cirrhipipra.

These early authors did not explicitly jus-
tify the order of taxa in their classification.
In Sclater's and Ridgway's classifications,
taxonomic order corresponds to the position
in the diagnostic keys, which were apparently
constructed for convenience. However, com-
ments in the text or footnotes of all three
authors suggest that proximity of taxa was
also meant to reflect evolutionary relation-
ship.

Sibley (1957) remarked that the piprid gen-
era were based only on male plumage from
Hellmayr's (1910) diagnosis, and that a ge-
neric revision of the family based on other
characters was necessary. But in the most re-
cent classification of the Pipridae, Snow
(1975, 1979) followed Hellmayr's generic
limits, with only two minor exceptions, be-
cause of the lack of additional systematic in-
vestigation on the group. Snow returned *Al-
locotopterus deliciosus* to *Machaeropterus,* and
Teleonema filicauda to *Pipra.* He also placed
the genera of piprids in a sequence to proceed
from "least" to "most" specialized in breed-

ing behavior and sexual dimorphism, stressing the lack of information for many genera. Snow (1975) made brief comments on interrelationships among piprid genera. He placed *Chloropipo* and *Xenopipo* near the beginning of the sequence as unspecialized manakins with other problematic genera that were subsequently removed from the family. He suggested that the plumage of *Antilophia* indicates affinities with *Pipra*, but placed it near the beginning of the sequence because of its apparent lack of elaborate displays (Sick, 1959, 1967). Snow considered *Heterocercus*, *Ilicura*, and *Masius* to be isolated genera without obvious affinities to other manakins, but apparently based on plumage, he placed the latter two genera late in the sequence of typical or "specialized" piprids. Based on details of behavior and plumage, Snow also suggested that *Machaeropterus* and *Corapipo* might be closely related to *Manacus*, and that *Chiroxiphia* is closest to *Pipra*.

Hypotheses of interspecific relationships within manakin genera have been presented recently in the form of proposed superspecies or species groups. Haffer (1967, 1970, 1974) identified several species groups of piprids, based on plumage similarity and patterns of geographic distribution (allopatry or parapatry). He (1967) recommended that all forms of *Manacus* be placed as semispecies in the single superspecies *Manacus manacus*, citing his observations of limited hybridization between populations of *Manacus* in Colombia, and the similarity of the courtship displays of the various geographic forms of *Manacus*. In the genus *Pipra*, Haffer (1970) recognized three superspecies including all species except *Pipra pipra*: the *Pipra aureola* species group including *aureola*, *fasciicauda*, and *filicauda* (previously placed in the monotypic genus *Teleonema*); the *Pipra erythrocephala* species group including *erythrocephala*, *rubrocapilla*, *chloromeros*, *mentalis*, and *cornuta*; and the *Pipra serena* species group including *serena*, *coronata*, *isidorei*, *coeruleocapilla*, *nattereri*, *vilasboasi*, and *iris*. Haffer (1970, 1974) hypothesized that the geographic patterns of species replacement in these groups were the result of primary isolation in forest refugia and secondary expansion during climatic cycles in the Pleistocene.

Snow (1975, 1979) recognized the *Pipra* aureola, erythrocephala, and serena species groups identified by Haffer (1970, 1974), except that he excluded *cornuta* from the *Pipra erythrocephala* group. Snow placed the Central American and Pacific South American forms of *Manacus* as subspecies of *Manacus manacus*, also following Haffer's (1967) recommendation. Elsewhere in the family, Snow also recognized species groups that included the members of *Corapipo*, *Heterocercus*, and *Chiroxiphia*, and *Machaeropterus regulus* and *pyrocephalus*. In *Chloropipo*, Snow recognized a species group including *flavicapilla*, *holochlora*, and *uniformis*. He questioned whether *C. unicolor* was related to other *Chloropipo* species because of differences in overall plumage and external morphology, but in the absence of any behavioral information, he hesitated to erect a new monotypic genus for *unicolor*.

S. M. Lanyon (1985) analyzed allozyme variation in the tyrannoids including seven species of piprids. In a variety of distance and cladistic analyses of the data with *Sapayoa* as the root or outgroup, the allozyme data supported two main piprid clades: one including *Machaeropterus regulus*, *Manacus manacus*, and *Pipra pipra*, and another including *Chiroxiphia pareola*, *Masius chrysopterus*, *Corapipo leucorrhoa altera*, and *Chloropipo holochlora*. He also placed *Neopelma* and *Tyranneutes* as the sister group to either of these piprid clades.

Prum and Johnson (1987) presented a cladistic analysis of male courtship display elements supporting a clade with *Ilicura* as the sister group to *Masius* and *Corapipo*. Prum (1988) did a cladistic analysis of the *Pipra serena* species group based on plumage characters in an investigation of patterns of biogeographic vicariance in Neotropical forest birds. Cracraft (1988) hypothesized that *Pipra cornuta* is the sister group to *Pipra erythrocephala* and *P. rubrocapilla*, based on a cladistic analysis of plumage characters.

Sibley and Ahlquist (1985, 1990) presented a phylogeny of the tyrannoids based on DNA-DNA hybridization distances including some piprid taxa, but the hypothesis was not highly resolved, included no reciprocal hybridizations, and provided little information about piprid phylogeny. Sibley and Monroe (1990) presented a classification of the piprids in a

subfamily Piprinae of an expanded Tyrannidae. Besides the change in the family-level status of the group, this classification was not based on any DNA-DNA hybridization evidence. Sibley and Monroe reversed the order of Snow (1979) to conform to Hellmayr (1929), but accepted Snow's changes of generic limits. Sibley and Monroe (1990) recognized the *Pipra aureola* species group of Haffer (1974) and Snow (1975, 1979), but they suggested new limits for the *Pipra erythrocephala* species group which included only *erythrocephala, rubrocapilla,* and *mentalis.* Further, they removed *Pipra coeruleocapilla* and *isidorei* from the *Pipra serena* species group, and placed them in their own *coeruleocapilla* group. At the specific level, they split *Manacus* into four species (*manacus, vitellinus, aurantiacus,* and *candei*), and *Corapipo leucorrhoa* into *leucorrhoa* and *altera.*

METHODS

Observations were made of 264 syringeal specimens of 37 species in all 11 genera of piprids using a Wild M5A dissecting microscope. Sixty-nine specimens were cleared and double stained with alcian blue and alizarin crimson to distinguish cartilage and bone (Dingerkus and Uhler, 1977) by Dr. W. E. Lanyon of the American Museum of Natural History. These specimens exhibited the shape, relative position, and composition of the syringeal supporting elements. One-hundred-ninety-five syringes from 33 species in 11 genera were removed from spirit specimens using the method of Ames (1971) and Cannell (1988). Observations were made of these uncleared specimens using reversible iodine stain of Bock and Shear (1972) to aid in the description of musculature and innervation. Most specimens were sexed by observations of the gonads. A list of all cleared and double-stained and iodine-stained piprid syringeal specimens observed is presented in the Appendix.

Illustrations of the syringeal material were prepared using a Wild M5A dissecting scope and a camera lucida. In figures 2 left, 3, 6, 7, 9, 10, 11, 13, 14, 15, 16, 18 left, 19, 20, 22, and 23, small and large stippling are used to illustrate ossified and cartilaginous elements, respectively. In figures 2 right, 4, 5, 8, 12, 17,

18 right, and 21, no stippling and small stippling are used to portray ossified and cartilaginous elements.

Monophyly of the piprids was accepted based on their possession of dorsally fused B1–2 syringeal elements (Prum, 1990b). The hypothesized sister group to the piprids is the cotingid clade, and their sister group is the tyrannids (Prum, 1990b). For this investigation the problematic tyrannoids that may be related to either cotingids or tyrannids were assumed to belong to the cotingids (Prum, 1990b).

Morphological variation in syringes of piprids was coded as 56 binary characters and three unordered multistate characters and polarized by outgroup comparison to other tyrannoids. Unknown character states were coded as (?). Hypothesized transition series were coded as a series of binary characters. Each character description proceeds from the distribution and description of the derived state to the distribution and description of the primitive state, and ends with a statement of the character polarity. Complex character descriptions include additional discussion. The distributions of hypothesized derived characters are summarized in table 2. Throughout the paper, specific characters are referred to by the character number in parentheses. Alternative derived states of the three complex, unordered characters (13, 54, and 57) are referred to by .1 or .2 following the character number.

The most parsimonious phylogenetic resolutions of the syringeal character data were identified using the PAUP computer program, version 3 (Swofford, 1989), on a Macintosh computer using the branch-and-bound algorithm, condensed zero branch lengths, and the consensus tree option on the unordered character set. For simplicity, the morphologically identical taxa were combined into single OTUs in the PAUP analysis. Some apparent autapomorphies in the results were used to support the monophyly of polytypic terminal taxa.

Throughout, I follow the taxonomy of Snow (1979) with a few exceptions. I recognize three species in the genus *Manacus*: *M. manacus, M. vitellinus,* and *M. candei.* Also, I recognize the two differentiated allopatric geographic forms formerly placed in *Pipra serena* as sep-

arate species: *Pipra serena* and *Pipra suavissima* (Prum, in prep.). For convenience, I refer to several species groups of *Pipra* as defined by Haffer (1970, 1974) and Snow (1975): the *Pipra serena* species group including *serena, suavissima, coronata, isidorei, coeruleocapilla, nattereri, vilasboasi,* and *iris*; the *Pipra aureola* species group including *aureola, fasciicauda,* and *filicauda*; and the *Pipra erythrocephala* species group including *cornuta, mentalis, chloromeros, erythrocephala,* and *rubrocapilla.*

SYRINGEAL MORPHOLOGY AND TERMINOLOGY

The tracheobronchial syrinx of piprids is composed of four morphological components: supporting elements, membranes, muscles, and nerves. Latin synonyms of morphological structures are from Baumel et al. (1979). Basic morphology and terminology of each of these character systems are outlined below.

SUPPORTING ELEMENTS

The syringeal supporting elements include tracheal and bronchial rings, and other non-ringlike supporting structures called accessory cartilages. King (1979, 1989) has proposed naming syringeal supporting rings based on their position relative to the bifurcation of the airway. However, a simplistic nomenclature based solely on the tracheal/bronchial dichotomy proposed by King (1979, 1989) results in the assignment of different names to homologous elements within and among species that vary in the relative position of the tracheobronchial junction. Although such a nomenclature may be convenient in functional analyses, this system would be an impediment to genuine evolutionary and comparative investigations.

In oscines, the names of the ringlike supporting elements are traditionally based on relative position to the tracheal tympanum or "drum" which is composed of three or four fused, ossified tracheal rings immediately cranial to the tracheobronchial junction (Ames, 1971). This drum is uniformly present in oscine birds (Ames, 1971). However, in suboscines the morphology of the supporting elements is much more variable,

leading to difficulties in identifying homologous elements among species. A tracheal drum, or tympanum, is not consistently present in suboscine species, and cannot be used as a landmark in assessing homology.

Since these two traditional systems for naming syringeal supporting elements are inappropriate for suboscines, Ames (1971) devised an alternative system based on the observation that tracheal and bronchial supporting elements typically differ in composition, i.e., the degree of ossification. He proposed naming the cranial, mostly tracheal, series of supporting rings "A elements," and the caudal, mostly bronchial series "B elements." In Ames's system, each ringlike supporting element is numbered in sequence in the A or B series, beginning with the first A and B elements near the tracheobronchial junction, and continuing cranially and caudally away from the tracheobronchial junction. The difficulty of this system is in establishing homology among the first supporting elements in the A and B series despite variation in morphology of elements and their relative position to the tracheobronchial junction. Ames (1971) differentiated the first A and B elements by differences in cross-sectional shape (flat vs. D-shaped), consistency (transparent and stiff vs. opaque, spongy, and flexible), and orientation of concavity (caudal vs. cranial). The first two criteria are indirect assessments of the degree of ossification, and the last criterion is highly variable among taxa and may be very difficult to assess once the syrinx has been removed from the body cavity. Further, I have observed significant variation among piprids in the degree of ossification of the first putative A and B elements, making it problematic to apply Ames's criteria.

In this investigation, I use the supporting element terminology proposed by Ames (1971), but I employ a different set of criteria for establishing homology among the initial A and B elements (in decreasing order of importance): (1) special similarities in shape, (2) relative position of syringeal muscle insertions, and (3) composition (ossified vs. cartilaginous). Within piprids, homologies are most easily established by the relative position of an element to the B1–2 elements, which are dorsally fused by a short cartilaginous bar

(Prum, 1990b) and distinctly widened and angled at their ventral ends. In piprids, putative homologs established by the first criterion are always consistent with hypotheses of homology supported by the second criterion—relative position to the insertion of the intrinsic syringeal musculature. In only a few critical instances, application of these criteria leads to different homology assignments than reported by Ames (1971) (discussed below). At higher levels within Tyrannoidea, establishment of supporting-element homologies is complicated by variation in the position of the insertions of syringeal musculature (such as the insertion of M. tracheolateralis on the A1/B1 membrane; Prum, 1990b). In these higher-level comparisons, it is necessary to invoke the third criterion of composition to identify putative homologs.

In describing the variation in shape of the syringeal supporting elements, I use terminology similar to that of Ames (1971). In this scheme, supporting elements are characterized as:

complete—element forms a closed ring,
incomplete—element "open" dorsally, ventrally, or medially in the form of a partial ring,
single—element composed of only a single ring,
double—element divided into a pair of left and right elements which may themselves be incomplete or complete.

Ames (1971) referred to incomplete double elements as "divided" and complete double elements as "double." In addition, supporting elements may vary in composition (either cartilaginous or ossified) and in the extent of ossification (either dorsally, ventrally, or medially, in double bronchial elements). Lastly, elements may be fused to one another entirely, along their dorsal or ventral margins, or by a bar of cartilage or bone.

The pessulus is a dorsoventrally oriented bar of cartilage or bone which forms the caudomedial margin of the tracheobronchial junction. Although the pessulus is probably not a single homologous element in all suboscine birds, it is a ubiquitous accessory syringeal supporting element in piprids. The pessulus may be cartilaginous or ossified, and

fused or unfused to other elements dorsally or ventrally.

In all tyrannids and the six genera of pipridlike tyrannoids, the syrinx also includes non-ringlike accessory cartilages in the medial tympaniform membranes, referred to as internal or medial cartilages (Lanyon, 1984a, 1985, 1986, 1988a, 1988c; McKitrick, 1985; Prum, 1990b), but these structures are absent in all true piprid genera described here. Two novel accessory cartilages occur in the piprids, and are evolutionarily independent of those in tyrannids. The paired medial bronchial cartilage bars of *Ilicura, Masius,* and *Corapipo* are dorsoventrally oriented at the cranial margin of the medial tympaniform membrane. Second, *Chiroxiphia* and *Antillophia* have a unique sheet of cartilage which forms the craniomedial walls of the bronchi and the ventral surface of the trachea at the tracheobronchial junction. Some individuals in a number of piprid species have disklike accessory cartilages on the ventral surface of the syrinx at the tracheobronchial junction which are irregularly distributed among and within species. They appear to be anomalies associated with the development of the tracheobronchial junction or the ventral insertion of the syringeal muscles. They were observed irregularly in specimens of several species: *Machaeropterus regulus* (4), *Chloropipo uniformis* (2), *Xenopipo atronitens* (1), *Pipra suavissima* (1), *Pipra mentalis* (2), *Pipra chloromeros* (1), and *Pipra erythrocephala* (1). Examples are illustrated in figures 14, 15, and 24, but they are not mentioned further in the taxonomic descriptions below.

MEMBRANES

As the trachea passes caudally into the thoracic cavity, it enters the interclavicular air sac (Saccus clavicularis) which surrounds the syrinx. The membranes of the syrinx are the connective tissue that comprises the "walls" of the respiratory tract and separate it from the interclavicular air sac. The most prominent syringeal membranes in most passerines are the medial or internal tympaniform membranes (Membrana medialis). They form the craniomedial surfaces of the bronchi and are generally considered to be the sources of sound generation in the tracheobronchial

passerine syrinx (Greenewalt, 1968; Stein, 1968; Gaunt, 1983; Gaunt and Gaunt, 1985; Brackenbury, 1989; Suthers, 1990). A pair of membranes on the lateral surfaces between the supporting elements in some oscines and some nonpasserines are sometimes called the external or lateral tympaniform membranes (Membrana lateralis). They have been hypothesized to be important in sound production in oscines (Chamberlain et al., 1968), but none of the lateral interannular membranes in piprids is drumlike or "tympaniform," so they are not likely to be sound sources during vocalization. In oscines, the lateral tympaniform membrane is located between A1 and 2, and not between A1 and B1, as indicated by Ames (1971: 88).

In many birds, the medial walls of the bronchi are connected by a transverse membrane called the interbronchial ligament (ligmentum interbronchialis) or bronchidesmus. In piprids and most other tyrannoids, the interbronchial ligament is present as a thin sheet of connective tissue between the caudoventral surface of the medial tympaniform membrane and the inner, dorsal surface of the interclavicular air sac on either side of the esophagus. The syrinx is also connected to the dorsal surface of the interclavicular air sac by thin membranous strands. In all piprids, a pair of membranous strands runs between the fused dorsal ends of the B1–2 elements and the interclavicular air sac on either side of the esophagus. In many specimens, these strands contain fibers from the vagus nerve (see Innervation), but they are also present in specimens that apparently lack these vagus nerve fibers. In cotingas and other tyrannoids, these strands are similar in position, but the B1–2 elements are not fused. With one exception, I observed little variation in the syringeal membranes of piprids, so these structures are not included in the syringeal descriptions below. However, a novel patch of fibrous tissue is present on the medial tympaniform membrane in *Pipra cornuta,* and it is described under that species.

MUSCULATURE

Syringeal musculature has been traditionally divided into two categories—extrinsic muscles that originate outside the syrinx and insert on syringeal supporting elements, and intrinsic muscles that originate and insert on the syringeal supporting elements (e.g., Ames, 1971). These categories, however, are frequently artificial since few syringeal muscles classified as "intrinsic" are composed exclusively of fibers originating on syringeal supporting elements.

Alternatively, muscles may also be classified as either tracheal or syringeal, depending on their origins, and each of these classes can then be distinguished into extrinsic and intrinsic subgroups, depending on the site of their insertion (King, 1989). This classification produces needless additional elaboration of essentially arbitrary distinctions by requiring recognition of the limits of the syrinx relative to musculature origins and insertions. Here, I use extrinsic and intrinsic in the former, traditional sense.

The two extrinsic syringeal muscles in passerines are M. tracheolateralis and M. sternotrachealis. In piprids and other tyrannoids, M. tracheolateralis originates on the cricoid cartilage of the larynx and continues caudad on the lateral surfaces of the trachea. In the absence of intrinsic syringeal muscles, M. tracheolateralis inserts on the A1–2 elements near the tracheobronchial junction. M. sternotrachealis originates on the inner surface of the craniolateral process of the sternum and inserts on M. tracheolateralis along the ventral or lateral surface of the trachea, between the tracheobronchial junction and the tracheal anastomosis with the interclavicular air sac.

The intrinsic syringeal muscles of passerine birds are composed of the differentiated caudal fibers of M. tracheolateralis (Ames, 1971). In piprids with intrinsic musculature, M. tracheolateralis inserts completely or partially on some A element(s) cranial to the tracheobronchial junction and immediately gives rise to a belly of partially independent muscle fibers that continue caudad to insert on other, more caudal A elements. Many variations on this general plan occur in piprids, and in only a few instances are these muscles completely "intrinsic"—i.e., entirely independent of M. tracheolateralis fibers. Typically, the deep fibers of M. tracheolateralis and the intrinsic muscles form insertions and origins on the A elements, while the su-

perficial fibers are continuous between the two muscles. However, the partially intrinsic syringeal muscles in piprids are as independent or differentiated from M. tracheolateralis as the intrinsic syringeal muscles in other tyrannoids or in oscines.

Within the guidelines of the existing literature, many of these intrinsic syringeal muscles deserve different names. But intrinsic muscles have apparently evolved independently multiple times within the family and have a variety of forms. In certain species they may be present in males and absent in females and immature males. Using the names applied to intrinsic syringeal muscles of oscines and other tyrannoids would mistakenly imply homology among these evolutionarily independent muscles. Rather than obscure the literature with an additional set of names for these muscular novelties, I will refrain from formal names, and merely refer to them descriptively as left or right, dorsal or ventral intrinsic muscles.

INNERVATION

As in oscines and most other birds, the syrinx of piprids and other tyrannoids is innervated by the left and right tracheosyringeal branches (Ramus syringealis) of the hypoglossocervical nerves (N. hypoglossocervicalis), which are formed by the union of the two roots of the hypoglossal (XII) cranial nerve and the first cervical nerve (fig. 1) (Köditz, 1925; Breazile and Yasuda, 1979; Bubień-Waluszewska, 1981). To my knowledge, the cranial nerves and the syringeal innervation of tyrannoids have not been previously described. My observations of a single specimen of *Pipra coronata* indicate that, unlike oscines and Old World suboscines, the hypoglossocervical nerve in this piprid does not exchange any fibers with either the vagus (X) or the glossopharyngeal (IX) cranial nerves before dividing into the laryngeolingual and tracheosyringeal branches (fig. 1).

From their origin in the laryngeal region, the left and right tracheosyringeal nerves of piprids continue caudad on the lateral surfaces of the trachea imbedded in the fibers of M. tracheolateralis. Typically in piprids, as M. tracheolateralis widens ventrally to cover the entire ventral surface of the trachea, the
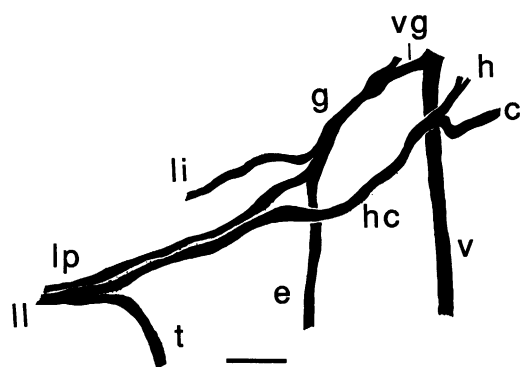
Fig. 1.   Lateral view of the plexus of the glossopharyngeal (IX), vagus (X), and hypoglossocervical (XII + C1) cranial nerves of *Pipra coronata* (UMMZ 225064). The syrinx is innervated by the tracheosyringeal branch of the hypoglossocervical nerve. Unlike the formation in other birds, the hypoglossocervical nerve does not exchange fibers with the vagus or the esophageal branch of the glossopharyngeal nerve. See text for further discussion. Abbreviations: **c** first cervical nerve; **e** esophageal branch of glossopharyngeal cranial nerve; **g** glossopharyngeal (IX) cranial nerve; **h** hypoglossal (XII) cranial nerve; **hc** hypoglossocervical nerve formed by the union of the hypoglossal cranial nerve and the first cervical nerve; **li** lingual branch of the glossopharyngeal cranial nerve; **ll** laryngeolingual branch of the hypoglossocervical nerve; **lp** larnyngeopharyngeal branch of the glossopharyngeal cranial nerve; **t** tracheosyringeal branch of the hypoglossocervical nerve; **v** vagus (X) cranial nerve; **vg** vagus-glossopharyngeal nerve connection. Scale bars in all figures equal 1 mm.

tracheosyringeal nerves veer caudoventrad to form a prominent X-shaped chiasma on the ventral midline of the trachea. The position of this ventral anastomosis varies between A20 and 35. The left and right nerves then continue craniolaterally from the chiasma, return to the lateral midlines of the trachea, and innervate M. tracheolateralis, M. sternotrachealis, and intrinsic syringeal muscles by small branches. This pattern is apparently derived in piprids, but has degraded in *Chloropipo* and *Xenopipo*.

In piprids and cotingids, a small branch of the vagus nerve that originates in the distal vagal ganglion innervates the trachea and bronchi. In piprids, these nerves usually attach to the dorsal ends of the B1 elements in membranous strands of connective tissue
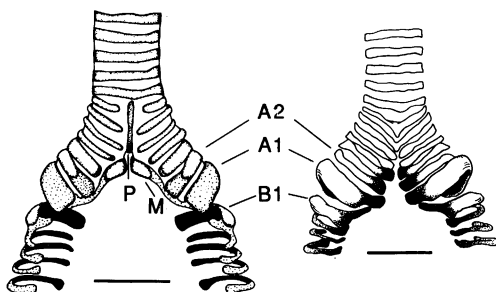
Fig. 2. Syringeal supporting elements of *Corapipo gutturalis* (AMNH 2256). **Left** dorsal view, **right** ventral view. Abbreviations: **A1** A1 supporting element; **A2** A2 supporting element; **B1** B1 supporting element; **P** pessulus; **M** medial cartilage.

which extend from these elements to the dorsal wall of the interclavicular air sac on either side of the esophagus. In some specimens, an additional branch innervates the dorsal surface of the trachea, following the arterial supply to meet the trachea between A8 and 12. Autonomic vagal nerve fibers are probably not involved in voluntary control of vocalization but in the control of mucous secretion in the airway. Köditz (1925) found similar vagal innervation of the syrinx in oscines and Old World suboscines, but Nottebohm and Nottebohm (1976) were unable to locate any vagal syringeal innervation in several oscines. However, these fibers are very small and may have been overlooked. In piprids, I did not find any branches of the esophageal branch of the glossopharyngeal nerve which innervate the M. tracheolateralis, M. sternotrachealis, or the intrinsic syringeal muscles, as reported in some oscine and nonpasserine birds (Köditz, 1925; Breazile and Yasuda, 1979).

SYRINGEAL MORPHOLOGY OF THE PIPRIDS

In each of the following descriptions of the syringeal morphology of piprid species, the supporting elements are described first, proceeding from A elements to the pessulus, other accessory cartilages, and the B elements. All piprid B elements are double and medially incomplete, and will not be described as such below. Unless otherwise indicated, B elements are cartilaginous. Next, the syringeal musculature is described beginning with M. tracheolateralis and any intrinsic muscles present, and ending with M. sternotrachealis. Lastly, the position of the major components of syringeal innervation is described, along with any differences from the typical pattern. In *Pipra cornuta,* a variation in the medial tympaniform membrane is described. The syringes of some species are described in reference to differences from another similar form, but each abbreviated description is only one reference away from a complete one.

Corapipo gutturalis (N = 2)

Supporting elements (fig. 2). A1–5 are double and medially incomplete, and A6–7 are single and dorsally incomplete. A1 is broad and thick; it is ossified for the ventrolateral half, and cartilaginous for the dorsal half and the ventral end. The ossified portion is enlarged or swollen, and tubular in shape. A2–7 are narrower and thinner than A1, and are fully ossified except for the ventral ends of A2–4. A8 and above are single, complete, fully ossified, and unfused. In lateral view, the syrinx conspicuously widens ventrally just caudal to the tracheobronchial junction, as a result of the prominent ventral lengthening of the double, medially incomplete A and B elements. A narrow, ossified pessulus is fused ventrally to A6, and is dorsally free or fused to half of A7 and A8. A1–2 are connected dorsally to partially ossified bars of cartilage that run dorsoventrally along the cranial edge of the medial tympaniform membrane to approach but not fuse to the ventral end of A3. These medial cartilage bars are fully ossified, except for their dorsal tips. B1 is broad, thick, and completely ossified except for its dorsal and ventral ends. The ossified portion of B1 is enlarged or swollen and tubular in shape like A1. All other B's are completely cartilaginous. B1–2 are fused by a short cartilaginous bar just before their dorsal ends, producing small dorsal extensions beyond the fusion from both elements. The ventral end of B1 is a thin cartilaginous bar that extends caudodorsad to the ventral end of A1.

Muscles. Apparently as in *Corapipo leucorrhoa* (fig. 4), but only cleared and stained specimens were observed.

Innervation. Not observed.

Corapipo leucorrhoa (N = 13)

Supporting elements. Like *Corapipo gutteralis* (fig. 2) except as follows: The double A4–6 elements are incomplete medially, but their ossified ventral ends and cartilaginous dorsal ends extend medially to give substantial support to the medial walls of the bronchi. The pessulus is fused dorsally to A8 and ventrally to A7. The medial cartilage bars are thinner and completely cartilaginous. The ventral widening of the syrinx and bronchi caudal to the tracheobronchial junction is even more pronounced than in *C. gutturalis,* though ossified portions of A1 and B1 are less extensive and less swollen.

Muscles (fig. 4). M. tracheolateralis is a robust, well developed muscle; it converges on the ventral midline between A30 and 35, and continues caudally to divide on the ventral midline into left and right halves around A10. It diverges toward the lateral surfaces of the trachea. The left and right halves insert partially on the ventrolateral and lateral surfaces of A6–8. The partial insertion gives rise to dorsal and ventral pairs of oblique intrinsic musculature. Each is distinct in fiber direction but both are partially continuous with M. tracheolateralis fibers. The ventral pair of intrinsic muscles originates on A5–7 on the ventral midline and on A4–5 or A2–4 on the lateral midline. Ventral fibers run directly caudad and the lateral fibers pass obliquely caudoventrad to insert as a fleshy mass of fibers on the cartilaginous ventral end of A1. The dorsal intrinsic musculature originates laterally at A4–5 and its fibers become continuous with those of the M. tracheolateralis dorsally. The fibers run caudodorsad forming a large belly to insert fleshily on the cartilaginous dorsal end of A2. M. sternotrachealis is moderately well developed and inserts broadly on the lateral and ventral surfaces of M. tracheolateralis at A15–20. Most fibers run parallel with the M. tracheolateralis and are assimilated rapidly into it. The ventralmost fibers fan out across the ventral surface of the trachea to insert on the ventral midline and form a conspicuous chevron-shaped insertion with the fibers of M. sternotrachealis of the other side. A few dorsal fibers may insert directly on the tracheal A elements on the dorsal edge of M. tracheolateralis.
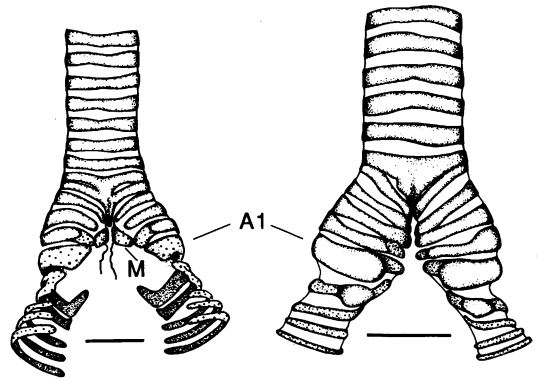
Fig. 3. Syringeal supporting elements of *Masius chrysopterus* (CM 1161). **Left** dorsal view, **right** ventral view. Abbreviations: **A1** A1 supporting element; **M** medial cartilages.

Innervation. Typical piprid pattern. Ventral anastomosis at A20–25.

Masius chrysopterus (N = 9)

Supporting elements (fig. 3). The ventral widening of the syrinx cranial to the tracheobronchial junction is similar to that of *Corapipo,* but not as prominent. A1–4 are double and medially incomplete. A1 is a broad, wide element, which is ossified except for the dorsal quarter and the ventral end. A2–4 are fully ossified except for their cartilaginous dorsal tips and the ventral tips of A2–3. The cartilaginous dorsal tips of A1–2 are weakly fused in one specimen. A5 is single and complete (ventrally incomplete in one specimen). A6 and subsequent A's are single, complete, fully ossified, and unfused. The dorsal ends of A2–3 are fused to a dorsoventrally oriented pair of narrow medial cartilages which form the cranial margin of the medial tympaniform membrane. The wide ossified pessulus is fused dorsally to A5–6 or A6–7 and ventrally to A5 or A6. B1 is ossified heavily for its ventral quarter, and is fused to the cartilaginous B2 dorsally by a short bar. The ventral end of B1 is prominently hooked dorsomedially to rest closely to A1. The ventral end of B2 is a thin, pointed dorsomedial hook. All subsequent B elements are cartilaginous and simply shaped.

Muscles. As in *Corapipo leucorrhoa* (fig. 4) except as follows. The ventral widening of the syrinx is less extreme and, correspond-
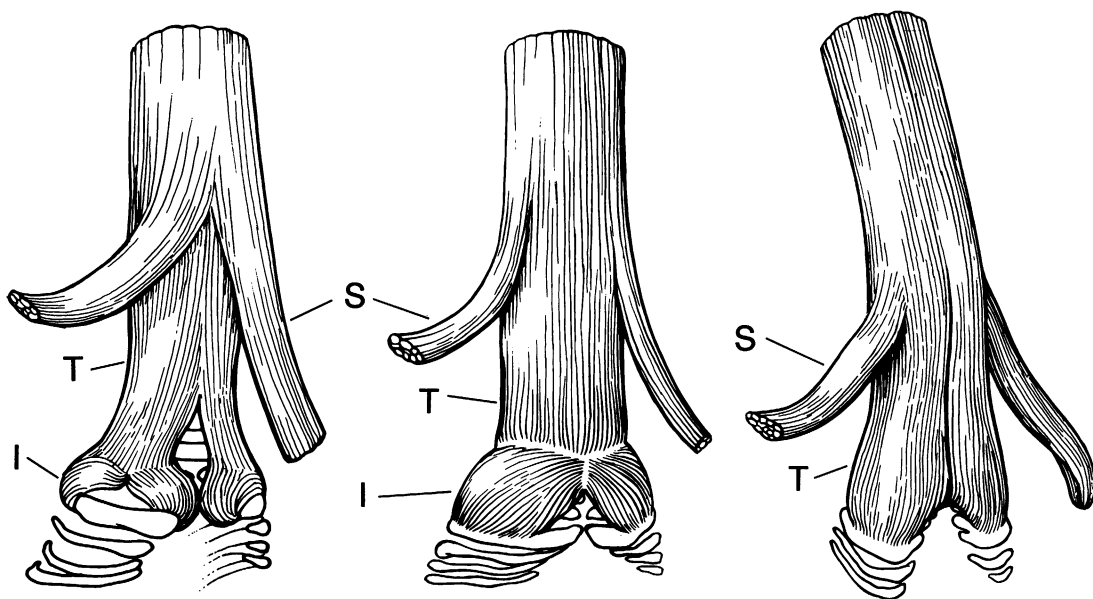
Fig. 4.   Ventrolateral view of syringeal muscles: **left** *Corapipo leucorrhoa* (LSUMZ 108683); **center** *Ilicura militaris* (FMNH 107028); **right** *Manacus manacus* (LSUMZ 112834). Abbreviations: **I** intrinsic syringeal muscles; **S** M. sternotrachealis; **T** M. tracheolateralis.

ingly, the oblique angle of the intrinsic muscle fibers is less exaggerated. M. tracheolateralis is weakly differentiated on the ventral midline near A10, but the two sides do not diverge laterally as in *Corapipo*. Rather, M. tracheolateralis inserts continuously along the lateral and ventral surfaces of A6–7. The insertion of M. sternotrachealis is the same except that it occurs between A10 and 15.

Innervation. Typical piprid pattern, but more well developed and visible than in most other piprids. Ventral anastomosis near A30. Each side sends a separate branch to innervate M. sternotrachealis and the intrinsic musculature.

Ilicura militaris (N = 5)

Supporting elements (fig. 5). A1 is double, medially incomplete, and completely cartilaginous. A2–A6 or A7 are double, medially incomplete, and fully ossified except for the dorsal ends of A2 and the ventral ends of A2–4. A7 or A8 and above are single, complete, fully ossified, and unfused. The pessulus is ossified, free dorsally, and possibly fused ventrally to A5, A6, or A7. A bar of

cartilage lies medial to the dorsal ends of A1 and A2, and is connected to them; it runs cranioventrad along the craniodorsal margin of the medial tympaniform membrane and ends adjacent to the pessulus in the tracheobronchial junction. All B elements are cartilaginous and thin. B1–2 are dorsally fused by a short bar; the dorsal ends of B1 extend slightly beyond the short bar. The ventral ends of B1–2 are thin and pointed, and closely nested to the caudal edge of A1. Subsequent B's are unspecialized in shape.

Muscles (fig. 4). M. tracheolateralis converges on the ventral midline above A35, and continues caudally without division to insert on the ventral and lateral surfaces of A6–7. A few of the dorsal fibers continue caudally to insert with the intrinsic muscles on the dorsal ends of A1. A pair of intrinsic muscles originates on the ventral surface of A4 and the ventrolateral surfaces of A5–6, and continues obliquely caudodorsad to insert on A1 from its dorsal end to the ventrolateral section. M. sternotrachealis is thin and moderately developed, and inserts simply on the lateral surface of M. tracheolateralis at A13–15 (A10–12 on right side of one specimen).
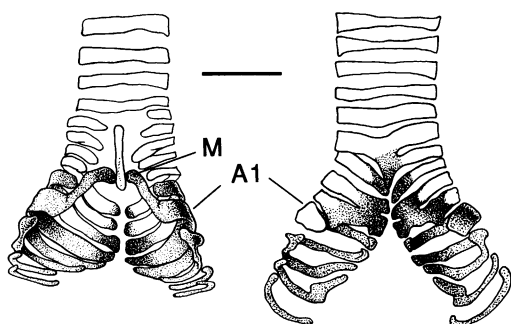
Fig. 5. Syringeal supporting elements. **Left** *Il-icura militaris* (FMNH 102023), dorsal view; **right** *Pipra coeruleocapilla* (FMNH 291664), dorsal view. Abbreviations: **A1** A1 supporting element; **M** medial cartilages.

Fig. 6. Syringeal supporting elements of *Manacus candei* (AMNH 6654). **Left** dorsal view, **right** ventral view. Abbreviation: **A1 + A2** fused A1 and A2 supporting elements.

The musculature of males is well developed whereas female musculature is thin and weakly developed.

Innervation. Typical piprid pattern. Ventral anastomosis near A25.

Manacus manacus (N = 13), *M. vitellinus* (N = 3), and *M. candei* (N = 1)

Supporting elements (fig. 6). A1–2 are double, medially incomplete, and ossified except for their cartilaginous dorsal tips. They are completely fused except for their rounded ventral ends which indicate the line of fusion between the elements. Both A1 and 2 are distinctly rough or grainy in texture unlike all other A's. A1 sometimes has a prominent ventrally flared shelf on its caudal margin. A3–4 are double, medially complete, and ossified except for their medial portions. In one specimen of *M. vitellinus* and the single specimen of *M. candei*, A3 is largely fused to A1–2 in the same manner. The cartilaginous medial sections of A3–4 and the dorsal ends of A1–2 are fused by short cartilaginous connections. The next one to six A elements (A5 alone to A5–10) are single, complete, unfused, and fully ossified except for a short section at the dorsal midline. These dorsal cartilaginous sections are connected by a continuous caudocranial dorsal bar of cartilage. Cranial to the last element in this dorsally cart'laginous series, all A's are single, complete, unfused, and fully ossified. The cartilaginous pessulus is fused dorsally and ven-

trally to A5. All B elements are completely cartilaginous. B1–2 are dorsally fused by a short cartilaginous bar. The ventral ends of B1–3 are angled abruptly craniad into small, squarish extensions at right angles to the cranial margins of the elements. B5–10 or B5–12 are each broader and flatter in cross section than B1–3, and are fused in a continuous cartilaginous lattice formed by their widened dorsal ends. This reinforced lattice provides additional support to the medial bronchial walls and the medial tympaniform membranes.

Muscles (fig. 4). M. tracheolateralis converges on the ventral midline at A30 to cover the entire ventral surface of the trachea. The muscle continues caudad but is weakly united along the ventral midline. It differentiates completely into left and right halves on the ventral midline at A12. These halves do not diverge laterally from one another, but continue caudad as adjacent muscle masses. Both sides insert by a thin sheet of connective tissue on A3 at the ventral midline and spiral caudodorsad to the ventrolateral surfaces of A2, and the lateral and dorsolateral surface of A1. The connective tissue sheet is continuous between the left and right sides across the ventral midline, even though the fibers of the left and right muscles are completely distinct. In males, M. tracheolateralis is a very robust and thick muscle with a prominent, but completely extrinsic belly caudal to the
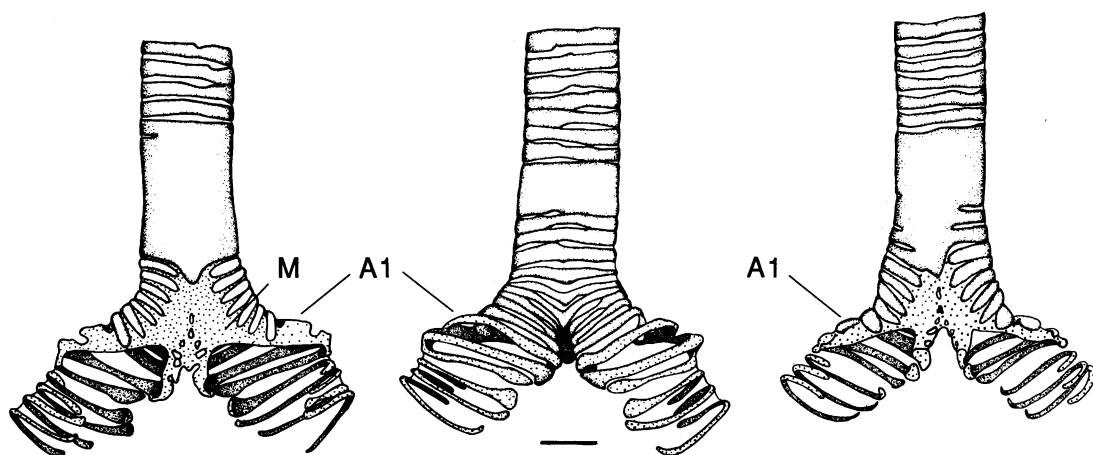
Fig. 7. Syringeal supporting elements: *Chiroxiphia caudata* (AMNH 2447), **left** dorsal view, **center** ventral view; *Antilophia galeata* (BMNH 1968.62.205), **right** dorsal view. Abbreviations: **A1** A1 supporting element; **M** medial cartilage.

lateral division at A12. In females, the muscle is the same in form but thin and weakly developed. M. sternotrachealis is a moderately well developed muscle and inserts on the dorsolateral surface of M. tracheolateralis at A11–13. Its fibers are incorporated rapidly into M. tracheolateralis.

Innervation. Usually the typical piprid pattern is present. The ventral anastomosis is near A30, and large branches innervate M. tracheolateralis and M. sternotrachealis caudally. In one specimen, the nerve continues caudad on the ventral midline as a single fiber for 1 mm before dividing again into left and right branches.

Chiroxiphia linearis (N = 7), *C. lanceolata* (N = 1), *C. pareola* (N = 10), and *C. caudata* (N = 7)

Supporting elements (fig. 7). The bronchi are prominently flared laterally and ventrally so that the medial surfaces are exposed in dorsal view. The trachea becomes increasingly widened toward the tracheobronchial junction caudal to a series of fused single A elements that form a tracheal drum. The structure of A elements can be described as five series of distinct element types. The specific A elements that comprise each series vary slightly among and within species (table 1). In all *Chiroxiphia*, the first series is made

of the A1 elements alone, which are double, medially incomplete, and cartilaginous. A1 is wide and indented craniad on the caudoventral margin. All other A elements are fully ossified. The second A series is composed of the next two to five A elements which are double, medially incomplete, unfused, and narrower than A1. The third series is composed of two or three A elements cranial to the second series which are single, ventrally fused, and dorsally incomplete. The fourth series is composed of between six and nine A elements which are fused together to form a prominent tracheal drum. The caudal one or two of the elements in the drum are typically completely fused dorsally and only partially fused ventrally, whereas the cranial elements in the series are entirely fused. The fifth series of A elements is made of the rest of the tracheal A's which are single, complete, unfused, and fully ossified. The A elements that comprise each of these series in the four species of *Chiroxiphia* are presented in table 1. The dorsal and ventral ends of the second series of A elements, the dorsal ends of the third A series, and the caudoventral margin of the drum are connected by a sheet of cartilage that forms the craniomedial surfaces of the bronchi and the dorsal surface of the tracheobronchial junction. The caudal margin of the cartilage sheet is indented craniad between its connections to the dorsal and

TABLE 1
Elements Comprising the Five A Element Series in *Chiroxiphia* and *Antilophia*

Species	A element series[a]				
	I	II	III	IV	V
Chiroxiphia linearis	1	2–5	5–8	8–15	14–16+
Chiroxiphia lanceolata	1	2–3	4–5	6–13	14+
Chiroxiphia pareola	1	2–4	5–8	7–14	14–15+
Chiroxiphia caudata	1	2–5	5–8	8–17	14–18+
Antilophia galeata	1	2–5	6–7	8–14	15+

[a] The five A element series are described in the text under the supporting elements of *Chiroxiphia* and *Antilophia*. The range of elements found in each A series in each species is given.

ventral ends of the first A elements, and it forms the cranial margin of the medial tympaniform membrane. A1 is fused dorsally to A2 and the caudolateral corner of the accessory cartilage sheet by a bar of cartilage. A1 and B1 are also fused by a thin cartilaginous bridge which has a small square projection on its craniolateral edge between the two elements. All B elements are cartilaginous. B1–2 are dorsally fused by a narrow cartilage strip. The ventral ends of B1–3 are widened and roundly angled dorsomedially. The ventral end of B1 is closely nested next to the ventral end of A1.

Muscles (fig. 8). M. tracheolateralis widens ventrally to cover the entire ventral surface of the trachea above A35–40, and continues caudally in a thin, weakly developed sheet of fibers to insert partially on the ventral and lateral surfaces of the A elements at the cranial margin of the drum (A13–17). The intrinsic musculature originates on the cranial portion of the drum. It is largely continuous with the fibers of M. tracheolateralis, and is weakly differentiated into dorsal and ventral portions from the origin. The ventral portion of the intrinsic muscle forms a large, prominent belly of fibers on the ventral and lateral surfaces of the trachea. The left and right sides are differentiated laterally on the ventral midline from origin to insertion, but they run parallel and adjacent to one another. This mass of muscle fibers attenuates rapidly at A5 on the ventral midline and A2 laterally, and each side inserts by a sheet of connective tissue that is attached to A4–5 at the ventral midline and spirals caudolaterally to insert on A3 and A2 on the lateral surface of the trachea. The connective tissue is continuous between the left and right sides across the ventral midline. In *pareola,* the muscle attenuates in the same manner and inserts by a connective tissue sheet on A4 on the ventral midline, but the sheet extends caudad to insert on the ventral end of A2 just lateral to the ventral midline on both sides, instead of spiraling caudally along the entire lateral surface as in *linearis* and *caudata.* The dorsal portion of the intrinsic musculature is composed of fibers that are continuous with M. tracheolateralis and the ventral intrinsic muscle, and of other fibers that originate directly on the A elements at the cranial margin of the drum. These dorsal intrinsic fibers originate in a broad fan on the most cranial elements of the drum at the dorsal edge of M. tracheolateralis and on the dorsolateral surfaces of the next three or four drum elements. The dorsal intrinsic musculature is continuous laterally with the ventral intrinsic fibers, but forms a distinct intrinsic belly on the dorsolateral surface of the trachea. The deep fibers insert with the ventral intrinsic belly by a connective tissue sheet on the dorsal ends of A2, but the more superficial fibers insert by a short, narrow strip of connective tissue to the dorsal end of A1. M. sternotrachealis is a thin and weakly developed muscle that inserts on the dorsal edge of M. tracheolateralis just cranial to its partial insertion at the cranial margin of the drum and to the origin of the dorsal intrinsic musculature. Fibers of M. sternotrachealis insert directly on the dorsalmost M. tracheolateralis fibers and on the tracheal A elements. The musculature of females is similar in form to that of males
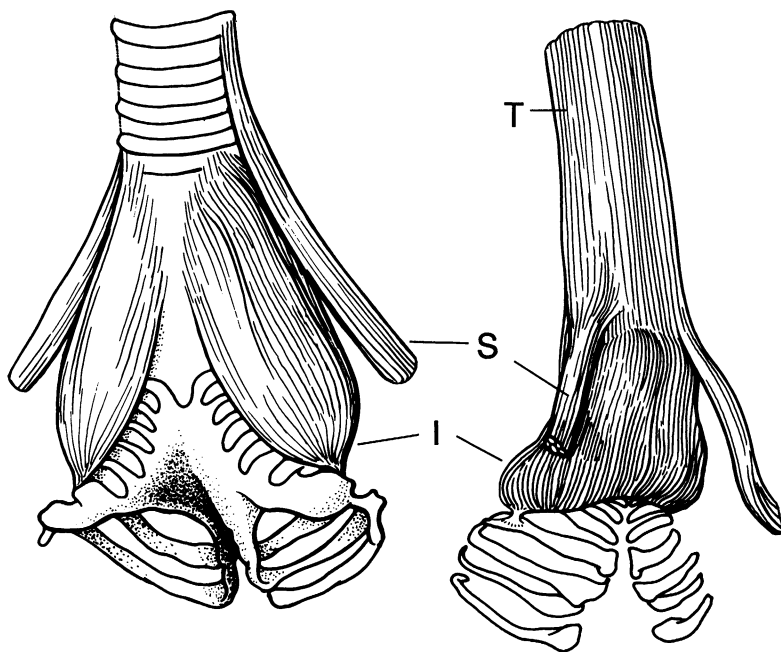
Fig. 8.   Syringeal muscles of *Chiroxiphia caudata* (FMNH 107323): **left** dorsolateral view, **right** ventrolateral view. Abbreviations: **I** intrinsic syringeal muscles; **S** M. sternotrachealis; **T** M. tracheo-lateralis.

but less well developed. The musculature of *lanceolata* is the same in general form, but no uncleared specimens were observed to document the details of the ventral intrinsic muscular insertion.

Innervation. All but four specimens (one each of *linearis* and *pareola,* and two of *caudata*) differ from typical piprid morphology. The left and right tracheal nerves converge on the ventral midline at A20–30, and continue caudad as a single large fiber along the ventral midline for 0.8 mm to more than 6.0 mm, before dividing once again into left and right branches that innervate the intrinsic muscles and M. sternotrachealis of each side. The three other specimens have the typical piprid pattern with a brief anastomosis.

Antilophia galeata (N = 6)

Supporting elements (fig. 7). Very similar to those of *Chiroxiphia.* The A elements form five series with the same characteristics including an extensive tracheal drum and medial bronchial cartilage sheet. The five series of A elements are composed of A1 (double,

medially incomplete, cartilaginous), A2–5 (double, medially incomplete, ossified), A6–7 (single, dorsally incomplete), A8–14 (single, fused into a drum), and A15 and above (single, complete, unfused). As in *Chiroxiphia,* A1 and all B's are cartilaginous, and all other A's are ossified. The syrinx of *Antilophia* differs from that of *Chiroxiphia* in that the elements of the second A series are wider than those of *Chiroxiphia* and more similar in shape to A1. Also, the cartilaginous dorsal bridge between A1 and B1 is shorter and lacks the square projection on its craniolateral margin found in *Chiroxiphia.*

Muscles. Generally as in *Chiroxiphia* (fig. 8). The ventral intrinsic muscles originate on A14 and insert spirally on A5 to A2; the dorsal intrinsic muscles are continuous with the ventral intrinsic fibers laterally, but they originate independently on the dorsal surface of A12–14 and insert on the dorsal end of A1 by a narrow tendon. M. sternotrachealis is more well developed than in *Chiroxiphia,* and inserts on the lateral surfaces of M. tracheolateralis and the trachea at A15–17.

Innervation. Four specimens have the dis-

tinct *Chiroxiphia* pattern in which left and
right tracheosyringeal nerves unite into a sin-
gle large fiber before innervating the intrinsic
muscles and M. sternotrachealis. One speci-
men has the typical piprid pattern of a simple
nerve anastomosis.

Machaeropterus regulus (N = 8)

Supporting elements (fig. 9). A1–2 are dou-
ble and medially incomplete. A1 is arched
cranially at the lateral midline and is carti-
laginous except for a small ossified oval near
the ventral end of the element (about a sixth
to an eighth of the entire element). A2 is fully
ossified except for its cartilaginous dorsal and
ventral tips. A3–4 are double, medially com-
plete, and generally ossified except for the
medial cartilaginous portions; one side of A4
is continuous dorsally with the pessulus in
all specimens. A5–6 are single and ossified,
but dorsally cartilaginous or incomplete. A7
and subsequent A elements are single, com-
plete, and fully ossified. The pessulus is fused
ventrally to A5 and is attached dorsally to
the dorsal tips of A4–6 or A5–6, and to the
ossified dorsal portion of A7. All B elements
are entirely cartilaginous. B1–2 are fused dor-
sally by a bar of cartilage. In most specimens
(N = 6 of 8), B3 is also dorsally fused to B1–
2 in the same manner. The ventral ends of
B1–3 are widened slightly and roundly turned
dorsad. The ventral end of B2 is a unique,
symmetrical spoon shape, and the distortion
of B3 is slight. All subsequent B elements are
thin and simple in shape.

Muscles (fig. 12). There is substantial vari-
ation in the degree of intrinsic differentiation
of the caudal portions of M. tracheolateralis.
The left side of M. tracheolateralis is much
more developed than the right, and it con-
tributes all of the fibers on the ventral surface
of the trachea. In both sexes the ventral sheet
of fibers divides on the ventral midline at
A10, and the left and right halves diverge
toward the lateral surfaces of the trachea. In
females, each side divides into dorsal and
ventral extrinsic portions on the lateral mid-
line at A2–4; the dorsal branch inserts just
lateral to the dorsal end of A1, and the ventral
portion passes obliquely caudoventrad to in-
sert on the ventral end of A1. In males, the
M. tracheolateralis is more well developed
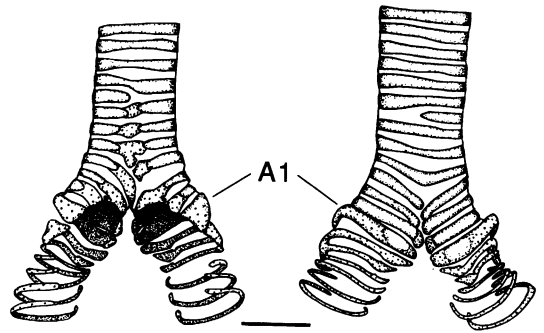
Fig. 9. Syringeal supporting elements of *Ma-
chaeropterus regulus* (LSUMZ 85891). **Left** dorsal
view, **right** ventral view. Abbreviation: **A1** A1
supporting element.

and partially inserts on A5 to produce in-
trinsic muscles. In one male, the left and right
sides partially insert on A5, and give rise to
partially intrinsic muscles that are mostly
continuous with M. tracheolateralis fibers, but
have some fibers originating on A4–5. In the
other male specimen, each side of M. tra-
cheolateralis inserts on the lateral surface of
A5. An intrinsic muscle originates on the dor-
sal margin of the M. tracheolateralis on A6–
9 and its fibers pass obliquely caudoventrad
over the insertion of M. tracheolateralis to
insert on the ventral end of A1. A few fibers
are continuous with the dorsalmost fibers of
M. tracheolateralis at A9, and some ventral
fibers of this muscle originate on A5 at the
ventral edge of M. tracheolateralis. Another
completely intrinsic muscle originates on the
dorsolateral surface of A5 and the lateral sur-
face of A4, and its fibers pass dorsoventrad
to insert on the third of A1 just dorsal to the
lateral midline. These two intrinsic muscles
are similar in fiber direction to the ventral
and dorsal extrinsic portions of M. tracheo-
lateralis in females, but have different origins
at least partially independent of this muscle.
The left M. sternotrachealis inserts on the left
ventrolateral and lateral surfaces of M. tra-
cheolateralis at A10–15, and the right side
inserts on the ventrolateral surfaces of M.
tracheolateralis and directly on the lateral
surfaces of the tracheal A elements at A10–
15. In females, M. sternotrachealis is weakly
developed and ribbonlike, but in males it is
a well developed muscle. The particularly
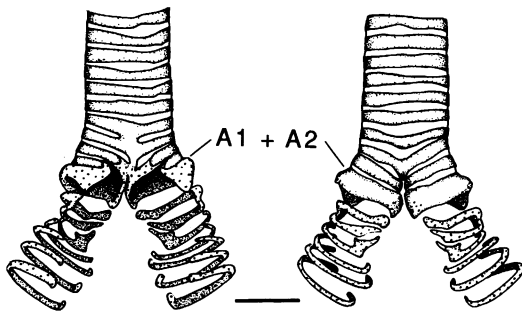
Fig. 10. Syringeal supporting elements of *Machaeropterus deliciosus* (AMNH 8713). **Left** dorsal view, **right** ventral view. Abbreviation: **A1 + A2** fused A1 and A2 supporting elements.
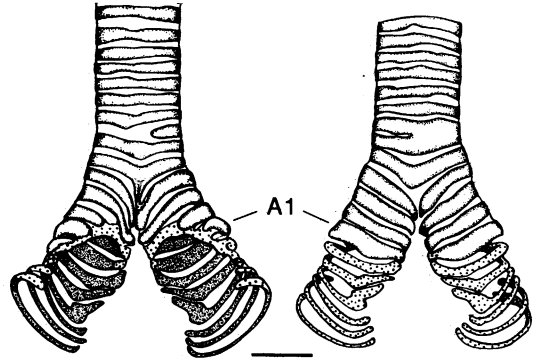
Fig. 11. Syringeal supporting elements of *Chloropipo holochlora* (KU 65552). **Left** dorsal view, **right** ventral view. Abbreviation: **A1** A1 supporting element.

large left side contributes a large volume of fibers to the mass of M. tracheolateralis.

Innervation. Typical piprid pattern. Ventral anastomosis at A20–25. A separate branch innervates M. sternotrachealis.

Machaeropterus pyrocephalus (N = 11)

Supporting elements. As in *M. regulus* (fig. 9) except as follows. A1–2 are fused for the short ventral section where A1 is ossified. There are no dorsally cartilaginous tracheal A elements. The lateral portion of A1 is not arched craniad. B3 is not dorsally fused to B1–2. The ventral ends of B1–3 are slightly widened, paddle shaped, and angled craniodorsad. All three are more distorted in shape than in *regulus*.

Muscles. The left side of M. tracheolateralis is much more developed than the right. The two sides converge on the ventral midline above A25, and the left side contributes most of the fibers that continue caudad on the ventral surface of the trachea. This sheet of fibers divides weakly on the ventral midline at A8–10 into separate left and right halves that continue caudad to diverge completely at A2 or A3. All fibers insert just lateral to the dorsal and ventral ends of A1. The muscle may be developed into strong bellies caudally, but is weakly differentiated laterally in three specimens. The left M. sternotrachealis inserts on the lateral surface of the M. tracheolateralis between A8 and 12, and is very well developed. The right M. sternotrachealis inserts on the ventral surface of M. tracheolateralis and on the lateral surface of

A8–12, because of the reduced fibers of the right M. tracheolateralis.

Innervation. Typical piprid pattern as in *M. regulus*.

Machaeropterus deliciosus (N = 6)

Supporting elements (fig. 10). A1–2 are double, medially incomplete, and fused together for the ventral two-thirds and at the dorsal ends. A1 is ossified for the ventral half (except for the tip) and cartilaginous for the dorsal half. A2 is completely ossified except for the dorsal tips. The cartilaginous ventral tip of A1 projects caudad from the caudoventral extremity of the fused A1–2 element. A3 or A3–4 are double, complete, and generally ossified but medially cartilaginous. A5 or A4–5 are single, complete, and fully ossified. In one specimen, A4–5 are dorsally fused to one another. A6 and subsequent A's are single, complete, fully ossified, and unfused. A cartilaginous pessulus is fused dorsally and ventrally to A4. All B elements are completely cartilaginous. B1–2 are dorsally fused by a short cartilaginous bar. The ventral ends of B1–3 are widened, paddle-shaped, angled craniad, and nested together. The cranial edge of these paddle-shaped elements is additionally distorted by a caudal concavity. All other B elements are simple in shape.

Muscles. M. tracheolateralis is thin and weakly developed in both males and females. It covers the ventral surface of the trachea caudal from A30, but in all specimens the
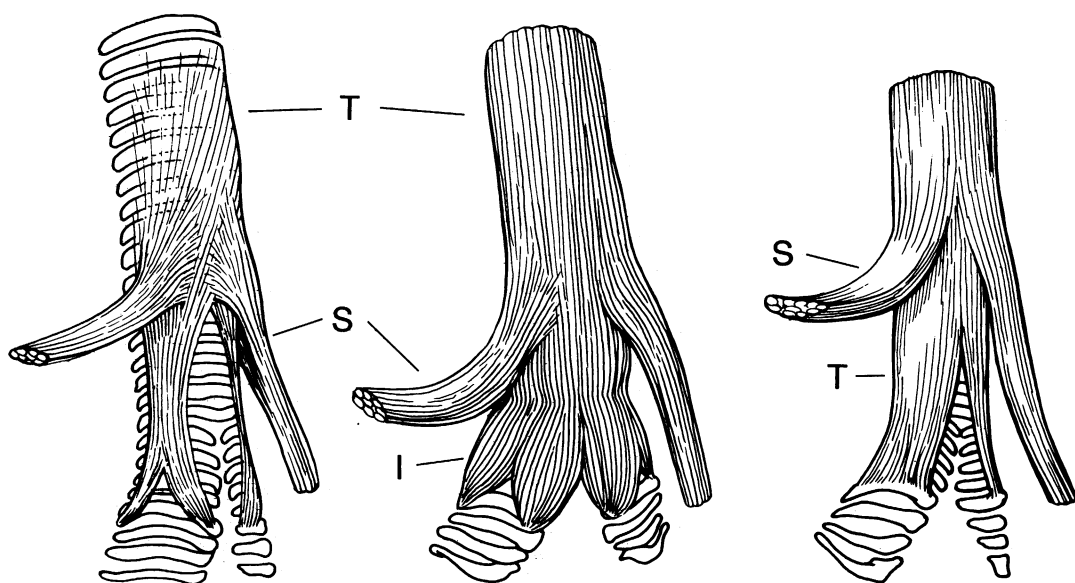
Fig. 12. Ventrolateral view of syringeal muscles: **left** *Machaeropterus regulus* (LSUMZ 114486), **center** *Chloropipo holochlora* (UMMZ 225050), **right** *Pipra coeruleocapilla* (USNM 512291). Abbreviations: **I** intrinsic syringeal muscles; **S** M. sternotrachealis; **T** M. tracheolateralis.

right side is much less developed or almost absent, and the left side contributes most of the fibers to the sheet of M. tracheolateralis. The thin sheet of muscle continues caudad and divides into left and right halves on the ventral midline at A7–8, before inserting on the ventral half of A1. M. sternotrachealis is a thin, ribbonlike muscle, and it inserts simply on the lateral portions of the M. tracheolateralis at A10–12.

Innervation. Typical piprid pattern. Nerve fibers minute. Ventral anastomosis at A20.

Chloropipo holochlora (N = 11)

Supporting elements (fig. 11). A1–2 are double, medially incomplete, and completely ossified. The cartilaginous extensions of the dorsal ends of A2 connect to A3. A3–4 are double, complete, and fully ossified, and their medial portions are straight instead of rounded. A5 and subsequent elements are single, complete, and fully ossified. These single elements are fused dorsally by a wide ossified bar between elements. This partial drum is made up of A5–6 (N = 4), A5–7 (N = 4), or A5–8 (N = 2). In one of these last specimens, the elements composing the drum are exten-

sively fused along their dorsal margins. A thin, ossified pessulus is fused dorsally and ventrally to A5. All B elements are completely cartilaginous. B1–2 are robust and dorsally fused by a short cartilaginous bar. The ventral ends of B1–3 are widened, angled dorsomedially, and closely nested together. Subsequent B elements are fused and unspecialized in shape. The shape of the ventral ends of B3 varies within the sample between nominate *holochlora* from Amazonian Ecuador and *litae* from the Pacific slope of Ecuador. In nominate *holochlora,* the ventral end of B3 is smaller, rounded caudally, and more strongly angled than in *litae,* which resembles other piprids more closely. An additional aberrant cleared-and-stained specimen from Amazonian Ecuador differs markedly from the rest of the sample (fig. 11). A3–4 are not straight medially, and the left A2 is cartilaginously complete medially. No tracheal A elements are fused, and the ventral ends of B3 are different in shape from those of all other specimens. This specimen may either indicate significant intraspecific variation, or be the result of hybridization or misidentification, but requires further investigation.

Muscles (fig. 12). The left and right Mm.

Fig. 13. Syringeal supporting elements of *Chloropipo unicolor* (LSUMZ 89472). **Left** dorsal view, **right** ventral view. Abbreviation: **A1** A1 supporting element.

tracheolaterales widen to cover the ventral surface of the trachea between A30 and 40. The fibers continue caudad until a slight constriction in muscle mass and a partial insertion on A8–9, where the muscle gives rise to left and right partially intrinsic muscles. The left and right bellies divide into dorsal and ventral intrinsic muscles on the lateral midline between A4 and 8. The dorsal portions are composed of lateral fibers that are continuous with M. tracheolateralis and, in some specimens, additional, completely independent fibers that originate on the lateral and dorsolateral surfaces on A4–8. The dorsal and ventral intrinsic muscles insert on the dorsal and ventral ends of A1. M. sternotrachealis is a well-developed muscle that inserts directly on the lateral fibers of M. tracheolateralis between A14 and 17. Female syringeal musculature is the same in general form as in males but less developed, and the dorsal intrinsic muscle is completely continuous with the fibers of the M. tracheolateralis.

Innervation. The tracheosyringeal nerve fibers are generally thin or degenerate. The small left and right fibers wander irregularly across the ventral surface of the trachea and exchange small secondary fibers at various points between A10 and 30. Small caudal fibers innervate the dorsal intrinsic musculature.

Chloropipo unicolor (N = 7)

Supporting elements (fig. 13). All A elements are fully ossified. A1–2 are double, and medially incomplete. A3–4 are double and complete. A5 and above are single and com-

plete. A5–7 are fused dorsally. The dorsal portion of A5 is chevron-shaped and extends medially to form the thin ossified pessulus which is fused ventrally to A5. A1–7 are closely fitted next to one another; the caudal edges of the double A elements, especially A1–2, are larger in diameter than the cranial edges, so that the bronchi widen laterally, giving the syrinx a unique inverted funnel shape. The B elements are very thin and the shapes of the ventral ends of B1–3 are unique. B1–2 are dorsally fused by a short bar of cartilage, but all other B's are unfused. B1 is larger in diameter than A1, resulting in a conspicuous gap between the elements. The ventral half to one-third of B1 is ossified, and its thin ventral end curves dorsomedially to approach the ventral end of A1. The ventral end of B2 angles dorsomediad, and is lightly ossified. The extreme ventral tip of B3 abruptly angles craniad 90° to nest close to B2. All subsequent B's are unspecialized in shape.

Muscles. Similar to those of *Chloropipo holochlora* (fig. 12). M. tracheolateralis covers the ventral surface of the trachea above A30, and continues in an undivided sheet to insert partially on the ventral and lateral surfaces of A6–7. These fibers are continuous with the intrinsic musculature that originates as a laterally differentiated pair at A6. The intrinsic muscles continue caudad and divide into dorsal and ventral bellies on the lateral midline at A4. These four muscles insert broadly on the ventral and dorsal thirds of A1. M sternotrachealis is well developed and inserts on the lateral and ventrolateral fibers of the M. tracheolateralis between A17 and 22. A few fibers insert directly on A17–22 at the dorsal edge of M. tracheolateralis. In females, the musculature is very thin and undeveloped, but in males it is well developed and robust.

Innervation. As in *Chloropipo holochlora.*

Chloropipo uniformis (N = 7)

Supporting elements (fig. 14). A1–2 are double, medially incomplete, and completely ossified. The caudal margin of A1 tapers narrowly toward the ventral end of the element. A3 is double, complete, and fully ossified. A4 is single but ventrally incomplete in at least
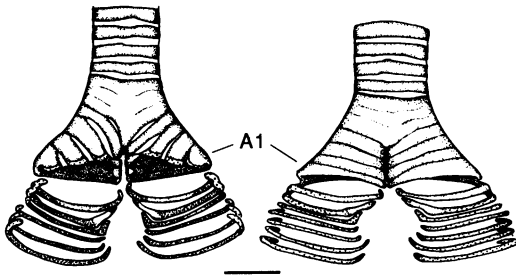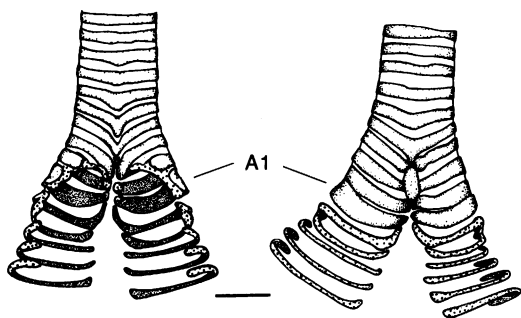
Fig. 14.   Syringeal supporting elements of *Chloropipo uniformis* (AMNH 7680). **Left** dorsal view, **right** ventral view. Abbreviation: **A1** A1 supporting element.
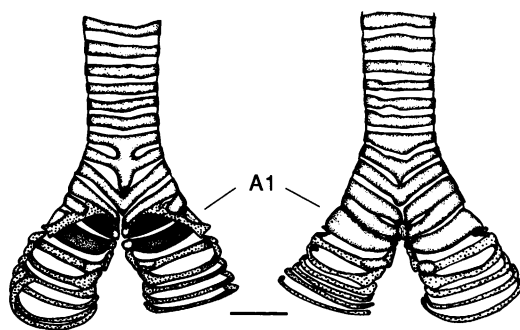
Fig. 15.   Syringeal supporting elements of *Xenopipo atronitens* (AMNH 8083). **Left** dorsal view, **right** ventral view. Abbreviation: **A1** A1 supporting element.

one specimen. The obliquely aligned left and right halves of A4 are fused dorsally in a prominent chevron shape, which extends medially to form the pessulus. A5 and subsequent A's are single, complete, and completely ossified. A5 has an ossified caudal projection on the dorsal midline that extends caudad into the area just craniad to the margins of the chevron-shaped A4 element. All B1 elements are completely cartilaginous. B1–2 are dorsally fused by a broad cartilaginous bar; all other B's are unfused. The ventral end of B1 is slightly widened and roundly curved craniomediad. The ventral end of B2 is widened asymmetrically. The caudal margin is straight, but the cranial margin flares craniad giving the B2 element a lopsided spatulate ventral end. B3 and subsequent B's are unspecialized in shape.

Muscles. Similar to those of *Chloropipo holochlora* (fig. 12). M. tracheolateralis is a moderately developed and uniform muscle that expands to cover the ventral surface of the trachea near A35. The fibers continue caudad and divide into left and right halves at A8–10. The left and right halves insert discontinuously on the lateral and ventrolateral surfaces of A5–6, and then give rise to the intrinsic musculature. These partially intrinsic muscles divide on the lateral midlines at A2 to insert on the dorsal and ventral ends of A1. M. sternotrachealis is moderately developed, and inserts on the lateral surface of M. tracheolateralis from A10–14. A few dorsal fibers insert directly on A10–13 at the dorsal edge of M. tracheolateralis. Muscula-

ture is well developed in males and thin in females.

Innervation. Nerve fibers not visible in most specimens. One male specimen has the typical piprid pattern with the ventral anastomosis at A25.

Xenopipo atronitens (N = 7)

Supporting elements (fig. 15). As in *Chloropipo uniformis* except as follows: A4 ventrally incomplete in at least one specimen. A5–6 (N = 4), A4–5 (N = 1), or A5–7 (N = 1) are fused dorsally by an ossified bar. A3 is medially incomplete on one side in one specimen. The ventral end of B1 abruptly turns dorsomediad with a distinct protruding corner on the ventral extreme of the element. The center of the ventral end of B1 is ossified. B1 is more abruptly angled than in *C. uniformis.* B2–3 are asymmetrically spatulate like B2 of *C. uniformis.*

Muscles. Similar to those of *Chloropipo holochlora* (fig. 12). Musculature is well developed and robust in the male specimens observed. It is similar to *C. uniformis* except as follows. M. tracheolateralis does not diverge ventrally before its insertion on A6 and the origin of the intrinsic musculature. The intrinsic muscles are differentiated laterally from their origin; they are more weakly differentiated dorsoventrally than in *uniformis* or *unicolor,* and divide at A2 to insert on the ventral and dorsal ends of A1. M. sternotrachealis is well developed and inserts on the lateral and ventrolateral fibers of M. tracheo-
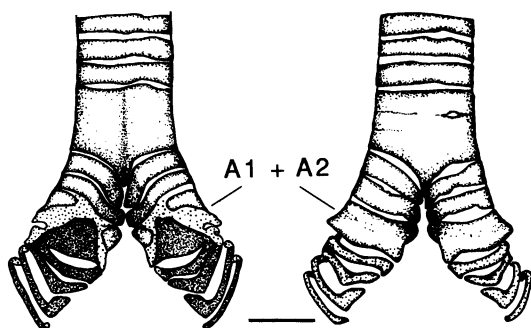
Fig. 16.   Syringeal supporting elements of *Heterocercus flavivertex* (AMNH 15204). **Left** dorsal view, **right** ventral view. Abbreviation: **A1 + A2** fused A1 and A2 supporting elements.

lateralis between A10 and 15. The ventralmost fibers insert on the ventral midline in a chevron pattern.

Innervation. Not well developed and difficult to see in most specimens. Main fibers anastomose on the ventral midline at A25, but secondary fibers on both sides continue directly caudad connecting the main fibers above and below the anastomosis.

Heterocercus flavivertex (N = 7) and
H. linteatus (N = 3)

Supporting elements (fig. 16). A1 is double, medially incomplete, ossified for the ventral two-thirds, and cartilaginous for the dorsal third. A2 is double, complete, and mostly ossified but medially cartilaginous. The cartilaginous medial portions of A2 are variable in extent. A1–2 are fused for the ventral two-thirds and at their dorsal ends. A3–4 are double, complete, and fully ossified; their medial portions are quite straight rather than rounded. A5–7 are single, complete, ossified, and fused into a partial drum (A5–8 in one *flavivertex* and one *linteatus*). The fusion of the elements at the dorsal midline is complete, and the entire dorsal margins of the elements are partially fused, but the presence of an ossified dorsal bar is still detectable. A8 and above are single, fully ossified, and unfused. The pessulus is ossified, wide dorsally, and fused dorsally and ventrally to A5. All B elements are cartilaginous. B1–2 are dorsally fused by a short cartilaginous bar. B1 is slightly widened at its ventral end, and B2–3 are

widened and angled dorsomedially at their ventral ends. B4 and subsequent elements are unfused and unspecialized in shape.

Muscles. M. tracheolateralis covers the entire ventral surface above A30 in a well developed, undivided sheet, and it inserts continuously on the ventral and lateral surfaces of the cranial margin of the drum at A7–8. The left and right intrinsic muscles are laterally differentiated on the ventral midline from their origin just caudal to this partial insertion. They form prominent bellies of fibers and insert along the entire surface of A1 without dorsoventral differentiation. M. sternotrachealis is a robust muscle that inserts on the ventrolateral and lateral surfaces of M. tracheolateralis at A11–14. The ventral fibers fan out cranioventrad across the ventral surface of the trachea to meet the fibers of the other side on the ventral midline. A few of the dorsal fibers also insert on the tracheal A elements at the dorsal margin of M. tracheolateralis. The musculature is less massive in female specimens but the intrinsic muscles are still completely developed.

Innervation. Typical piprid pattern. Ventral anastomosis at A18–25.

Pipra coronata (N = 11), *P. isidorei* (N = 1),
P. coeruleocapilla (N = 7), *P. nattereri*
(N = 8), and *P. iris* (N = 6)

Supporting elements (fig. 5). A1–2 are double and medially incomplete. A1 is completely cartilaginous, and A2 is ossified with cartilaginous dorsal and ventral tips. A3–4 are double, complete, and ossified except for the medially cartilaginous sections. A3–4 are partially ossified medially in *iris* and most *nattereri*. The cartilaginous medial portions of A3–4 are partially fused in *isidorei, iris, nattereri,* and two of six specimens of *coronata*. The cartilaginous ends of A2 extend medially and fuse to the medial portions of A3 in *coeruleocapilla*. A5 and subsequent elements are single, complete, and usually entirely ossified. In two specimens of *coronata,* A5 is dorsally cartilaginous, and in one specimen A5–6 are dorsally cartilaginous. All subsequent A elements are single, complete, and entirely ossified. A thin cartilaginous pessulus is fused dorsally and ventrally to A5 (fused dorsomedially to one A4 in one spec-

imen of *coronata*). In three specimens of *iris* and most *nattereri*, the pessulus is partially or mostly ossified. All B elements are entirely cartilaginous. B1 and B2 are fused dorsally by a short cartilaginous bar. The ventral ends of B1–3 are widened, paddle-shaped, and angled craniad. B3 is the most exaggerated in shape. The ventral ends of B1–3 of *P. coronata* are less specialized in shape than the other species. Subsequent B elements are thin and unspecialized in shape.

Muscles (fig. 12). M. tracheolateralis widens ventrally to cover the entire ventral surface of the trachea by A25, and continues caudally in a thin sheet of fibers to divide into left and right halves at A7–10. The left and right extrinsic muscles generally insert as a single continuous sheet of fibers from the ventrolateral to dorsolateral surfaces of A1. In three of six *coronata* and two of seven *coeruleocapilla,* M. tracheolateralis divides on the lateral midline at A2–4 into two weakly differentiated dorsal and ventral groups of fibers which insert on the dorsolateral and ventrolateral surfaces of A1. This dorsolateral differentiation is produced by the underdevelopment of the lateral fibers rather than by the development of separate dorsal and ventral groups of fibers. There are no prominent bellies in the M. tracheolateralis before insertion. M. sternotrachealis is moderately well developed and inserts directly on the lateral and ventrolateral surfaces of M. tracheolateralis. The insertion varies in extent from A9–15 to A12–18. A few of the dorsalmost fibers of M. sternotrachealis usually insert directly on the A elements at the dorsolateral margin of the M. tracheolateralis. In two of five *coronata,* the left M. sternotrachealis is more strongly developed than the right, but in general there is limited asymmetry in syringeal musculature in these species.

Innervation. Typical piprid pattern. Ventral anastomosis between A25 and 30.

Pipra suavissima (N = 6)

Supporting elements (fig. 17). A1–2 are double and medially incomplete. A1 is cartilaginous and arched craniad along its lateral portions. Its caudoventral margin tapers craniad. A2 is ossified except for its cartilag-
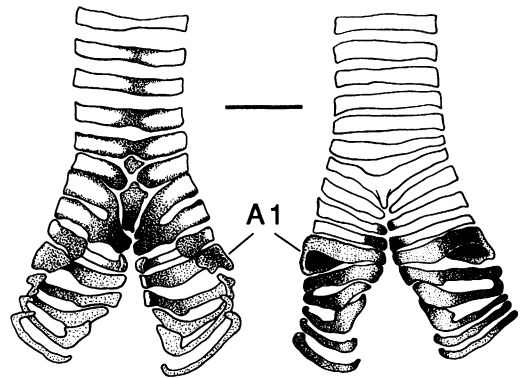
Fig. 17. Syringeal supporting elements of *Pipra suavissima*. **Left** dorsal view (AMNH 816768), **right** ventral view (AMNH 9366). Abbreviation: **A1** A1 supporting element.

inous ventral and dorsal tips. A3–4 are double, complete, and entirely ossified except for cartilaginous medial sections, which are fused together. A5 and above are single and complete. The A5–8 or A5–12 are ossified except for a small cartilaginous portion on the dorsal midline. Subsequent A's are entirely ossified. The cartilaginous pessulus is fused ventrally to A5, and dorsally it is closely associated with but not fused to the cartilaginous dorsal portion of A5. All B elements are entirely cartilaginous. B1–2 are fused dorsally by a short cartilaginous bar. The ventral ends of B1–3 are widened and spatulate, and angled craniodorsad to nest close to one another and to the tapered ventral end of A1. The ventral ends of B1–2 are slightly widened, but B3 is the most distorted. All subsequent B elements are thin and unspecialized.

Muscles. Generally weakly developed. M. tracheolateralis divides laterally on the ventral midline at A7. The insertion of M. tracheolateralis differs in the three uncleared specimens. In one adult male, it inserts on the lateral and ventral surface of A1; in an immature plumage male, M. tracheolateralis is weakly differentiated into ventral and dorsal bundles to insert on the dorsal and ventral ends of A1. In another adult male, M. tracheolateralis inserts on the lateral and ventral surfaces of A2, and a portion of the dorsalmost fibers extend to insert on the dorsal end of the cartilaginous A1. M. sternotrachealis

Fig. 18. Syringeal supporting elements of *Pipra serena* (ROM 127643). **Left** dorsal view, **right** ventral view. Abbreviation: **A1** A1 supporting element.

is thin and inserts on the lateral surfaces of M. tracheolateralis at A12–15.

Innervation. Typical piprid pattern with ventral anastomosis at A25.

Pipra serena (N = 2)

Supporting elements (fig. 18). *Pipra serena* is similar in general form to *P. suavissima*, but much larger and distorted in shape. The diameter of the syrinx of *suavissima* at A1 is 2.5–2.6 mm, and at A10, the diameter is 1.2–1.3 mm. In nominate *serena*, the widths at A1 and A10 are 3.8 or 3.9 mm and 2.6 or 2.7 mm, respectively. In the two specimens of *serena* (one male and one female), the entire trachea and syrinx are twisted and dorsoventrally compressed into a distorted oval shape, and the tracheobronchial junction is displaced craniad by an extensive series of double, complete bronchial A elements. A1 is double, medially incomplete, and cartilaginous. It is very broad in its dorsal half and consistently tapers toward the ventral end. A2 is double, medially complete, and ossified for its ventrolateral two-thirds. It is connected medially to A3 by a thin cartilaginous strip, but it is not truly complete medially. A3–5 are double, complete, and ossified except for the medial third. The cartilaginous medial portions of A2–5 are connected by an oval plate of cartilage that is supported in the middle of medial wall of each bronchus by the dorsal and ventral ends of A2–5. This plate of cartilage is buckled or depressed into the lumen of each bronchus. A6 is single,

complete ventrally, and fully ossified except for its dorsal tips which are fused to the cranial end of the medial bronchial cartilaginous plate or to the cartilaginous pessulus. A7–14 or 15 are single, complete, and fully ossified except for a short cartilaginous portion on the dorsal midline. All subsequent A elements are single, complete, and entirely ossified. The cartilaginous pessulus is fused ventrally to A6, and is attached dorsally to the dorsal tips of A7 and to the medial, bronchial cartilaginous plate. All B elements are completely cartilaginous. The slightly widened ventral ends of B1 are slightly angled craniad. B2–3 elements are very wide ventrally and thin dorsally. The difference between the broad ventral ends and narrow dorsal ends of these elements produces a strong distortion in the shape of the bronchi. B1–2 are dorsally fused together in an acute angle and not by a short cartilaginous bar. The more distorted, spatulate ventral ends of B2–3 are acutely angled craniad to nest close to one another and to B1 and A1. Subsequent B elements are thin, simple, and not distorted in shape.

Muscles. These observations are based only on cleared-and-stained specimens in which the musculature is only partially preserved. Muscles are not very well developed, apparently similar to those of *P. suavissima*. The ventral division of M. tracheolateralis is not preserved. The muscle appears to insert on A2 and dorsally on A1 as in one specimen of *suavissima*. M. sternotrachealis is thin and inserts on the lateral sides of the trachea at A14–15.

Innervation. Not observed.

Pipra pipra (N = 17)

Supporting elements (fig. 19). A1 is double, medially incomplete, and ossified for its ventral half. The dorsal and ventral ends of A1 are wider than the lateral portions, resulting in a prominent arch-shaped indentation along the caudal margin of the element. A2 is double and mostly ossified, but its medial bronchial portions may be incomplete (N = 5), medially complete and cartilaginous (N = 4), or medially complete and ossified (N = 6). A1–2 are fused for the ventral two-thirds of their length. A3–4 (N = 12) or A3–5 (N = 3)
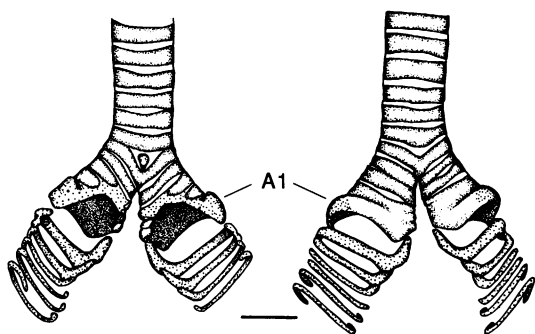
Fig. 19. Syringeal supporting elements of *Pipra pipra* (AMNH 9358). **Left** dorsal view, **right** ventral view. Abbreviation: **A1** A1 supporting element.
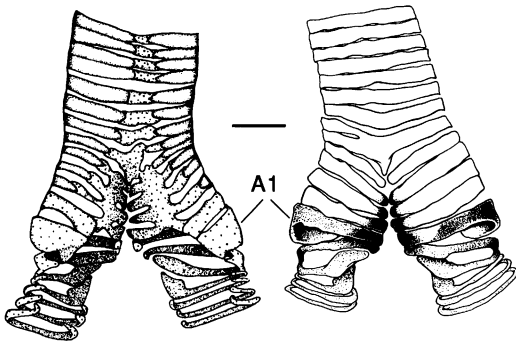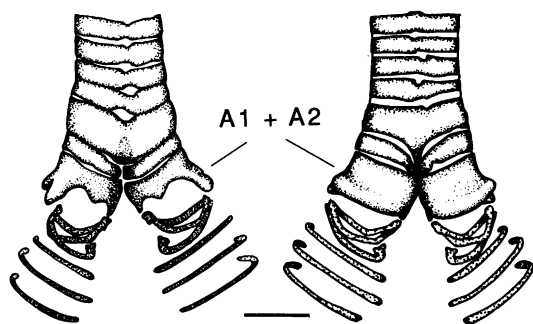

Fig. 20. Syringeal supporting elements of *Pipra fasciicauda* (AMNH 2301). **Left** dorsal view, **right** ventral view. Abbreviation: **A1 + A2** fused A1 and A2 supporting elements.

are double, complete, and fully ossified. Subsequent A elements are single, complete, and ossified. The left and right halves of the first single element are oblique to the tracheal A elements, giving this element a prominent chevron shape. In most specimens (N = 10), no tracheal A elements are fused dorsally, but in five specimens the first two single A elements are dorsally fused by an ossified bar. In all three cleared-and-stained specimens, which are dorsally unfused, a free floating piece of cartilage is located between the first and second single elements in the position of the ossified dorsal bar in other specimens. A very narrow pessulus is fused dorsally and ventrally to the first single element, A5 or A6. All the B elements are cartilaginous. B1–2 are dorsally fused by a cartilaginous bar. The ventral ends of B1–3 are widened and roundly curved craniomedially. Subsequent B's are unspecialized in shape.

Muscles. M. tracheolateralis widens to cover the ventral surfaces of the trachea between A30–35. It continues caudally as a single sheet of fibers, and differentiates into left and right halves between A8 and 10. The left and right sides continue caudad adjacent to one another on the ventral midline before separating laterally at A2–4. Each side divides into dorsal and ventral groups of fibers on the lateral midline at A2–4. The ventral and dorsal fibers insert on the ventral end and ventrolateral surface of A1. These caudal portions of M. tracheolateralis are completely extrinsic and differentiate without intermediate insertions or constrictions. M. ster-

notrachealis is a broad, well developed muscle, and it inserts on the lateral surfaces of M. tracheolateralis from A11–17. The dorsal fibers insert on the A elements at the dorsal edge of M. tracheolateralis, while the ventral fibers fan out obliquely over the ventral surface of the trachea. Musculature in females is very thin and undeveloped but the same as in males in general form.

Innervation. Typical piprid pattern in most specimens. Ventral anastomosis at A20. In one specimen, the small lateral fibers of the tracheal nerves exchange several tiny diagonal fibers across the ventral surface of the trachea between A15 and 25.

Pipra aureola (N = 3), *P. fasciicauda* (N = 5), and *P. filicauda* (N = 8)

Supporting elements (fig. 20). All A elements are completely ossified. A1–2 are double and completely fused. A2 is complete. A1 is medially incomplete and somewhat straighter dorsally than A2, and its dorsal ends form prominent rounded projections at the caudodorsal corners of the fused element. The caudomedial edge of A2 is sculpted in a distinctive double-arched curve. A3 is double, complete, and unfused. A4–5 are single and completely fused into a short tracheal drum. The thin ossified pessulus is fused dorsally and ventrally to A4. A6 and subsequent elements are single, complete, ossified, and unfused. All B elements are cartilaginous, thin, and fragile, and the bronchi are very weakly supported. The dorsal ends of B1–2
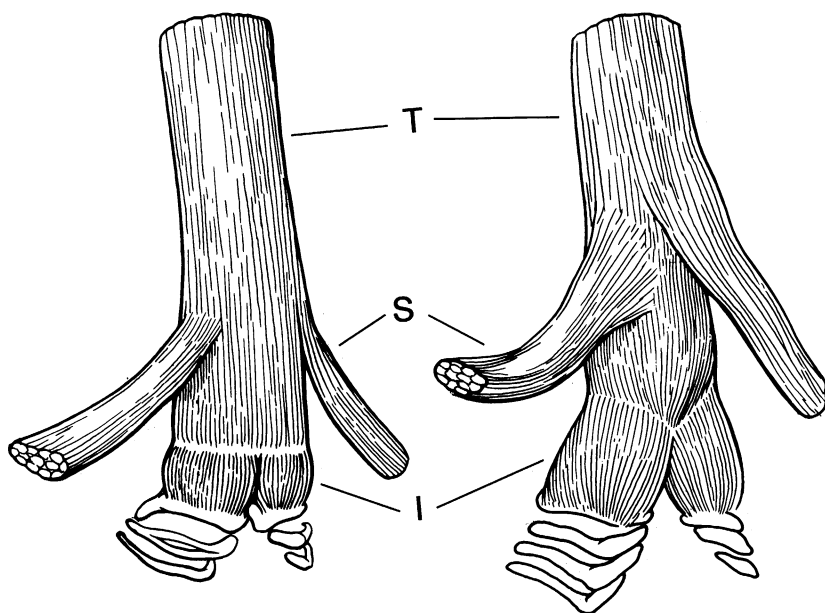
Fig. 21.   Ventrolateral view of syringeal muscles: **left** *Pipra filicauda* (UMMZ 225067), **right** *Pipra rubrocapilla* (LSUMZ 114486). Abbreviations: **I** intrinsic syringeal muscles; **S** M. sternotrachealis; **T** M. tracheolateralis.

run directly into one another and are fused in an arrowhead shape, instead of by a perpendicular cartilaginous bar. These fused dorsal ends of A1–2 are located very close to the protruding dorsal end of A1. The ventral end of B2 is widened, angled craniad underneath the ventral end of B1, and fused to the medial side of that element. The blunt ventral end of B3 is turned abruptly craniad in a right angle. Subsequent B elements are thin and unspecialized in shape.

Muscles (fig. 21). In males, M. tracheolateralis is a robust, well-developed muscle that widens ventrally to converge on the ventral midline between A30 and 35. It continues caudally in single well-developed mass without lateral differentiation until a partial insertion on A4–5. This insertion gives rise to a pair of partial intrinsic muscles that are differentiated on the ventral midline from their origin at A4–5. The left and right muscles form prominent bellies that are adjacent on the ventral midline, and insert along the lateral and ventrolateral surfaces of the combined A1–2 elements. The intrinsic muscles insert on the middle of the fused element, approximately where A1–2 are fused, leaving

the caudal edge of A1 exposed in ventral and lateral view. M. sternotrachealis is a short but very robust muscle. The thick bundle of fibers tapers rapidly to insert by a sheet of connective tissue on the lateral surface of M. tracheolateralis at A12–15. Few M. sternotrachealis fibers are continuous with the M. tracheolateralis. In females, M. tracheolateralis is less well developed and massive. One female specimen has weakly developed but completely differentiated intrinsic muscles, and another has no intrinsic muscles. M. sternotrachealis is thinner but the same in the form of insertion.

Innervation. Typical piprid pattern, with a ventral anastomosis at A26. The main nerve fibers innervate the massive Mm. sternotracheales and smaller branches innervate the intrinsic musculature.

Pipra mentalis (N = 7)

Supporting elements (fig. 22). A1–2 are double, fully ossified, and completely fused. A1 is medially incomplete, and A2 is complete, except for a thin dorsomedial suture. The caudoventral and caudolateral margins

of this fused element are flared outward and at right angles to one another, forming squared supports for the laterally spread bronchi. A3 (N = 2) or A3–4 (N = 5) are double, complete, and completely ossified. The medial portions of these complete double elements are straight instead of rounded. The next 2–4 cranial elements (A4–8) are single, complete, fully ossified, and fused extensively at their dorsal margins. All subsequent elements are single, complete, ossified, and unfused. The ventral ends of B1–3 are distinctly shaped into a prominent "fish hook" profile; they broaden ventrolaterally, turn acutely dorsomediad, and gradually narrow toward the ventral tip. They are closely nested together at the ventral margin of A1–2. The ventral end of B1 is ossified ventral to the bend in the element. Because of their widened ventral ends, the dorsal portions of B1–2 approach one another at an acute angle and are directly fused instead of being connected by a separate cartilaginous bar. B4 and subsequent elements are not specialized in shape.

Muscles. In adult males, M. tracheolateralis converges ventrally to cover the entire ventral surface of the trachea, and continues caudad in a single, undivided sheet of fibers to insert partially on the ventral and lateral surfaces of the cranial margin of the drum (A6–8). A pair of intrinsic muscles originates caudal to this insertion and is laterally differentiated. The left and right intrinsic muscles are strongly developed into prominent bellies that insert on the entire length of A1. In some specimens, M. sternotrachealis originates from a pair of fleshy raphes on the medial surface of the craniolateral process of the sternum. The two origins fuse immediately to form a single well-developed muscle. M. sternotrachealis inserts on the lateral sides of M. tracheolateralis at A15–18. Dorsally a few fibers insert on the A elements at the dorsal margin of M. tracheolateralis, and ventrally, a few fibers fan out across the ventral surface of the trachea. In females, M. tracheolateralis is a thin, undeveloped sheet of fibers. It does not insert on the cranial edge of the drum, but it divides on the ventral midline at A6–8, and inserts on A1 without any prominent intrinsic bellies.

Innervation. Typical piprid pattern. Ventral anastomosis between A30 and 35.
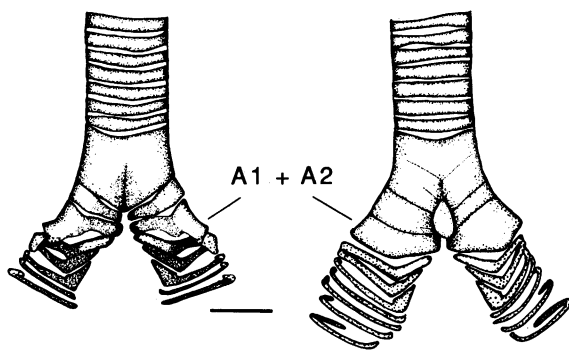
Fig. 22. Syringeal supporting elements of *Pipra mentalis* (LSUMZ 95070). **Left** dorsal view, **right** ventral view. Abbreviation: **A1 + A2** fused A1 and A2 supporting elements.

Pipra cornuta (N = 10)

Supporting elements. Similar to those of *Pipra mentalis* (fig. 22) except as follows: A1–2 are completely fused and squared on the caudoventral margin, but the elements are more robust in shape and the lateral flare of the bronchi is reduced. A2 is medially incomplete. A3 is double, complete, and fully ossified. The dorsomedial corner of A3 is broadened caudally to nest next to the craniodorsal end of the medially incomplete A2. A4–6 are fused extensively along their dorsal margins into a partial drum. The ventral end of B1 is similar in shape but is thinner, and less acutely angled (about 90°). The ventral end of B1 is ossified beyond the dorsomedial bend. The ventral ends of B2–3 are smaller, cartilaginous, and not acutely angled.

Muscles. In males, M. tracheolateralis is well developed, covering the ventral surface of the trachea above A30. The left side of M. tracheolateralis is more well developed, producing a pronounced asymmetrical bulge in musculature left of the ventral midline. On the lateral surfaces, M. tracheolateralis inserts on A6 and gives rise to a pair of intrinsic muscles; however, the ventral fibers continue caudad without any intermediate insertion to insert on the ventral ends of A1. These ventral fibers are not laterally differentiated until immediately prior to their insertion on A1. The well-developed left and right intrinsic muscles insert on the lateral and ventrolateral surfaces of the syrinx, whereas the caudal extrinsic fibers of M. tracheolateralis cover the
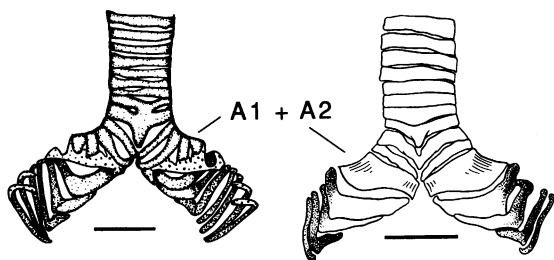
Fig. 23. Syringeal supporting elements of *Pipra erythrocephala* (AMNH 8081). **Left** dorsal view, **right** ventral view. Abbreviation: **A1 + A2** fused A1 and A2 supporting elements.

ventral eighth of the syringeal circumference. Musculature in female specimens is weakly developed, and is similar generally in shape to that of female *Pipra mentalis*. M. tracheolateralis is not differentiated into intrinsic muscles. Its fibers extend caudally to insert on A1 without any significant partial insertion on the drum. M. sternotrachealis has a single origin, and inserts on the lateral surface of M. tracheolateralis at A13–16.

Innervation. Typical piprid pattern. Ventral anastomosis near A30. The main fibers divide into a pair of prominent smaller fibers caudal to the insertions of Mm. sternotracheales. They continue caudad to innervate the intrinsic muscles, and innervate the Mm. sternotracheales from their medial surface.

Pipra chloromeros (N = 10)

Supporting elements. Generally similar to those of *P. mentalis* (fig. 22). A1–2 are double, ossified, and completely fused. A1 is medially incomplete. A2 is complete and has a distinct dorsomedial suture. A3–4 are double, complete, and completely ossified. A5–6 (N = 11) or A5–7 (N = 2) are single, ossified, and extensively fused at the dorsal margins. A7 or A8 and subsequent elements are single, complete, ossified, and unfused. An ossified pessulus is formed by the dorsomedial portion of A5 and is fused ventrally to A5. The ventral ends of B1–3 are widened and angled dorsomediad into "fish hook" shapes, which are more exaggerated than in *P. mentalis*. The bronchi are more laterally flared than in *mentalis*. The ventral half or third of B1 is ossified, and the ventral ends of B2 are also os-

sified. B4 and subsequent elements are not specialized in shape.

Muscles. Similar to those of *P. rubrocapilla* (fig. 21). M. tracheolateralis inserts in a continuous sheet on A8–9 laterally and on A5–6 at the ventral midline. The insertion is chevron shaped. The left and right intrinsic muscles originate just caudal to this insertion, the ventral fibers originate on A4, and the lateral fibers on A8–9. A few of the most dorsal fibers originate on A8–9 just dorsal to the inserting fibers of M. tracheolateralis. M. sternotrachealis has a single origin, and inserts on the lateral and ventrolateral surfaces of M. tracheolateralis between A14 and 19. In females, the musculature is thin and undeveloped as in female *mentalis,* but the change in fiber direction before insertion of the left and right halves of M. tracheolateralis on A1 reflects the chevron-shaped origin found in male intrinsic musculature.

Innervation. Typical piprid pattern. Ventral anastomosis at A30.

Pipra rubrocapilla (N = 9)

Supporting elements. As in *Pipra chloromeros* except as follows: A2 is complete but medially cartilaginous. The dorsomedial suture between the medial and dorsal portions of A2 is still visible. A5–7 (N = 4) or A5–8 (N = 4) are extensively fused dorsally into a partial drum. Ventral ends of both B1 and B2 are ossified.

Muscles (fig. 21). As in *Pipra chloromeros.* M. tracheolateralis inserts and intrinsic musculature originates on A7–8, at the cranial margin of the partial drum. M. sternotrachealis inserts on the lateral and ventrolateral surface of M. tracheolateralis at A12–16.

Innervation. Typical piprid pattern. Ventral anastomosis at A25.

Pipra erythrocephala (N = 11)

Supporting elements (fig. 23). As in *Pipra chloromeros* except as follows: The dorsal ends of A1 are cartilaginous. A2 is complete but partially cartilaginous medially. In most specimens the dorsomedial suture is observable. The bronchi are more laterally flared, caudally exposing the medial walls of the bronchi. A5–6 are fused only by a narrow bar on the dorsal midline. Subsequent A ele-

ments are unfused. B1 is very robust; because of the lateral spread of the bronchi, the rounded lateral portion of B1 elements arch craniad between their ventral and dorsal ends.

Muscles. As in *Pipra chloromeros* and *rubrocapilla* (fig. 21), except as follows: M. sternotrachealis inserts on the M. tracheolateralis at A15–19.

Innervation. Typical piprid pattern. Ventral anastomosis at A30. Innervates both the intrinsic muscle and the M. sternotrachealis.

SYRINGEAL CHARACTER ANALYSIS

The characters are organized into subheadings A Elements (1–19), B Elements (20–39), Accessory Cartilages (40–42), Syringeal Shape (43–44), Extrinsic Musculature (45–47), Intrinsic Musculature (48–56), Innervation (57–58), and Membranes (59). In each character description, derived state and its distribution are followed by the primitive state and its distribution (summarized in table 2). See Methods for details.

A ELEMENTS

1. Double, complete A elements. In all piprids except *Masius, Corapipo,* and *Ilicura,* one or two A elements are double and complete, providing support to the medial bronchial walls. Three double, complete A elements are present in *Pipra serena* and a few individuals of *Pipra pipra.* Double, complete A elements are found in some cotingids (*Pipreola, Ampelioides, Porphyrolaema, Cotinga, Conioptilon,* and *Procnias*) and in some tyrannid clades. In the tyrannid clades, medially complete A elements have been hypothesized to be independently derived (W. E. Lanyon, 1984a, 1985, 1986, 1988a, 1988c). Since both ingroup states are present in the immediate outgroup to piprids, the cotingids, it is also necessary to refer to more distant outgroups. Based on outgroup comparison to furnarioids and Old World suboscines and to the oscines, medially complete, double A elements are derived within tyrannoids. These medially complete, double A elements in piprids are hypothesized here to be derived independently of those in cotingids. The piprids *Chiroxiphia* and *Antilophia* are so specialized in the morphology of their tracheobronchial junction that it is not possible to determine

confidently whether they are derived or primitive for this character, and they are coded as unknown (?).

2. Double, complete, fully ossified A3–5 elements. In *Chloropipo, Xenopipo, Heterocercus, Pipra pipra,* the *Pipra aureola* species group, and the *Pipra erythrocephala* species group, one or more of the double, complete A elements are fully ossified. The number of fully ossified, double A elements varies among these taxa from one to three. In the *Pipra serena* species group, *Machaeropterus,* and *Manacus,* the double complete A elements are medially cartilaginous. In syringeal development of tyrannoids, formation of cartilaginous supporting elements precedes ossification (Ames, 1971). The medially ossified, double A elements are apparently a terminal addition to the ontogeny of the complete but medially cartilaginous double A's found in other piprids. Completely ossified double A elements are not present in any cotingids and only in a few tyrannids in which they are hypothesized as independently derived. The completely ossified double A's are hypothesized to be derived by ontogenetic criteria (Fink, 1982) and by outgroup comparison.

3. Double, complete A2 elements. In *Heterocercus, Pipra pipra,* the *Pipra aureola* species group, and the *Pipra erythrocephala* species group (except *P. cornuta*), the A2 elements are double and complete. This morphology is absent in other piprids, cotingids, and almost all tyrannids, and is here hypothesized to be derived.

4–5. Double, complete, medially ossified A2 elements. In the *Pipra aureola* species group, and in *P. mentalis* and *P. chloromeros,* the A2 elements are completely ossified medially. In *P. mentalis* and *P. chloromeros,* the medial portion of A2 connects to the dorsal and lateral portion in a conspicuous dorsomedial suture. In *P. erythrocephala* and *P. rubrocapilla,* the medial portions of A2 are cartilaginous, but the suture is still present, indicating that in these taxa such elements have become secondarily cartilaginous. In *Pipra pipra* and *Heterocercus,* the complete, double A2's are variably ossified and not as robust or consistent as in the *Pipra* species above. These medially ossified A2's are absent in other piprids, cotingids, and most tyrannids, and are hypothesized here to be de-

TABLE 2

Distribution in the Piprids of the Derived States of 59 Syringeal Morphology Characters

(Characters are coded: 0 primitive state; 1 derived state; 2 alternative, unordered derived state. Character descriptions and polarity assessments are given in the text.)

Species	Characters																								
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Corapipo gutturalis	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0
Corapipo leucorrhoa	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0
Masius chrysopterus	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0	0
Ilicura militaris	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0
Machaeropterus deliciosus	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Machaeropterus regulus	1	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	1	1	0	0	0	0	0
Machaeropterus pyrocephalus	1	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	1	0	0	0	0
Manacus manacus	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0
Manacus vitellinus	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0
Manacus candei	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0
Chiroxiphia linearis	?	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	1	0	0	0	1	1
Chiroxiphia lanceolata	?	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	1	0	0	0	1	1
Chiroxiphia pareola	?	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	1	0	0	0	1	1
Chiroxiphia caudata	?	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	1	0	0	0	1	1
Antilophia galeata	?	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	1	0	0	0	1	0
Chloropipo holochlora	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0
Chloropipo unicolor	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0
Chloropipo uniformis	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0
Xenopipo atronitens	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	1	0	0
Heterocercus linteatus	1	1	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0
Heterocercus flavivertex	1	1	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0
Pipra pipra	1	1	1	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0
Pipra coronata	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0
Pipra isidorei	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0
Pipra coeruleocapilla	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0
Pipra nattereri	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0
Pipra iris	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0
Pipra suavissima	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0
Pipra serena	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0
Pipra aureola	1	1	1	1	0	0	1	1	0	1	0	0	0	0	1	1	0	0	0	1	1	0	0	0	0
Pipra fasciicauda	1	1	1	1	0	0	1	1	0	1	0	0	0	0	1	1	0	0	0	1	1	0	0	0	0
Pipra filicarda	1	1	1	1	0	0	1	1	0	1	0	0	0	0	1	1	0	0	0	1	1	0	0	0	0
Pipra cornuta	1	1	0	0	0	0	1	1	1	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0
Pipra mentalis	1	1	1	1	0	0	1	1	1	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0
Pipra chloromeros	1	1	1	1	0	0	1	1	1	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0
Pipra rubrocapilla	1	1	1	1	1	0	1	1	1	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0
Pipra erythrocephala	1	1	1	1	1	0	1	1	1	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0
Outgroups	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

rived in the *Pipra aureola* and *P. erythrocephala* species groups (4). The cartilaginous medial portions of A2, which retain the medial suture, are hypothesized to be secondarily derived in *P. erythrocephala* and *P. rubrocapilla* (5).

6–8. A1–2 partially or completely fused. In *Manacus,* A1–2 and sometimes A1–3 are extensively fused together, but the elements retain their distinct characters; the lines of fusion between the elements and their shapes are easily discernible. The outer surfaces of A1–2 are also distinctly rough in texture. In *Machaeropterus deliciosus, Heterocercus,* and *Pipra pipra,* A1–2 are fused for the ventral half to two-thirds of their length and at their dorsal ends into single composite elements. In the *Pipra aureola* and *P. erythrocephala*

TABLE 2—(*Continued*)

Characters																																	
26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59
0	1	0	0	0	0	0	0	0	0	1	0	1	0	1	1	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	1	0	0
0	1	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	1	0	0
0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0
0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0
0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0
0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0
0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0
0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0
0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0
0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0
0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0
0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0
0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0
0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0
0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0
0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0
0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	2	0	0
0	1	0	0	1	0	1	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	2	0	0	2	0	0
0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	2	0	0	2	0	0
0	1	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	2	0	0
0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0
0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0
0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
0	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1	1	0
0	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1	1	0
0	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1	1	0
0	1	0	0	1	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	1
0	1	0	0	1	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0
0	1	0	0	1	0	0	1	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0
0	1	0	0	1	0	0	1	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0
1	1	0	0	1	0	0	1	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

groups, the A1–2 elements are completely fused forming a single composite element without apparent distinctions between the elements. Fused double A elements are absent in other piprids, cotingids, and most tyrannids, and are hypothesized to be derived in piprids. The A1–2 fusion of *Manacus* differs markedly in character and detail from the fused A1–2 of these other piprids and is here hypothesized as independently derived (6). The partially and completely fused states are hypothesized to be derived in the following transition series: (7) A1–2 partially fused into a single composite element, derived in *Machaeropterus deliciosus, Heterocercus, Pipra pipra*, the *Pipra aureola*, and *P. erythrocephala* species groups; (8) A1–2 completely fused into a single, composite element; derived in

the *Pipra aureola* and *P. erythrocephala* species groups.

9. Caudoventral and caudolateral margins of A1 flared and square. In the *Pipra erythrocephala* species group, the caudoventral and caudolateral margins of the A1 elements are flared outward and at right angles to one another, forming squared supports for the laterally spread bronchi. This morphology is unique in tyrannoids and is hypothesized to be derived.

10. Double arch-shaped indentation on caudomedial edge of A2. In the *Pipra aureola* species group, the caudomedial edge of A2 is "indented" or "incised" in a double arch shape or double s-curve. This morphology is unique in tyrannoids and hypothesized as derived.

11. Arch-shaped caudolateral edge of A1. In *Pipra pipra,* the caudolateral edge of A1 is indented or arched craniad (i.e., the element thins at the lateral midline). This unique morphology is hypothesized to be derived.

12. A1 element broad and expanded. In *Masius* and *Corapipo,* A1 is a robust, broad element. The mode of ossification produces a pronounced bulge or inflation of the element. This morphology is unique in tyrannoids and is hypothesized to be derived.

13. Completely or largely cartilaginous A1. In *Ilicura, Chiroxiphia, Antilophia,* and the *Pipra serena* species group, the A1 element is completely cartilaginous. In *Machaeropterus regulus* and *M. pyrocephalus,* the A1 element is almost completely cartilaginous except for a conspicuous ossified oval in the center of the ventral quarter of the element. In almost all other tyrannoids, the A1 elements are completely ossified. Both the completely cartilaginous and the mostly cartilaginous state of A1 are derived in piprids, but the state found in *Machaeropterus regulus* and *pyrocephalus* may be intermediate to the completely cartilaginous A1 or it may be independently derived. The completely cartilaginous (13.1) and mostly cartilaginous (13.2) states of the A1 element will be coded here as unordered derived states of a single complex character.

14-16. Fused, single A elements. In some piprids, a pair or series of single, tracheal A elements is fused. These elements are fused by an ossified dorsal bar in *Masius chrysop-*

terus, Xenopipo atronitens, Chloropipo holochlora, Chloropipo unicolor, Pipra erythrocephala, and some individuals of *Machaeropterus deliciosus,* and *Pipra pipra.* In *Masius,* this dorsal bar is a direct, cranial extension of the pessulus which is fused dorsally to the first two dorsally complete elements, whereas in these other taxa, the dorsal bar is not a continuation of the pessulus. Single, tracheal A elements can also be fused extensively along their dorsal margins (as in some *Chloropipo holochlora* and *Heterocercus*), or completely fused dorsally (as in the *Pipra erythrocephala* species group except *erythrocephala*), or, they can be fused entirely along their dorsal and ventral margins (as in the *Pipra aureola* species group). Fused tracheal elements are not present primitively in cotingids, and are absent in tyrannids. The fused tracheal drum of *Chiroxiphia* and *Antilophia* is composed of a different series of A elements and is different in many other details; it is here hypothesized to be independently derived (see 17). The coding of the variation in this derived character in piprids is made more complex by several factors, including the different types or degrees of fusion, intraspecific variation in fusion, and apparent reversals in degree of fusion. However, morphological details indicate that these tracheal fusions evolved in a transition series from lack of fusion, to fusion by a dorsal bar, to extensive or nearly complete dorsal fusion. In species with extensive dorsal fusion, the most complete fusion occurs at the dorsal midline and a remnant of a dorsal bar is observable. Likewise, in species with extensive or complete fusion, occasional anomalies or interruptions in fusion occur between the ventral or lateral margins of elements, but not at the dorsal margins. In individuals of *Pipra pipra* that lack dorsal fusion, independent (but normally fused) floating pieces of cartilage are present between the elements in the position of the dorsal bar, indicating that these individuals are anomalous, incompletely fused specimens within a derived taxon. These tracheal fusion characters will be coded as the following derived characters (the latter two form a transition series):

(14) A5–6 or A6–7 fused dorsally by a cranial extension of the pessulus; derived in *Masius.*

(15) Partial or extensive dorsal fusion of A elements by a dorsal bar; derived in *Chloropipo holochlora, C. unicolor, Xenopipo, Heterocercus,* and *Pipra* (except the *Pipra serena* species group).

(16) Dorsal and lateral fusion or complete fusion; derived in a transition series from (15) in the *Pipra aureola* species group and the *Pipra erythrocephala* species group (except *erythrocephala*).

17. Extensive tracheal drum. In *Chiroxiphia* and *Antilophia,* an extensive tracheal drum is formed by the partial or complete fusion of a series of six to nine single A elements between A6 and 17. In most individuals, the cranialmost elements are entirely fused and difficult to differentiate, whereas the caudal elements of the drum are usually only fused dorsally. The caudodorsal margin of the drum often has a short caudal projection between the most cranial, dorsally incomplete pair of A elements. This morphology is unique in tyrannoids and is here hypothesized as derived.

18. Chevron-shaped A4 element at tracheo-bronchial junction. In *Chloropipo uniformis* and *Xenopipo atronitens,* the left and right halves of the single A4 element are oriented parallel to the double, bronchial A's and oblique to the more cranial, single, tracheal A's. The left and right halves are dorsally fused in a conspicuous chevron shape. The caudodorsal end of this element extends mediad and forms the pessulus. In a few *C. uniformis* and *X. atronitens,* the single A4 element is ventrally incomplete. In both *C. uniformis* and *Xenopipo atronitens,* the caudodorsal end of A5 extends caudad into the space cranial to the chevron-shaped A4. A few other piprids have obliquely oriented, fused halves of the first single A element (e.g., *Pipra pipra*), but in none of these species are these elements ventrally incomplete, strongly distorted, or a major contribution to the pessulus. Also, in none of these does the next, cranial element extend caudally in a similar manner. This unique morphology in *C. uniformis* and *Xenopipo atronitens* is hypothesized to be derived.

19. Dorsally incomplete or cartilaginous tracheal A elements. In *Manacus, Pipra serena, P. suavissima, Machaeropterus regulus, Chiroxiphia,* and *Antilophia,* a series of single, tracheal A elements are dorsally incomplete or dorsally cartilaginous. The number of elements and the series vary among taxa: *Manacus* (A5–10 or 12), *P. serena* (A6–11), *P. suavissima* (A6–8), *Machaeropterus regulus* (A5–6), *Chiroxiphia* (A4–5 to A6–8), and *Antilophia* (A6–7). In two specimens of *P. coronata,* A5 is single and dorsally cartilaginous. It is difficult to distinguish dorsally incomplete and dorsally cartilaginous A elements within or among species because the cartilaginous dorsal area may appear to be either an organized continuation of the elements or a generalized strip of cartilage related to the pessulus or accessory cartilages. However, dorsally cartilaginous tracheal A elements are not found in any other piprids or cotingids. In tyrannids, they have been hypothesized to be independently derived in tody-tyrants (Lanyon, 1988c). Dorsally cartilaginous, single A elements in piprids are here hypothesized to be derived. The one variable taxon, *Pipra coronata,* is coded as primitive or absent for this character because only a small minority of the specimens have this trait.

B ELEMENTS

20. B1-2 dorsally fused. In all piprids, B1–2 are dorsally fused by a short cartilaginous bar. This morphology is unique in suboscines and has been hypothesized to be a synapomorphy of the family (Prum, 1990b).

21. B1-2 fused directly. In *Pipra aureola, P. fasciicauda,* and *P. filicauda,* the B1–2 elements are directly fused at their dorsal ends in an acute angle, or arrowhead shape, and not by a distinct cartilaginous bar. This unique morphology is hypothesized to be derived secondarily from (20).

22. B1-2 broadly fused dorsally. In *Chloropipo uniformis* and *Xenopipo atronitens,* the dorsal ends of B1–2 are broadly fused by a wide cartilaginous connection. This morphology is unique among tyrannoids and is hypothesized to be derived secondarily from (20).

23. Caudal series of B elements dorsally fused. In *Manacus,* a series of caudal B elements (B5–10 to B5–12) are broadened and flattened, and their widened dorsal ends are fused to one another in a lattice. This mor-

phology is unique in tyrannoids and hypothesized as derived.

24-25. A1 dorsally fused to B1-2. In *Chiroxiphia* and *Antilophia,* A1 is dorsally fused to B1-2 by a thin strip of cartilage. In *Chiroxiphia,* the strip is longer than in *Antilophia* and it has a distinct square projection on its craniolateral edge which is absent in *Antilophia.* This fusion is absent in all other piprids and all other tyrannoids, and is here hypothesized to be derived in *Chiroxiphia* and *Antilophia* (24). The presence of the longer cartilaginous A1–B1 bridge with the square craniolateral projection in *Chiroxiphia* is hypothesized to be secondarily derived in that genus (25).

26. Lateral section of B1 arched craniad. In *P. erythrocephala,* the lateral portion of the double, medially incomplete B1 element is arched craniad. As a result, the B1–2 meet dorsally at an acute angle, and are fused directly to one another, instead of being fused by a perpendicular cartilaginous bar. This unique, derived morphology is associated with the extreme lateral flare of the bronchi in this species, and is hypothesized to be derived.

27-35. Specialized ventral ends of B1-3. The ventral ends of B1–2 of all piprids are widened, paddle shaped, or angled in some specialized manner. The B3 of the majority of piprids is also specialized in a similar manner, and the three elements are typically nested together next to the caudoventral margin of A1. No similarly shaped elements occur in any of the outgroups examined, making it difficult to polarize the variation in these structures within the group. Some restricted variations, however, appear to be derived within piprids because of their highly distinctive shapes. This set of morphologies is coded here as the following binary characters in a complex transition series:

(27) Ventral ends of B1–2 widened and angled dorsad or craniad; derived in all piprids.

(28) Specialized ventral ends of B1–2 reduced but still present; derived in *Ilicura.*

(29) Ventral end of B2 angled craniad underneath B1 and fused to the ventromedial surface of B1; derived in the *Pipra aureola* species group.

(30) B3 widened and angled craniad with B1–2; derived in all piprids except *Ilicura, Masius, Corapipo,* and *Chloropipo uniformis.*

(31) Ventral ends of B3 reduced to a short, blunt process angled craniad at 90°; derived and present in *Manacus* and the *Pipra aureola* species group.

(32) B1–3 elements very thin and ventral ends of B1–3 angled dorsad, as in other piprids, but distinctly thinner and spindly in shape; derived in *Chloropipo unicolor.*

(33–34) In all of the *Pipra erythrocephala* species group except *cornuta,* ventral ends of B1–3 are very broad, acutely angled dorsad, and pointed at the tip in a unique "fish hook" shape. These specialized ventral ends are nested closely together and next to the cranioventral margin of the laterally and ventrally flared A1 (see 9). In *P. cornuta,* the B1 element is prominently crooked in a right angle that is less exaggerated than the others in this species group. The B2–3 elements of *cornuta* are not acutely angled dorsad or "fish hook" shaped, but are more similar to the less specialized shapes present in *Chloropipo holochlora,* the *Pipra serena* species group, and *Machaeropterus deliciosus,* which are probably primitive in the group. The ventral ends of B1–3 in the *Pipra erythrocephala* group are hypothesized to be derived in an ordered transition series: (33) ventral end of B1 widened and angled into a large hook shape, derived in the *Pipra erythrocephala* group; (34) ventral ends of B1 further distorted and ventral ends of B2–3 widened and angled acutely into "fish hook" shapes, derived in *Pipra erythrocephala, rubrocapilla, chloromeros,* and *mentalis.*

(35) In *Chloropipo uniformis* and *Xenopipo atronitens,* ventral ends of B1–2 asymmetrically widened. The caudal margin is straight, but the cranial margin veers craniad at the ventral end of the element producing a lopsided, spatulate, ventral end to the element. This morphology is unique among piprids and is hypothesized to be derived.

36-39. B1 or B1-2 elements partially ossified. In *Masius, Chloropipo unicolor, Xenopipo,* and the *Pipra erythrocephala* species group, the ventral quarters or ventral ends of the B1 elements are ossified. In *Corapipo,* the broad B1 element is almost completely ossified. The ossified portions of B1 elements in *Masius* and *Corapipo* are enlarged or swollen in a unique manner. In *Pipra rubrocapilla, P. erythrocephala, P. chloromeros,* and *Chloropipo unicolor,* the ventral ends of the B2

elements are also ossified. In all other piprids and most other tyrannoids, the B elements are completely cartilaginous. In some cotingids and tyrannids, the central portion of the more caudal B elements are ossified, but these morphologies are independent of those of piprids. The partially ossified B elements in piprids are hypothesized to be derived in the following transition series of binary characters:

(36) Ventral ends of B1 elements ossified and enlarged; derived in *Masius* and *Corapipo*.

(37) Ventral ends of B1 elements ossified but not enlarged; derived in *Chloropipo unicolor, Xenopipo atronitens,* and *Pipra erythrocephala* species group.

(38) B1 almost completely ossified; derived in *Corapipo.*

(39) Partially ossified ventral ends of B2 elements; derived in *Pipra erythrocephala, P. rubrocapilla,* and *P. chloromeros.*

ACCESSORY CARTILAGES

40–41. Medial bronchial cartilage bars. In *Masius, Corapipo,* and *Ilicura,* a pair of accessory cartilaginous bars is fused to the dorsal ends of A1–2 and continues ventrad or cranioventrad toward the tracheobronchial junction and the pessulus. These paired medial bronchial cartilages form the cranial or craniodorsal margin of the medial tympaniform membrane. These structures are unique in tyrannoids and hypothesized to be derived in these three genera (40). In *Corapipo gutturalis,* the medial bronchial cartilages are enlarged and ossified. This morphology is hypothesized to be additionally derived in this species (41).

42. Accessory cartilaginous sheet. In *Chiroxiphia* and *Antilophia,* a sheet of cartilage forms the caudoventral surface of the trachea and the ventral and medial walls of the bronchi at the tracheobronchial junction. The sheet is connected to the dorsal ends of all dorsally incomplete elements (from A1–6 to A1–8), and is also connected to the ventral ends of A1–2. The tracheal portion of the cartilaginous sheet is bowed outward or cylindrically rounded, and its caudal margin in both bronchi is indented craniad where it supports the cranial edge of the medial tympaniform membrane. This morphology is unique in

piprids and is here hypothesized to be derived. Similar cartilage sheets are present in *Neopelma, Tyranneutes, Tityra, Lipaugus* (sensu stricto; Prum, 1990b), and *Calyptomena* (Eurylaimidae; R. O. Prum, in prep.), but these structures are hypothesized to be independently evolved.

SYRINGEAL SHAPE

43. Trachea and syrinx greatly enlarged and distorted in shape. The syrinx of *Pipra serena* is similar to that of *P. suavissima* but the trachea and bronchi are greatly enlarged and twisted. Associated with this increase in size are a number of changes or distortions of primitive morphological details. In *suavissima* and other members of the *Pipra serena* species group, there are small cartilaginous connections between the cartilaginous medial sections of the double, complete A elements. In *serena,* an expanded oval plate of cartilage is supported in the medial bronchial wall by the cartilaginous medial sections of these double A's. The number of dorsally cartilaginous single A's increases from three to six in *suavissima* to nine or ten in *serena.* The shape of the B1–3 elements is also tremendously distorted by increase in the diameter of the bronchi. This suite of derived characters is clearly an autapomorphy of *serena.* Its presence in *serena* implies that the reorganization of primitively present morphological details is the result of a single, radical change in syringeal ontogeny in this species.

44. Tracheobronchial junction flared into funnel shape. In *Chloropipo unicolor,* the edges of A1–7 are closely fitted next to one another; the caudal margins of these elements (especially A1–2) are larger in diameter than the cranial edges, so that the entire syrinx flares laterally in an inverted funnel shape. This morphology is unique among tyrannoids and is here hypothesized to be derived.

EXTRINSIC MUSCULATURE

45. Mm. tracheolaterales highly asymmetrical. In *Machaeropterus,* the left and right Mm. tracheolaterales are asymmetrically developed. The right side is underdeveloped; the left side contributes almost all of the fibers to the ventral sheet of muscle that is usually formed by the union of the left and right sides.

The right M. sternotrachealis partially inserts onto the lateral surface of the tracheal A elements because the fibers of the right M. tracheolateralis are underdeveloped or missing. Many other piprids have limited muscular asymmetry associated with the asymmetrical position of the trachea to the mid-sagittal plane, but in no other piprids is the asymmetry as extreme or consistent among individuals as in *Machaeropterus*. This condition is not found in any cotingids or tyrannids and is here hypothesized to be derived.

46. Ventral division of M. tracheolateralis cranial to insertion. In *Corapipo, Machaeropterus regulus,* and *Chloropipo uniformis,* the continuous sheet of ventral muscle fibers formed by the left and right Mm. tracheolaterales divides on the ventral midline at A10 into differentiated left and right halves which veer laterad before insertion and differentiation into intrinsic musculature. In most piprids with intrinsic muscles, the ventral sheet does not differentiate laterally at all or until immediately before insertion. In *Manacus, Chiroxiphia,* and *Antilophia,* M. tracheolateralis is differentiated into left and right halves between A12 and 17, but these halves continue caudad as adjacent bellies and do not divide and veer laterad to form separate bodies of fibers on the lateral surfaces of the trachea. The unique morphology of *Corapipo, Machaeropterus regulus,* and *Chloropipo uniformis* is hypothesized to be derived.

47. M. sternotrachealis inserts by thin membrane. In the *Pipra aureola* species group, M. sternotrachealis is a well-developed and robust muscle that narrows abruptly before insertion by a thin sheet of connective tissue to the lateral surface of M. tracheolateralis. None of the fibers of M. sternotrachealis is continuous with M. tracheolateralis, as they are in all other piprids and other tyrannoids. This unique morphology is hypothesized as derived.

INTRINSIC MUSCULATURE

The intrinsic syringeal muscles of piprids are very diverse and have arisen a number of independent times within the clade. There are no morphological details to support the hypothesis that the entire class of "intrinsic" musculature novelties in piprids are homologous. Variation in the intrinsic syringeal musculature of piprids is difficult to polarize because the immediate outgroup, the cotingids, generally lacks intrinsic syringeal muscles, and the more distant outgroups, the tyrannids and furnarioids, have very different syringeal muscles that are unlikely to be homologous with those of piprids (Ames, 1971; Prum, 1990b). A combination of inferences from outgroup comparison, differences in the intrinsic muscles of piprids, and limited evidence from ontogeny is used to polarize variation in piprid intrinsic musculature.

Several groups of piprids lack intrinsic syringeal muscles. The *Pipra serena* species group, *Machaeropterus deliciosus,* and *M. pyrocephalus* have Mm. tracheolaterales that converge on the ventral midline, continue caudad as a single sheet, and then differentiate into right and left halves on the ventral midline to insert directly on A1. Most specimens of the *Pipra serena* species group and *Machaeropterus deliciosus* show no dorsoventral differentiation in the left and right halves and insert continuously on A1. But in *M. pyrocephalus* and a few specimens of the *Pipra serena* species group, the left and right sides are differentiated weakly into dorsal and ventral bundles of fibers that insert on the dorsal and ventral ends of A1. In *Pipra pipra,* the Mm. tracheolaterales are strongly differentiated into four (left and right, dorsal and ventral) bellies that do not have any intermediate insertion before A1, and are thus completely extrinsic. In *Manacus,* M. tracheolateralis divides on the ventral midline into two large bellies of completely extrinsic musculature.

All other piprids have some form of intrinsic musculature. In *Corapipo, Masius,* and *Ilicura,* there are two distinct forms of oblique intrinsic musculature that are clearly derived, and share an additional derived detail with one another which indicates that the forms are historically related. *Chiroxiphia* and *Antilophia* have distinctive, derived intrinsic muscles that share a derived form of insertion with the extrinsic muscles of *Manacus.* In *Machaeropterus regulus* males, the caudo-

dorsal and caudoventral fibers of M. tracheolateralis have developed into variable, partially intrinsic muscles which are absent in females. Each of these forms of intrinsic musculature is quite distinct and is hypothesized here to have an independent origin.

The two main remaining forms of intrinsic musculature are certainly derived within piprids, but it is difficult to determine whether both are independently derived or whether one state is primitive to the other in a complex transition series. In *Chloropipo* and *Xenopipo*, M. tracheolateralis inserts on the trachea at A6–9, and gives rise to left and right intrinsic muscles, which themselves differentiate into dorsal and ventral bellies at A2–4, to insert on the dorsal and ventral ends of A1. In *Heterocercus*, the *Pipra aureola* species group, and males of the *Pipra erythrocephala* species group, M. tracheolateralis inserts on the lateral and ventral surfaces of A4–9, and gives rise to a laterally differentiated pair of intrinsic muscles that insert on the entire surface of A1, without any dorsoventral differentiation. Among these latter species there is additional variation in the insertion of Mm. tracheolaterales and the origin of the intrinsic muscles. In *Heterocercus*, the *Pipra aureola* species group, *P. mentalis*, and *P. cornuta*, the insertion and origins of these muscles are straight along the tracheal circumference and perpendicular to the tracheal axis. In *Pipra erythrocephala*, *P. rubrocapilla*, and *P. chloromeros*, M. tracheolateralis inserts on A8–9 on the lateral surfaces of the trachea and on A5 on the ventral midline, in an oblique, chevron pattern. The intrinsic muscles originate immediately caudal to this insertion in a similar chevron pattern. Females, immature males, and a fledgling of the *Pipra erythrocephala* species group, and one of two female specimens of the *aureola* species group completely lack intrinsic musculature; M. tracheolateralis does not insert on any tracheal elements before differentiating laterally on the ventral midline and inserting on the entire A1.

An additional unique variation is present in *Pipra cornuta* males; the paired, lateral intrinsic muscles are restricted to the lateral and ventrolateral surfaces of the syrinx, and the ventral fibers of Mm. tracheolaterales insert directly on the ventral ends of A1. The syringes of *P. cornuta* females lack intrinsic muscles and resemble those of females of other species in the *erythrocephala* species group.

It remains problematic to determine the polarity among the two pairs of intrinsic muscles in *Chloropipo* and *Xenopipo*, and the single pair in *Heterocercus*, and the *Pipra aureola* and *Pipra erythrocephala* species groups. Given the information available, they are treated as unordered alternative states of a complex character. The additional variations found within subsets of the *Pipra erythrocephala* species group are hypothesized to be derived as well.

The variation in piprid syringeal musculature will be coded as the following series of binary characters and as a single, unordered, complex character.

48. Single pair of ventrolaterally oblique intrinsic muscles. In *Ilicura*, M. tracheolateralis inserts continuously on the ventral and lateral surfaces of A6; a pair of intrinsic muscles originates on the ventral surface of A4 and on the lateral surface of A5. These fibers pass obliquely caudodorsad to insert on the dorsal and lateral surfaces of A1. This oblique pair of intrinsic muscles is unique among piprids and cotingids, and is hypothesized to be derived. These muscles are only superficially similar to the independently derived Mm. obliquus ventrales of tyrannids (Ames, 1971; Prum, personal observ.).

49. Two highly differentiated, oblique pairs of intrinsic muscles. In *Corapipo* and *Masius*, M. tracheolateralis inserts on the ventral and lateral surfaces (*Masius*) or lateral surfaces (*Corapipo*) of A6–8, and is partially continuous with two pairs of intrinsic muscles. The ventral pair originates on the ventral surfaces of A5–7 and on the lateral surfaces of A2–4 or A4–5; these fibers run caudad or caudoventrad to insert as a fleshy mass on the ventral end of A1. The dorsal pair of intrinsic muscles originates on the lateral surface of A4–5; these fibers run caudodorsad to insert on the dorsal end of A1 in a large fleshy belly. This morphology is unique among piprids and is hypothesized to be derived.

50. Dorsal fibers of M. tracheolateralis continuous with dorsal intrinsic musculature. In *Ilicura*, *Corapipo*, and *Masius*, the dor-

salmost fibers of M. tracheolateralis do not insert on the tracheal A elements, but continue parallel along the dorsal margin of the intrinsic muscle fibers to insert with them on the dorsal end of A1 in a characteristic, stereotyped manner. In other piprids, M. tracheolateralis fibers are generally continuous with intrinsic musculature, but they are not restricted to a well-defined group of dorsal fibers. The morphology in *Corapipo, Masius,* and *Ilicura* is unique among piprids and cotingids and is hypothesized to be derived.

51. Oblique, partially intrinsic ventral muscles. In *Machaeropterus regulus,* M. tracheolateralis diverges ventrally at A10, and forms two separate bundles of fibers on the lateral surfaces of the trachea (see 46). In females, each side divides into dorsal and ventral portions at A2–4 which insert on the dorsal and ventral ends of A1. The ventral portion in particular has a distinct, oblique lateroventral fiber direction. In males, M. tracheolateralis inserts on A5 and gives rise to two variable, partially intrinsic dorsal and ventral muscles that insert on the dorsal and ventral ends of A1. These muscles have the same fiber direction as those of females. Lateroventrally oblique intrinsic muscles are found only in *Corapipo* and *Masius,* but these muscles are different in form, sexual dimorphism, and degree of development from the musculature in *M. regulus.* The morphology in *M. regulus* is hypothesized to be independently derived.

52. Intrinsic or extrinsic muscles insert by spiral sheet of connective tissue. In *Chiroxiphia* and *Antilophia,* M. tracheolateralis inserts partially on A13–17 and gives rise to a well-developed, partially intrinsic belly of fibers that is cryptically divided from its origin at the ventral midline into adjacent left and right groups of fibers. In *Manacus,* M. tracheolateralis is differentiated on the ventral midline into left and right portions of fibers at A10 that continue caudad as adjacent parts of a single well-developed belly of completely extrinsic musculature. In all three genera, the left and right sides insert by a single, laterally continuous sheet of connective tissue on a series of elements beginning with A3 (*Manacus*) or A4–5 (*Chiroxiphia* and *Antilophia*) on the ventral midline and spiraling caudodorsad to the ventrolateral and lateral surfaces of A2 (*Chiroxiphia* and *Antilophia*) or

A1 (*Manacus*). In *Chiroxiphia pareola,* the connective tissue inserts on A4 at the ventral midline and extends caudad immediately lateral to the ventral midline on both sides to insert on A2 from its ventral end. This feature is a synapomorphy of the polytypic biological species *pareola* which is not coded in this character analysis. The dorsal intrinsic muscles of *Chiroxiphia* and *Antilophia* have additional independent origins and insertions (see 53). The form of ventral differentiation and the complex insertion of the ventral intrinsic muscle in these three genera are unique in tyrannoids and are hypothesized to be derived.

53. Dorsal intrinsic muscle inserts by tendon on dorsal end of A1. In *Chiroxiphia* and *Antilophia,* the dorsal portion of the intrinsic musculature originates on the dorsolateral surface of the A elements at the cranial margin of the tracheal drum and inserts partially by a narrow strip of tendon on the extreme dorsal end of A1. This morphology is unique among tyrannoids and is here hypothesized to be derived.

54. One or two pairs of laterally differentiated intrinsic muscles. In *Heterocercus,* and *P. aureola* and *P. erythrocephala* species groups, M. tracheolateralis inserts on the cranial margin of the fused tracheal drum (A5–9) and gives rise to a single pair of laterally differentiated intrinsic muscles that insert on A1. In *Chloropipo* and *Xenopipo,* M. tracheolateralis inserts on A5–7 and gives rise to four laterally and dorsoventrally differentiated bellies of intrinsic muscles that insert on the dorsal and ventral ends of A1. In all these genera, the intrinsic muscle fibers are caudocranially oriented and not oblique. These morphologies are not found in any other piprids or other tyrannoids and are hypothesized here to be derived. However, it cannot be determined which state is primitive relative to the other or whether they are independently derived. They will be coded here as unordered, derived states: (54.1) a single pair of nonoblique intrinsic muscles, present in *Heterocercus, Pipra aureola* species group, and *Pipra erythrocephala* species group; (54.2) two pairs of nonoblique intrinsic muscles, present in *Chloropipo* and *Xenopipo.*

55. Extrinsic Mm. tracheolaterales fibers insert on A1 ventral to lateral pair of intrinsic muscles. In male *Pipra cornuta,* the pair of

intrinsic muscles is restricted to the lateral and ventrolateral surfaces of the syrinx. The ventral extrinsic fibers of Mm. tracheolaterales continue caudad to insert directly on the ventral ends of A1. Mm. tracheolaterales remain laterally undifferentiated until immediately before insertion. This morphology is unique among piprids and other tyrannoids, and is hypothesized to be derived.

56. Chevron-shaped ventral insertion of M. tracheolateralis. In *Pipra erythrocephala, P. rubrocapilla,* and *P. chloromeros,* M. tracheolateralis inserts on the lateral surface of A9 and on the ventrolateral surfaces of the next caudal series of elements in a spiral to A5 at the ventral midline. The left and right sides combine to form a V-shaped or chevron-shaped insertion in ventral view. The left and right intrinsic muscles originate immediately caudal to the insertion of M. tracheolateralis. In all other piprids with intrinsic muscles, the insertion of M. tracheolateralis and the origins of intrinsic muscles are straight across the trachea. The chevron-shaped M. tracheolateralis insertion and intrinsic muscle origin in *Pipra erythrocephala, P. rubrocapilla,* and *P. chloromeros* are unique in tyrannoids, and hypothesized to be derived.

INNERVATION

57. X-shaped ventral anastomosis of the tracheosyringeal nerves. In all piprids except *Chloropipo* and *Xenopipo,* the tracheosyringeal nerves anastomose on the ventral midline of the trachea between A20 and 35 before innervating the M. sternotrachealis, M. tracheolateralis, and the intrinsic musculature. In other tyrannoids including the cotingids, *Neopelma, Tyranneutes,* and the tyrannids, the tracheosyringeal nerves pass down the lateral surfaces of the trachea sometimes exchanging smaller secondary nerve fibers. In *Chloropipo* and *Xenopipo,* the nerve fibers are poorly developed and difficult to observe. Most frequently, the nerves appear as a fine network of tiny fibers across the ventral surface of the trachea, but a few specimens with observable nerves in *C. uniformis* and *X. atronitens* have suggestions of piprid ventral anastomosis. The ventral anastomosis of the tracheosyringeal nerves is here hypothesized to be derived in piprids (57.1). The alternative state found in *Chloropipo* and *Xenopipo*

is hypothesized to be derived as well (57.2). Both states are scored as unordered alternative derived states of a single character.

An additional variation in the pattern of syringeal innervation was not coded as an independent character because it was not completely fixed within any species. In most specimens of every species of *Manacus, Chiroxiphia,* and *Antilophia,* the tracheosyringeal nerves combined into a single fiber on the ventral surfaces of the trachea for several millimeters before splitting into left and right branches to innverate the syringeal muscles. In the few remaining specimens, the typical X-shaped chiasma was present. Although intraspecific variation in this novelty makes it difficult to code formally, it is a unique variation among tyrannoids and may consitute strong evidence for monophyly of these three genera.

58. Main branches of tracheosyringeal nerves innervate M. sternotrachealis. In the *Pipra aureola* species group, the main branches of the tracheosyringeal nerves veer laterad from the ventral chiasma and pass directly into the medial surface of Mm. sternotracheales. The nerves innervate the caudal fibers of M. tracheolateralis and the intrinsic muscles by smaller secondary branches. In other piprids, M. sternotrachealis is innervated by small branches of the tracheosyringeal nerves. The morphology in the *Pipra aureola* species group is unique in tyrannoids and is here hypothesized to be derived.

MEMBRANES

59. Fibrous mass on medial tympaniform membrane. In *Pipra cornuta,* there is a thick, round fibrous mass in the center of the medial tympaniform membrane, medial to the B1–4 elements. The interbronchial ligament arises just caudal to this fibrous mass. These structures occur sporadically in the syringes of other tyrannoids, but are hypothesized to be independently evolved. The novelties found in *Pipra cornuta* are unique among piprids and are hypothesized here to be derived.

PHYLOGENETIC ANALYSIS

The 59 derived syringeal character states supported two different maximally parsimonious phylogenetic hypotheses with zero

branch lengths collapsed. Each had a length of 76 and a consistency index of 0.82. The strict consensus tree based on these two trees included 22 resolved clades and was identical to one of the two shortest trees (fig. 24). Both trees included a single large trichotomy about which none of the characters were informative. The two shortest trees differed only in the resolution of the relationships of a single species: *Chloropipo unicolor*. At least 25 distinct combinations of syringeal characters were identified among the 40 species of piprids. Thirteen lineages were diagnosed by syringeal autapomorphies. Twelve of the 59 characters were autapomorphies of presently recognized biological species (11, 14, 26, 28, 32, 41, 43, 44, 48, 51, 55, 59). With these autapomorphies removed, the shortest phylogenetic hypotheses had a length of 64 and a consistency index of 0.77.

The monophyly of a number of traditional genera and recently recognized species groups was supported by one or more syringeal synapomorphies (fig. 24). These corroborated groups include *Corapipo, Manacus, Machaeropterus*, the *Machaeropterus regulus-pyrocephalus* clade, *Chiroxiphia*, the *Pipra aureola* clade (including *aureola, fasciicauda*, and *filicauda*), and the *Pipra erythrocephala* clade (including *erythrocephala, rubrocapilla, chloromeros, mentalis*, and *cornuta*). The following monotypic genera and species were also diagnosed by syringeal autapomorphies: *Masius* (14), *Ilicura* (13.1, 28, 48), *Corapipo gutturalis* (41), *Machaeropterus deliciosus* (7), *M. regulus* (51), *Chloropipo unicolor* (32, 44), *C. uniformis, Pipra pipra* (11), *Pipra cornuta* (55, 59), *Pipra erythrocephala* (−16, 26), and *Pipra serena* (43). However, the monophyly of *Pipra* and of *Chloropipo* was not supported in the consensus tree or any of the six supported resolutions. Neither *Heterocercus* nor the *Pipra serena* species group was supported as monophyletic by any derived syringeal characters.

The first, basal clade in the piprid syringeal consensus tree was composed of the three genera *Corapipo, Masius*, and *Ilicura*. This clade is supported as the sister group to the rest of the piprids. Within this clade, *Ilicura militaris* was the sister group to *Masius chrysopterus* and *Corapipo*, and *C. leucorrhoa* and *C. gutturalis* were sister groups.

The rest of the piprids belonged to a monophyletic group made up of three clades with unresolved interrelationships. The first clade was the genus *Machaeropterus*, within which *deliciosus* was supported as the sister group to *regulus* and *pyrocephalus*.

The second clade included *Manacus, Chiroxiphia, Antilophia*, and the *Pipra serena* species group. In this clade, *Manacus* was the sister group to *Chiroxiphia* and *Antilophia*. Interrelationships of species within *Chiroxiphia* and *Manacus* were not resolved. The members of the *Pipra serena* species group form an unresolved, paraphyletic set of lineages related to the *Manacus-Chiroxiphia-Antilophia* clade. In both of the shortest trees, *Pipra serena* and *P. suavissima* are most closely related to these three genera but are not a diagnosable clade. *Pipra coronata* and the other members of the species group were an undiagnosable set of lineages at a basal position in the clade.

The third clade within this large assemblage of piprids included *Chloropipo, Xenopipo, Pipra pipra, Heterocercus*, the *Pipra aureola* clade, and the *Pipra erythrocephala* clade. The monophyly of *Chloropipo* plus *Xenopipo* was supported; and *Xenopipo atronitens* was the sister group to *Chloropipo uniformis*. The relationships of *C. unicolor* to this clade were not completely resolved. The two most parsimonious syringeal trees supported either *unicolor* as the sister group to *uniformis* and *atronitens*, or an unresolved trichotomy of *holochlora, unicolor*, and *uniformis-atronitens* clade.

The sister group to *Chloropipo* and *Xenopipo* included *Heterocercus* and the rest of the genus *Pipra*. Within this clade, *Pipra pipra* was the sister group to *Heterocercus*, the *Pipra aureola* clade, and the *Pipra erythrocephala* clade. The monophyly of the *Heterocercus* was not supported by any syringeal synapomorphy, so the three species of *Heterocercus* were the undiagnosable primitive sister taxa to the *Pipra aureola* and *erythrocephala* clades. The relationships among the species of *Heterocercus* or the *Pipra aureola* clade were unresolved because no informative syringeal variations were identified. However, the syringeal characters supported a single resolution of the phylogeny of the five species in the *Pipra erythrocephala* clade:
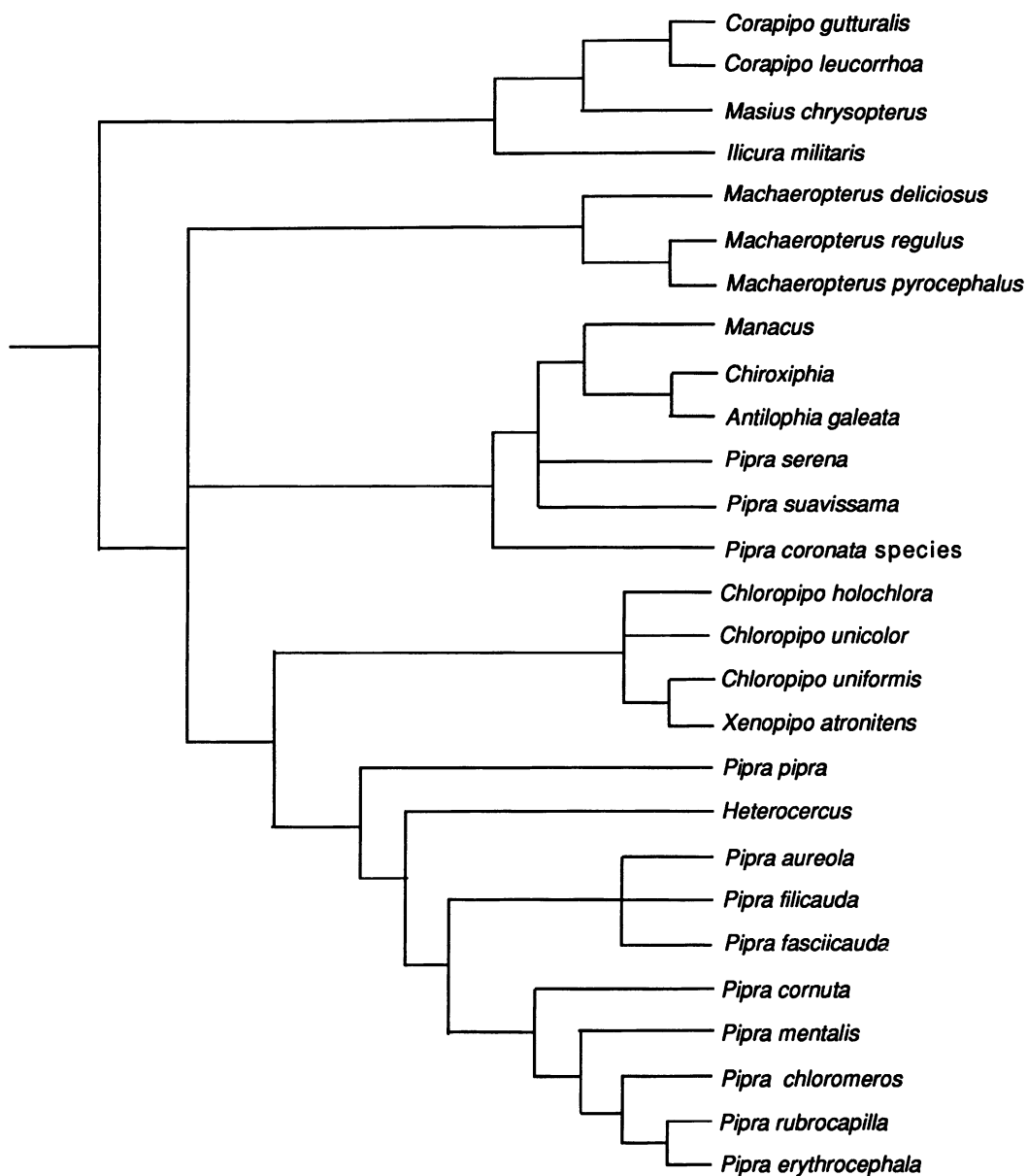
Fig. 24.   One of two maximally parsimonious phylogenetic hypotheses based on 59 syringeal characters for the piprids. Each input tree had a length of 76 and a consistency index of 0.81. This phylogenetic hypothesis is same as the strict consensus tree of the two maximally parsimonious trees. The other shortest tree differed only in the placement of *Chloropipo unicolor*; *C. unicolor* is the sister group to *Chloropipo uniformis* and *Xenopipo atronitens* in the other tree (see fig. 25).

cornuta as the sister group to the other four species; *mentalis* as the sister group to the remaining three; and *chloromeros* as the sister group to *erythrocephala* and *rubrocapilla*. *Pipra erythrocephala* and *P. cornuta* were both distinguished by syringeal autapomorphies.

In none of the maximally parsimonious resolutions of the data were *Pipra pipra* or the *Pipra serena* species group most closely related to each other or to the remainder of the genus *Pipra*.

The syringes of *Chloropipo flavicapilla*,

Heterocercus aurantiivertex, and *Pipra vilas-boasi* were unavailable for examination (Wood et al., 1982), but the relationships of these species to other piprids are discussed below.

ALTERNATIVE PHYLOGENETIC HYPOTHESES FOR THE PIPRIDS

A phylogenetic analysis of piprid syringeal characters supports a well-resolved phylogenetic hypothesis for the 40 species of the family. These results corroborate cladistically some traditional piprid taxa that have not been diagnosed before, and support many novel phylogenetic hypotheses among manakin genera. Parsimonious optimizations of the evolution of the syringeal characters are shown on the resolved syringeal hypothesis of phylogeny in figure 25. Here, the relative strength of support of the various piprid clades is discussed, and the syringeal hypothesis of phylogeny is compared to previous phylogenetic hypotheses and classifications of the family.

The monophyly of the *Ilicura-Masius-Corapipo* clade is supported by two synapomorphies (40, 50). The *Masius-Corapipo* clade is diagnosed by three syringeal synapomorphies (12, 36, 49) including details of both supporting elements and musculature. The monophyly of *Corapipo* was supported also by two characters (38, 46). This resolved hypothesis for the phylogeny of the four species in these three genera is exactly congruent with the previous hypothesis for their interrelationships based on a cladistic analysis of male courtship display elements (Prum and Johnson, 1987). Plumage similarities that lead Snow (1975) and Hellmayr (1910) to hypothesize close relationships between *Corapipo* and *Manacus,* and between *Masius* and *Antilophia* are apparently convergent.

The large clade composed of the rest of the piprids is supported by two derived syringeal characters: (1) complete, double A elements, and (30) specialized ventral ends of the B3 elements. Within this assemblage, there are three main clades with unresolved relationships. The first includes only the genus *Machaeropterus* whose monophyly was supported by a single syringeal character (45). The monophyly of the *M. regulus-pyrocephalus* clade was supported by (13.2) a unique

pattern of partial ossification of the A1 elements. This result confirms Snow's (1975, 1979) placement of *deliciosus* back in *Machaeropterus* and the monophyly of Snow's *regulus-pyrocephalus* species group.

The next large clade in this assemblage includes *Chiroxiphia, Antilophia, Manacus,* and the *Pipra serena* species group. Within this clade, the *Chiroxiphia-Antilophia* clade is conclusively supported by a suite of four derived characters (17, 24, 42, 53). Snow (1975) hypothesized that these two genera may each be related to *Pipra,* based on behavior and plumage, respectively, but they have not been previously associated with one another.

The *Chiroxiphia-Antilophia* clade shares a unique, derived musculature character with *Manacus* (52). Most specimens of these three genera also have a unique, probably derived form of syringeal innervation in which the left and right tracheosyringeal nerves combine into a single large fiber (described in 57). This novelty was not used as a character because a few individuals of all genera had the general piprid X-shaped pattern. However, this unique character provides further corroboration of the *Chiroxiphia-Antilophia-Manacus* clade. The monophyly of *Manacus* is supported by a unique, dorsal fusion of a caudal series of B elements (23) and several other synapomorphies (6, -13.1, 31). The monophyly of *Chiroxiphia* is supported by a single derived character (25). This novel hypothesis for the interrelationships of these three genera is congruent with the large body size and with plumage and soft part colors of females in these genera.

The monophyly of the *Pipra serena* species group was not supported in any of the most parsimonious resolutions. Although the syringes of these species are identifiable and generally similar to one another, these similarities are not arguably derived. All members of the group have completely cartilaginous A1 elements (13.1) that are shared with the *Chiroxiphia-Antilophia* clade and *Ilicura. Pipra serena* and *P. suavissima* share the derived dorsally cartilaginous, single A elements with *Manacus, Chiroxiphia, Antilophia,* and *Machaeropterus regulus* (19).

The syringeal morphology of the *Pipra serena* species group is generally similar but not arguably derived within the family, so no sy-

40, 50

12, 36, 49

38, 46

41

Corapipo gutturalis

Corapipo leucorrhoa

14

Masius chrysopterus

13.1, 28, 48

Ilicura militaris

45

7

Machaeropterus deliciosus

19, 46, 51

13.2

Machaeropterus regulus

Machaeropterus pyrocephalus

6, -13.1, 23, 31

Manacus

52

25

Chiroxiphia

17, 24, 42, 53

Antilophia galeata

19

Pipra serena

43

Pipra suavissama

13.1

Pipra coronata species

20, 27, 57.1

54.2, 57.2

Chloropipo holochlora

32, 44

Chloropipo unicolor

37

-15, -30, -37, 46

Chloropipo uniformis

18, 22, 35

Xenopipo atronitens

11

Pipra pipra

1, 30

Heterocercus

2, 15

10, 21, 29, 31, 47, 58

Pipra aureola

54.1

Pipra filicauda

3, 7

Pipra fasciicauda

-3, -4, 55, 59

Pipra cornuta

4, 8, 16

Pipra mentalis

9, 33, 37

Pipra chloromeros

34

Pipra rubrocapilla
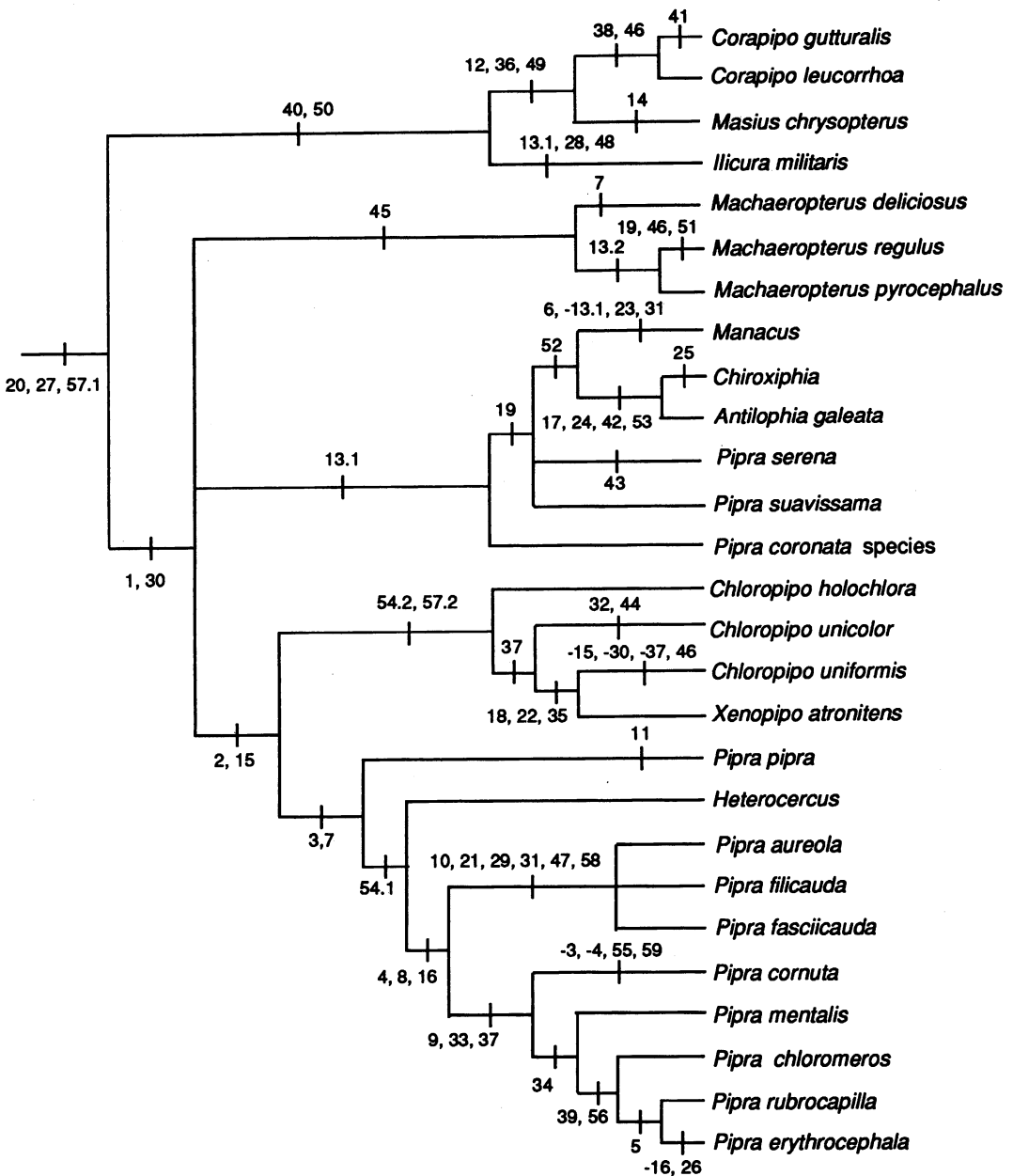
39, 56

5

Pipra erythrocephala

-16, 26

Fig. 25. Hypotheses for the evolution of the 59 syringeal characters within one of the maximally parsimonious phylogenetic hypotheses for the piprids. The alternative derived states of the three unordered, multistate characters (13, 54, and 57) are indicated as decimals following the character number (#.1, #.2). Hypothesized reversals are indicated by a minus sign preceding the character number. All character optimizations are unambiguous except for characters 4 and 37. Both of these are hypothesized to have evolved once and to be lost secondarily once, but it would be equally parsimonious to hypothesize two independent origins. Character 4 is hypothesized to a synapomorphy of the *Pipra aureola-erythrocephala* clade with a reversal in *Pipra cornuta,* but it may also be independently derived in the *Pipra aureola* clade and the *erythrocephala* clade, excluding *cornuta.* Character 37 is hypothesized to be a synapomorphy of *Chloropipo unicolor, C. uniformis,* and *Xenopipo atronitens,* with a reversal in *uniformis*; but it could be hypothesized to be independently evolved in *unicolor* and *atronitens,* as in the other maximally parsimonious hypothesis based on these data (fig. 24).

ringeal characters support the monophyly of the group. Haffer (1970) recognized the species group based on overall plumage similarity. Subsequently, a cladistic analysis of plumage characters was used to support the monophyly of the *Pipra serena* species group (Prum, 1988). However, this analysis was confounded by the inappropriate use of *Pipra pipra* and other *Pipra* species as an outgroup, since the syringeal characters analyzed here indicate that *Pipra pipra* is not closely related to the *Pipra serena* group. Furthermore, additional errors were made in the analysis (Prum, 1988). The iris color of *Pipra serena* and *suavissima* was coded as white, and the iris color of *nattereri, iris,* and *vilasboasi* was coded as dark, when the opposite is the case. Furthermore, an alternative equally parsimonious resolution of the plumage characters would place *exquisita* as more closely related to *nattereri-vilasboasi-iris* than to *coronata* (J. Haffer, personal commun.). The monophyly of the *Pipra serena* species group may ultimately be supported by several derived traits that are found only in members of this species group but have also been subsequently lost in other members, such as the white or blue rump patch. Derived plumage and iris color traits still support the *serena-suavissima* clade and the *nattereri-vilasboasi-iris* clade within the species group, but other aspects of the phylogeny of the species group are unresolved. As in syringeal morphology, plumage of the *Pipra serena* species group shows a uniformity and similarity which is not certain to be derived, but the overall evidence implies that the assemblage is highly likely to be monophyletic. No syringeal evidence was found to refute or corroborate Sibley and Monroe's (1990) placement of the two Andean species, *coeruleocapilla* and *isidorei,* in a separate species group.

Two syringeal synapomorphies support a clade including *Chloropipo* and *Xenopipo* (54.2, 57.2). Within this group, a clade including *Chloropipo uniformis* and *Xenopipo atronitens* is diagnosed by three derived syringeal characters (18, 22, 35). The syringeal characters do not resolve the relationships among the other species in this group: *C. holochlora* and *C. unicolor.* It is equally parsimonious to explain the single derived character shared by *unicolor* and *atronitens*—(37)

ossified ventral end of the B1 elements—as either a synapomorphy of a clade including *unicolor, atronitens,* and *uniformis* with a subsequent reversal in *uniformis,* or as two independent derivations in *unicolor* and *atronitens.* The hypothesis of a single origin fully resolves the relationships of these species while the independent origin hypothesis produces an unresolved trichotomy with *holochlora, unicolor,* and the *uniformis-atronitens* clade.

The syrinx of *Chloropipo flavicapilla* was not available for observation in this study, because no spirit specimens of the species were available (Wood et al., 1982). However, derived plumage characters support a clade including *flavicapilla, unicolor, uniformis,* and *atronitens,* resolving the ambiguity in the syringeal data (Prum, in prep.).

Snow (1975) and Wolters (1977) hypothesized that *Chloropipo flavicapilla, C. holochlora,* and *C. uniformis* comprise a species group or a separate subgenus from *C. unicolor.* However, the syringeal characters strongly support *uniformis* as the sister group to *Xenopipo atronitens.* Both *atronitens* and *unicolor* have been separated at various times from other *Chloropipo* species based on black male plumage, which is probably independently derived in these two species within the group (Prum, in prep.). The *Chloropipo flavicapilla-holochlora-uniformis* species group is a paraphyletic assemblage composed of the sexually monomorphic or mostly green plumaged members of this clade.

The genus *Pipra* is currently recognized to include 16 species, many of which have mostly black male plumage with distinct patches of bright red, yellow, white, or blue. The syringeal characters of these species indicate that the genus is polyphyletic and composed of three main clades. The *Pipra aureola* and *Pipra erythrocephala* clades share three derived, detailed syringeal traits (4, 8, 16), and constitute a well-supported monophyletic group. A single syringeal muscle character indicates that they are most closely related to *Heterocercus*: (54.1) presence of a single pair of intrinsic muscles. Two derived syringeal characters support *Pipra pipra* as the sister group to these three clades (3, 7). The seven species of the *Pipra serena* species group are not closely related to this clade. The tradi-

tional plumage characters used to define the genus *Pipra* are apparently homoplasious and phylogenetically uninformative.

The genus *Heterocercus* is not diagnosed by any syringeal characters, and anatomical specimens of one of the three species in the genus, *aurantiivertex*, were unavailable (Wood et al., 1982). However, all three species of *Heterocercus* share three derived plumage characters that unambiguously support the monophyly of the genus: (a) silky, elongate, erectile white throat feathers; (b) a graduated tail with the outer rectrices shortest; and (c) a narrow, central crown patch of red, yellow, or orange. The first two characters are unique among piprids and all other tyrannoids. This derived crown patch character is unique among piprids but has been independently derived in some tyrannids.

The syringeal data indicate that the plumage and size traits, and notions about undeveloped display behavior that were traditionally used to align *Heterocercus* with *Schiffornis* are homoplasious or inaccurate. Parkes (1961) redescribed the unique type specimen of *Pipra anomala* Todd as a hybrid between *Heterocercus linteatus* and *Pipra aureola*. He remarked that the hybrid provided evidence for a closer relationship between the two genera than implied by Hellmayr's (1929) placement of *Heterocercus* as distant from *Pipra* and nearest to *Schiffornis*. These syringeal data indicate that the two species involved in this hybridization are even more closely related than Parkes (1961) hypothesized.

The *Pipra aureola* clade, previously recognized as a species group by Haffer (1970) and Snow (1975, 1979), is diagnosed by six syringeal synapomorphies (10, 21, 29, 31, 47, 58). No syringeal variation among the three species in this clade was observed. In contrast, each of the five species of the *Pipra erythrocephala* clade have a distinct set of derived syringeal characters that completely resolve their interrelationships. The entire clade is supported by three derived traits (9, 33, 37), and each branch within is supported by additional synapomorphies : (34) derived in all but *cornuta*, (39, 56) derived in all but *mentalis* and *cornuta*, and (5) derived in *erythrocephala* and *rubrocapilla* alone.

Haffer (1970) hypothesized that these five species constitute a superspecies and this was accepted by the American Ornithologists' Union (1983), but Haffer did not resolve their cladistic interrelationships. Snow (1979) recognized the *erythrocephala* species group excluding *cornuta*, and a single syringeal synapomorphy also supports the monophyly of that assemblage. Based on plumage, *chloromeros* is perhaps most similar to *mentalis*, but the clade including *chloromeros, erythrocephala*, and *rubrocapilla* is well supported by two syringeal synapomorphies. Cracraft (1988) hypothesized that *Pipra cornuta* is the sister group to *erythrocephala* and *rubrocapilla* based on plumage characters, but a large number of syringeal characters support the placement of *cornuta* as the sister group to all other species in the clade. Sibley and Monroe (1990) recognized a species group including *mentalis, erythrocephala*, and *rubrocapilla* only, but the syringeal characters strongly indicate that this assemblage is not monophyletic. *Pipra chloromeros* shares (39) ventrally ossified B2 elements, and (56) chevron-shaped origin of intrinsic muscles with *erythrocephala* and *rubrocapilla* that are both absent in *mentalis*.

The various lineages in the syringeal hypothesis of phylogeny have different degrees of relative confidence. The relationships among *Corapipo, Masius*, and *Ilicura* are well supported, and congruence with a previous behavioral hypothesis of phylogeny of these genera increases the confidence in this hypothesis (Prum and Johnson, 1987). Sister-group relationships between *Chiroxiphia* and *Antilophia*, the *Pipra aureola* and *Pipra erythrocephala* clades, *Machaeropterus regulus* and *M. pyrocephalus*, and *Chloropipo uniformis* and *Xenopipo atronitens* are also well supported by two or more derived characters. However, other higher level clades are less well supported or dependent on additional, possibly overly simplified, hypotheses of character evolution. Homoplasy or mistakes in polarization of some characters, such as (1) complete double A elements, or (30) specialized ventral ends of the B3 elements, could eliminate support for some major piprid clades. Further, no characters resolve a major trichotomy in the hypothesis, and any error in characters supporting the monophyly of these three clades would yield additional

instability in the higher-level phylogeny of the family. Although this is the first comprehensive morphological investigation of piprid phylogeny, it is not a complete solution to the phylogenetic interrelationships of the family, and should be augmented with comparative analyses of other character systems.

Two phylogenies including some piprids based on biochemical data have been presented. S. M. Lanyon (1985) did an analysis of allozyme variation of tyrannoids that included seven piprid species. He identified 14 allozymes that varied among these taxa and supported two main clades, which included *Machaeropterus regulus, Manacus manacus,* and *Pipra pipra*; and *Chiroxiphia pareola, Chloropipo holochlora, Masius chrysopterus,* and *Corapipo leucorrhoa.* The distance trees also placed *Neopelma* and *Tyranneutes* as the sister group to either of these two groups of piprids, and *Schiffornis* as the sister group to all other piprids. None of the derived syringeal characters described here are congruent with either of the two groups supported by allozyme variation. Furthermore, a cladistic analysis of other morphological characters indicates that *Schiffornis, Neopelma,* and *Tyranneutes* are most closely related to non-piprid tyrannoids (Prum, 1990b). The lack of congruence between the syringeal and allozyme data may be the result of extensive homoplasy in either data set, but this cannot be evaluated appropriately until a more complete molecular analysis of piprids is performed.

Sibley and Ahlquist (1985, 1990) have published two analyses of DNA-DNA hybridization distances for piprids. *Pipra erythrocephala* was used as a driver in comparisons to 13 other piprid species. Piprids were also used as tracers in comparisons to *Pipreola arcuata, Schiffornis turdinus,* and other suboscines, but no reciprocal hybridizations were performed. Values of Delta $T_{50}H$ for comparisons between *Pipra erythrocephala* and other piprids ranged from 2.1 (to *Heterocercus flavivertex*) to 3.2 (to *Masius chrysopterus*). These values seem to imply some congruence with the syringeal hypothesis of phylogeny, which places the *Pipra erythrocephala* clade near *Heterocercus,* and *Masius* in a small clade that is the sister group to the rest of the piprids. But these points of congruence conflict with other Delta $T_{50}H$ values reported: e.g., *Pipra erythrocephala* to *P. mentalis,* 2.2; *P. erythrocephala* to *P. filicauda,* 2.7. The former is shorter than the distance to *Heterocercus,* and the latter is larger than other distances reported to species of *Chiroxiphia, Manacus, Machaeropterus, Chloropipo,* and the *Pipra serena* species group. The available DNA-DNA hybridization distances contradict the monophyly of most traditional piprid genera and species groups, many of which are strongly supported by syringeal synapomorphies. Larger complete matrices with reciprocal hybridizations are required before these inconsistencies in DNA-DNA hybridization distances can be evaluated.

I used these syringeal data and an earlier version of the syringeal hypothesis of phylogeny (Prum, 1989) in an analysis of the evolution of piprid display behavior (Prum, 1990a). Phylogenetic analysis of the separate syringeal and behavioral data sets, the combined data sets, and superimposition of the behavioral characters on the syringeal consensus tree revealed a high degree of congruence between the two data sets, and demonstrated the tradeoffs among the alternative phylogenetic tests of behavioral hypotheses of homology. Since that publication, I observed additional piprid specimens which led me to reevaluate some characters and to change the coding of others. For example, additional specimens of *Machaeropterus pyrocephalus* led me to reexamine this species; *pyrocephalus* turned out to lack dorsally cartilaginous A elements which I had erroneously coded as present (Prum, 1989). This change led to additional resolution of the phylogeny of the group, including unambiguous support of the monophyly of *Machaeropterus.* However, these changes did not substantially affect the results of the behavioral analysis presented in Prum, 1990a.

SYRINGEAL VARIATION, FUNCTION, AND EVOLUTION

PREVIOUS DESCRIPTIONS OF PIPRID SYRINGES

Previous descriptions of the syringeal morphology of piprids come from three authors.

Müller (1847, 1878) described the syringes of *Pipra pipra, P. erythrocephala, Chiroxiphia pareola,* and *Manacus manacus.* Lowe (1942) made additional observations of *Manacus vitellinus.* Ames (1971) observed a total of 10 individuals from 8 species—*Pipra erythrocephala, Pipra mentalis, Chiroxiphia caudata, Chiroxiphia lanceolata, Ilicura militaris, Corapipo gutturalis, Manacus vitellinus,* and *Manacus candei.* Ames (1971) also described the syringes of *Schiffornis* and *Piprites* as piprids, but these genera are not members of the monophyletic assemblage of piprids analyzed here (Prum and Lanyon, 1989; Prum, 1990b).

Previous descriptions of piprid syringeal morphology are largely congruent with these findings, but they are limited in detail because the stains and preparations employed here were not used. Most apparent differences from Ames's (1971) descriptions result from differences in the initial identification of homologous supporting elements. Ames's homology criteria were based largely on indirect observation of ossification, and this typically led to the identification of the first ossified double element as A1. The criteria utilized here emphasize special similarities in shape of elements over their composition, and as a result completely cartilaginous A1 elements were identified in *Ilicura, Chiroxiphia, Antilophia,* and the *Pipra serena* species group. In Ames's descriptions of three species from the two former genera, the cartilaginous A1's were identified as B1's. For example, the intrinsic muscles of *Ilicura militaris* were described by Ames as inserting on B1, but similarities in the dorsal fusion of B1–2 to other piprids favor the hypothesis described here—that these muscles insert on a cartilaginous A1.

Likewise, the cartilaginous A1 of *Chiroxiphia* was identified by Ames as B1. This homology assignment is a little more difficult, because the first three double, cartilaginous elements (either A1–B2, or B1–3) in *Chiroxiphia* and *Antilophia* are dorsally fused by strips of cartilage. The former situation is found nowhere else in piprids, and the latter is found only in some specimens of *Machaeropterus regulus.* However, in *Chiroxiphia* and *Antilophia* the ventral ends of the second through fourth double, cartilaginous ele-

ments are spatulate, as are B1–3 of almost all other piprids, indicating that these elements are B1–3 and that the A1 in these genera is cartilaginous.

Hypotheses of homology among supporting elements established by these conserved special similarities in shape are consistent with other details in shape and in the position of intrinsic muscle insertions.

INTRASPECIFIC VARIATION

Intraspecific variation in syringeal morphology may be geographic, sexual, ontogenetic, or random individual variation (Ames, 1971). The substantial samples of individuals of some species make it possible to access some aspects of intraspecific syringeal variation in piprids. Most piprids show limited individual variation in syringeal supporting elements, and somewhat more variation in syringeal musculature. Although no sexual dimorphism was observed in syringeal supporting elements, significant sexual dimorphism is present in syringeal musculature of some species.

Syringeal supporting elements have a stereotypical shape within a species. Intraspecific variations are more likely to occur in the extent of fusion or ossification of supporting elements. *Pipra pipra, Machaeropterus regulus, Manacus manacus,* the *Chiroxiphia* species, and *Chloropipo holochlora* have some variation in the fusion of elements in the observed samples. In *Chiroxiphia,* the number of elements incorporated in the tracheal drum varied by one or two within each species (table 1). Specimens of *Manacus* vary in the degree of fusion of the double A elements. In all specimens, A1–2 are completely fused, but in one individual of *M. vitellinus* and one of *M. candei,* A1–3 are fused. Specimens of *Pipra pipra* vary in the presence of dorsal fusion of single, tracheal A elements. In most *Machaeropterus regulus* (N = 6 of 8), the dorsally fused B1–2 are additionally fused to B3.

The most variable sample observed was of *Chloropipo holochlora.* It varied in the degree of fusion of the first single, tracheal A elements (A5–7 or A5–8) ranging from fusion by an ossified dorsal bar, to fusion along their dorsal and ventral margins into a nearly complete drum. One anomalous specimen lacked

dorsal fusion entirely (fig. 11). There is also some variation in degree of ossification of the medial section of A2, the first double, medially complete element. This variation does not appear to be geographically based; some extremes in syringeal structure come from the same geographic regions.

Another type of intraspecific variation is found in *Pipra pipra*. In 3 of 15 specimens, an additional double, complete A element is present. This type of variation is interesting in that it changes the relative position of the tracheobronchial junction to the syringeal supporting elements, but does not result in any significant change in the overall form of the syrinx.

Ames (1971) described occasional asymmetrical, "extra" supporting elements in tyrannoids, and these do occur in low frequency within piprids. These additional rings or half rings are developmental accidents, and usually do not change the shape of the syrinx in any significant fashion.

There is limited individual variation and significant sexual variation in syringeal musculature of most species. In the *Pipra serena* species group, there is some minor variation in the extent of the insertion of M. tracheolateralis on A1. In most specimens, M. tracheolateralis inserts continuously along the lateral surface of A1, whereas in a few, M. tracheolateralis fibers are absent on the lateral midline. This variation appears to be more related to underdevelopment of the muscle in these specimens rather than a well-marked dorsoventral differentiation. In three specimens of *Pipra suavissima,* the M. tracheolateralis inserts on A1, A2, or both.

In general, most females have less robust and well developed musculature than males, although the musculature of males and females is identical in general form. In *Chloropipo holochlora,* the intrinsic muscles are well differentiated in males but only partially intrinsic in females. In *Machaeropterus regulus,* the two males in the small sample showed significant differences in the independence or intrinsic distinctness of the oblique caudal fibers of M. tracheolateralis, whereas females showed no indication of intrinsic musculature. In the most extreme case, intrinsic syringeal muscles are found only in

mature males. In males of the *Pipra erythrocephala* clade, M. tracheolateralis inserts on the cranial margin of the tracheal drum; right and left intrinsic muscles originate just caudal to that insertion, and insert themselves on A1. Both M. tracheolateralis and the intrinsic muscles are strongly developed into large bellies of muscle fibers. In females, fledglings, and immature males (sex determined by observations of the gonads), M. tracheolateralis continues caudad in a thin sheet of fibers to insert directly on the A1 elements after separating on the ventral midline at A4–8. The muscle has no traces of intermediate insertions before A1 or developed bellies of muscle fibers. The *Pipra aureola* clade is apparently intermediate; one female specimen completely lacks intrinsic muscles and another has weak but completely differentiated intrinsic musculature.

Other piprids differ from the *Pipra erythrocephala* and *Pipra aureola* group in that females and young males have syringeal musculature that is identical in form to adult males but is significantly less developed in mass. This is true of *Ilicura, Corapipo, Masius, Antilophia,* and *Chiroxiphia.*

The sexual dimorphism and ontogeny of M. tracheolateralis and the intrinsic musculature in the *P. erythrocephala* clade support Ames's (1971: 138–140) hypothesis that passerine intrinsic syringeal musculature is ontogenetically derived from undifferentiated M. tracheolateralis fibers. However, it contradicts Ames's (1971: 95–96) generalization that the ontogeny of syringeal musculature is complete by the time of fledging.

Many individuals differ in the degree of symmetry of the syringeal musculature. This muscular asymmetry is associated with the consistent asymmetry of the trachea, which is situated on the right side of the neck and twists clockwise as it proceeds caudad into the interclavicular air sac. Because of this twist, the left M. sternotrachealis has to travel farther from its origin on the craniolateral process of the sternum to its insertion on the trachea. The left M. tracheolateralis is also more exposed ventrally than the right and may be less constricted in development. For the most part, if any asymmetry is present, the left M. tracheolateralis and M. sternotra-

chealis contribute more to the total mass of extrinsic musculature. Usually, intrinsic musculature is not noticeably asymmetrical.

Asymmetry of M. tracheolateralis is extreme in the three species of *Machaeropterus* (character 45). This extreme asymmetry does not appear to be correlated only with the general underdevelopment of the syringeal muscles in this genus. For comparison, the species in the *Pipra serena* group also have poorly developed Mm. tracheolaterales, but they do not have exaggerated asymmetry.

EVOLUTION OF INTERSPECIFIC VARIATION

The syringeal morphology of piprids has undergone an extensive radiation in both supporting element structure and musculature. In this regard, the piprids are similar to other tyrannoids (Ames, 1971; Lanyon, 1984a, 1985, 1986, 1988a, 1988b, 1988c; Prum and Lanyon, 1989) and differ from the oscine passerines, which are characterized by a complex but generally stereotyped syrinx (Ames, 1971, 1975, 1987; Warner, 1972). However, the extent of the interspecific variation in piprids is extreme even within in the generally diverse suboscine groups. Of the 40 species in the family, 25 distinct combinations of syringeal novelties are identifiable. Only a few oscine families are known to have diagnosable syringeal characters (Ames, 1971, 1975, 1987; Warner, 1972; B. D. Cutler *in* Baptista and Trail, 1988).

This extensive variation in syringeal morphology in piprids is used here to reconstruct the phylogeny of the family, but it is of additional interest as an example of syringeal diversification in birds. It may be preferable to make inferences about the process of syringeal evolution in the context of an independent hypothesis of phylogeny based on some other data set, but this syringeal data set is the only complete hypothesis available. However, the patterns of variation are so complex that any phylogenetic hypothesis would indicate that the piprid syrinx has undergone significant changes in supporting element shape, composition and fusion, form and development of musculature, and innervation patterns.

Some syringeal apomorphies have evolved independently many times within this hypothesis of phylogeny for the family. For example, intrinsic syringeal muscles have arisen independently at least four times within the piprids, and have radiated into eight distinct forms. Within the *Manacus-Chiroxiphia-Antilophia* clade, dorsal and ventral intrinsic muscles have evolved subsequent to the evolution of a novel extrinsic muscle insertion. Oblique intrinsic musculature evolved a single time in the *Ilicura-Masius-Corapipo* clade, and subsequently diversified into the distinct single pair and double pair of intrinsic muscles found in these genera. The ventral oblique pair present in *Ilicura* is similar in position and fiber direction to the M. obliquus ventralis present in many tyrannids. Some supporting element novelties have also evolved multiple times within the piprids, such as tracheal fusion of A elements (14–17), and ventral ossification of B elements (36–39).

A striking example of apparently rapid syringeal evolution comes from two sister species, *Pipra serena* and *P. suavissima*. These two differentiated, allopatric geographic forms are currently placed as subspecies of *Pipra serena* (Snow, 1979), but I recognize them here as separate species. *Pipra serena* is found in Suriname, French Guiana, Amapá and Pará Provinces, Brasil. *Pipra suavissima* is found in the western Guiana Highlands region of southern Venezuela, Guyana, and northern Amazonas and Roraima Provinces, Brasil. The males of these two populations differ in the distribution and tone of yellow in the plumage, and the females are similar in plumage but differ in the tone of blue on the crown. The two forms were first combined as subspecies of *Pipra serena* by Hellmayr (1910, 1929). Derived plumage similarities indicate that the two forms are sister taxa (Prum, 1988), but differences in plumage, song, and syringeal morphology between these two allopatric forms indicate that they are separate species with distinct evolutionary histories (Prum, in prep.).

The syrinx of *P. suavissima* is similar to those of other members of the *P. serena* species group, but it is slightly larger and has a series of dorsally cartilaginous single A ele-

ments (fig. 17). The syrinx of *P. serena* has all the typical characters of other members of the species group and the specific features of *P. suavissima,* but is tremendously enlarged in size, distorted in shape, and characterized by a suite of unique morphological details (fig. 18). This suite of features of the syrinx of *Pipra serena* (43) appears to be correlated with its increase in size and the resulting exaggeration and distortion of primitive structures. These rearrangements may have been caused by a single change or mutation in the developmental program of the syrinx.

The doubling in size and tremendous distortion in shape of the syrinx of *serena* have evolved since common ancestry with *suavissima*. These changes have been relatively more rapid and extensive than the change in plumage coloration. The absolute age of these sister species is unknown, but it is apparent that *serena* has undergone a rapid acceleration in the rate of syringeal evolution by the acquisition of a suite of major apomorphies. This extent of syringeal variation between sister species is unprecedented in other birds, and is especially striking given the degree of overall plumage similarity. While it is difficult to compare rates of morphological evolution, such a rapid rate of diversification is probably rare for avian morphological systems.

This case raises the possibility that the evolution of syringeal diversity in the piprids proceeded through the accumulation of apomorphies in rapid "revolutions" in syringeal organization (Gould and Eldredge, 1977).

FUNCTIONAL CONSEQUENCES OF
SYRINGEAL VARIATION

The consensus among functional morphologists is that the medial tympaniform membranes are the main sound sources in the tracheobronchial passerine syrinx (Greenewalt, 1968; Gaunt, 1983; Gaunt and Gaunt, 1985; Brackenbury, 1989; Suthers, 1990). In the absence of direct observations of the medial tympaniform membrane during vocalization, these observations of piprid syringeal morphology confirm that the medial tympaniform membrane is the only feasible vibratile sound source in the piprid syr-

inx. The other potential sound sources—the lateral membranes and the semilunar membrane—are reduced or absent in piprids.

Attempts to correlate syringeal structure with vocal ability have been limited by the extreme complexity of the problem. Ames (1971) summarized the general trend of syringeal and vocal complexity in passerines. He observed that although the simplest syringes do produce simple songs, strong correlations are lacking between syringeal and vocal complexity. Ames concluded that advances in neural control may be more important in the evolution of vocal complexity within the passerines. Gaunt (1983) hypothesized that complex syringeal musculature is necessary for the evolution of vocal complexity, defined as rapid frequency and amplitude modulations. He hypothesized that antagonistic pairs of intrinsic syringeal muscles are necessary to perform fine adjustments of membrane tensions and relative position of syringeal supporting elements. Gaunt found a rough correlation indicating that syringeal muscle complexity was necessary but not sufficient to explain the distribution of avian vocal complexity. No other significant patterns of relationship between syringeal structure and vocal ability have been documented.

All observed variations in supporting elements and musculature of piprid syringes can be hypothesized to have direct or indirect affects on vocalization through the control of the tension, relative position, support, or size of the medial tympaniform membranes. But the actual functional consequences of these structural variations cannot be evaluated or interpreted in terms of present theories of avian vocalization.

Direct electromyographic observations of the extrinsic muscles of some species of birds indicate that they are important in vocal modulation (Brackenbury, 1989), but no direct observations of intrinsic muscle activity during vocalization have been made. The insertion of M. tracheolateralis or intrinsic musculature on the double A elements probably functions to alter the position of these elements and control the acoustical properties of the medial tympaniform membranes they support. However, this apparent functional association does not explain the vari-

ety in dorsoventral differentiation, insertion, and fiber direction of M. tracheolateralis or the intrinsic muscles of piprids.

Piprid intrinsic musculature may insert on the cartilaginous dorsal and ventral ends of A1 (in the oblique muscles of *Corapipo* and *Masius*), on the entire length of a completely ossified A1 (in *Heterocercus,* and the *Pipra aureola* and *Pipra erythrocephala* clades), on the entire cartilaginous A1 (in *Ilicura militaris*), or in a complex insertion on a number of cartilaginous and ossified A elements (in *Chiroxiphia* and *Antilophia*). Intrinsic muscles also vary in the degree of dorsoventral differentiation. In some piprids, the left and right intrinsic muscles are not divided or differentiated into dorsal and ventral bundles of fibers (e.g., *Pipra aureola* and *Pipra erythrocephala* clades), and in others dorsoventral differentiation is complete as in the oblique intrinsic muscles of *Corapipo* and *Masius*.

The simpler extrinsic musculature of some piprids also varies in dorsolateral differentiation. In *Pipra pipra,* M. tracheolateralis is laterally and dorsoventrally differentiated into four parts that insert on the dorsal and ventral ends of A1, but these differentiated caudal parts are completely continuous with M. tracheolateralis and lack any intermediate tracheal insertion or belly. In the *Pipra serena* species group, M. tracheolateralis inserts broadly along A1, but in some individuals of several species, the fibers are weak along the lateral midline producing a partial dorsolateral differentiation.

M. sternotrachealis has been hypothesized to act antagonistically to M. tracheolateralis by pulling the syrinx caudad and lessening tensions on the medial tympaniform membrane (Brackenbury, 1989). In most piprids, Mm. sternotracheales are robust and strongly developed, especially in males. They insert broadly on the lateral and ventral surfaces of Mm. tracheolaterales. The fibers are typically helically coiled between origin and insertion. The one major variation in M. tracheolateralis in piprids is present in the *Pipra aureola* clade. In these three species, Mm. tracheolaterales are short and very robust, and the fibers are straight and not coiled. The muscle attenuates sharply before inserting on the lateral surface of M. tracheolateralis by a thin ligament, and unlike those of

other piprids, few of these M. sternotrachealis fibers are continuous with M. tracheolateralis. Such an insertion would potentially have very different action on the syrinx during vocalization.

The composition and shape of syringeal supporting elements may also have significant effects on vocal control and modulation. Supporting elements should vary significantly in rigidity and mobility depending on whether they are cartilaginous or ossified, independent or fused. The variations in the shape, degree of ossification, and fusion of supporting elements in piprids present a wide array of potential acoustic consequences.

Independent association of some muscular and supporting element novelties may indicate that these structures function together in vocalization. In two phylogenetically independent instances, M. tracheolateralis inserts and the intrinsic muscles originate near the cranial margin of a drum of fused tracheal elements (e.g., *Chiroxiphia* and *Antilophia*; most *Chloropipo, Xenopipo, Heterocercus,* the *Pipra aureola* and *Pipra erythrocephala* clades). A fused drum between the origin and insertion of an intrinsic muscle may serve to minimize tracheal compression and maximize displacement of the caudal A elements during contraction of that muscle. These genera are similar to oscines, in which complex intrinsic muscles originate on the cranial margin of a fused tracheal drum. In contrast, well-differentiated oblique intrinsic muscles appear in the absence of fused tracheal elements in *Corapipo, Masius,* and *Ilicura.* However, these intrinsic muscles act obliquely on the tracheal rings, potentially avoiding tracheal compression and eliminating the necessity of any tracheal fusion. There are additional exceptions to these trends. *Chloropipo uniformis* has intrinsic muscles but has secondarily lost any tracheal fusion. Some specimens of *Machaeropterus deliciosus* have the first two single, tracheal A elements fused dorsally into a partial drum, but this species lacks any intrinsic syringeal musculature.

Piprids also vary in the degree and form of support of the medial tympaniform membrane. In all piprids, B1-2 are dorsally fused, giving additional support to the craniodorsal margin of the medial tympaniform membrane. In the *Pipra aureola* clade and *Ilicura,*

the B elements are quite thin and fragile, and support for the medial tympaniform membrane is minimal. In contrast, in *Manacus,* a caudal series of B elements (typically B5–10) is widened and fused dorsally into an extensive lattice that gives substantial support to each bronchus and to the dorsal edge of the medial tympaniform membrane. In *Corapipo, Masius,* and *Ilicura,* the cranial or craniodorsal margin of the medial tympaniform membrane is supported by an accessory bar of cartilage, subsequently ossified in *C. gutturalis.* In *Chiroxiphia* and *Antilophia,* the ventral wall of the trachea and the ventromedial walls of the bronchi at the tracheobronchial junction are formed by an accessory cartilage sheet that also supports the cranial margin of the medial tympaniform membrane. These structural novelties apparently support or reinforce the medial tympaniform membrane, but their functional roles remain enigmatic.

Gaunt (1983) has discussed the problem of the exaggeration of the stereotypy of the "typical" syrinx in many discussions of avian vocal mechanisms. The syringeal diversity in the piprids provides an opportunity to take advantage of syringeal variation, and investigate the relationship between form and function in vocalization. A rigorous comparative approach to test hypotheses about the evolution of syringeal morphology and function would be to document the phylogenetic patterns in morphological and functional diversity, and test hypotheses for the sequence of morphological and functional transformations based on their hierarchical distribution (Lauder, 1981; Schaefer and Lauder, 1986). Parallel transformational sequences from independent clades would support or refute generalizations about the evolution of the system. Advances in the phylogenetic relationships of tyrannoids will permit detailed investigations of syringeal morphology, function, and evolution that are not possible through gross correlations.

THE TWO-VOICE MODEL AND THE SUBOSCINE SYRINX

Greenewalt (1968) and Stein (1968) documented that the syrinx of many birds contains two acoustically independent sound sources. They identified many examples of simultaneous, harmonically unrelated notes in sonagrams of vocalizations of many oscines and some nonoscine birds. Greenewalt (1968: 60–61) concluded that the ability to vocalize using two independent sound sources could be found in members of "almost every family for which representative recordings are available." Greenewalt's (1968: 61) two-sound-source model "start[s] with the premise that birds can . . . activate their two acoustical sources (the two medial tympaniform membranes) separately and independently, that this ability occurs in all groups of birds, and that the ability to modulate frequency or amplitude or both is available for either sound source." The morphological prerequisites for two-voice sound production are 1) two discrete potentially vibratile membranes, 2) laterally independent syringeal musculature, and 3) independent neural control over the two sides of the syrinx.

Greenewalt's conclusions on the uniformity and ubiquity of the two-voice ability in birds underestimated both their morphological and vocal diversity. Variations in syringeal morphology provide interesting opportunities to test comparatively the morphological assumptions of Greenewalt's two-sound-source model.

The oscines meet the three morphological criteria of the model. They have a pessulus that divides the two medial tympaniform membranes, and they have independent innervation of the intrinsic musculature of both sides of the syrinx. Evidence in support of the two-voice model in oscines has come from several sources. Most recently, Suthers (1990) has gathered direct evidence for the two-voice model in oscines, by recording air pressure in both bronchi during singing. Nottebohm (1971, 1972, 1976) investigated the neurological basis of lateralization and control of the two syringeal sound sources in three oscines (*Serinus serinus, Fringilla coelebs,* and *Zonotrichia leucophrys*), and concluded that selective denervation of one side of the oscine syrinx can result in degradation of some notes in the repertoire with no effect on the form of other notes.

Nottebohm and Nottebohm (1976) did a similar investigation of neural control of vocalizations in the Orange-winged Parrot

(*Amazona amazonica*). Parrots have paired, vibratile lateral tympaniform membranes, and tracheal nerves that anastomose into a single fiber on the ventral surface of the trachea before dividing again into the left and right branches that innervate the intrinsic muscles. Nottebohm and Nottebohm (1976) showed that the left and right tracheal nerves contribute equally to normal vocal control in *Amazona*; selective denervation of one side of the syrinx led to general degradation of all vocalizations, and not to selective loss of a set of independent vocal phrases, as in oscines. Nottebohm and Nottebohm (1976) also failed to detect simultaneous, harmonically unrelated notes in a preliminary investigation of parrot vocalizations.

Variation in the syringeal morphology of the piprids and other suboscines provides additional opportunities to test the two-voice model. In piprids, the medial tympaniform membranes are separated laterally by a pessulus, but the tracheal nerves anastomose on the ventral midline cranial to the innervation of the caudal portion of M. tracheolateralis, M. sternotrachealis, or the intrinsic muscles. Histological or physiological investigations are necessary to confirm that the tracheosyringeal nerves of piprids are not laterally independent despite this anastomosis. However, additional evidence of the absence of neural lateralization in piprids comes from *Chiroxiphia, Antilophia,* and a few specimens of *Manacus.* In these taxa, the tracheosyringeal nerves continue caudad as a single fiber for 0.8–6.0 mm after the ventral anastomosis before dividing again into left and right fibers that innervate the syringeal musculature. This pattern is similar to that of psittacids; Greenewalt's model predicts that piprids should be unable to produce two, acoustically independent sounds.

In other tyrannoids, a pessulus is also present but the tracheosyringeal nerves do not anastomose ventrally. In most cotingids, the nerves remain on the lateral surfaces of the trachea to innervate the muscles of the two sides. In many tyrannids, the tracheosyringeal nerves remain separated on the left and right sides of the trachea, but they exchange secondary, horizontal fibers across the ventral surface of the trachea before innervating the intrinsic muscles.

Elsewhere in suboscines, the pittas (Pittidae) and broadbills (Eurylaimidae) have independent innervation of the two sides of the syrinx, but some species lack a pessulus dividing the medial tympaniform membranes and most lack intrinsic muscles (Köditz, 1925; Ames, 1971; Prum, in prep.). The furnarioids have paired dorsal and ventral tracheal membranes and a single undivided medial tympaniform membrane (Ames, 1971; Prum, personal observ.), but the innervation of the furnarioid syrinx has not been described. The morphological prerequisites of the two-voice model are absent in some of these species, leading to the prediction that they should be unable to produce two independent sounds.

Previous analyses of suboscine vocalizations have not been thorough enough to document accurately the systematic distribution of two-voice ability within this diverse clade. Stein (1968) did not include any suboscines in his analysis. Greenewalt (1968) apparently analyzed some North American tyrannids and other suboscines, but found evidence of two independent sound sources only in the cotingid *Procnias nudicollis,* the Bare-throated Bellbird. Like other cotingas, *Procnias* meets all three morphological criteria for two-voice production: independent medial tympaniform membranes, laterally independent syringeal innervation, and laterally independent muscles. But *Procnias* also has well developed intrinsic muscles which are absent in nearly all other cotingas (Prum, personal observ.). No information is available on two-voice vocal ability in other tyrannoids, furnarioids, or Old World suboscines.

Additional surveys of suboscine vocalizations could provide an important comparative test of Greenewalt's two-voice model. This test is complicated by the possibility that Greenewalt's morphological criteria may be necessary but not sufficient to explain the evolution of the behavior. Some tyrannids appear to "fit the bill" but apparently lack two-voice control, indicating a possible additional role for neural control, as hypothesized by Ames (1971) and Gaunt (1983). Furthermore, laterally differentiated intrinsic muscles may be an additional prerequisite for two-voice ability, as in *Procnias.* A phylogenetic test of Greenewalt's model would compare the phylogenetic distribution of these

morphological traits and two-voice ability, and examine the sequence of functional change in independent lineages. Despite recent confirmation of two-voice model in oscines (Suthers, 1990), comparative tests would evaluate the generality of the model.

VOCAL LEARNING, LEK BEHAVIOR, AND SYRINGEAL EVOLUTION

The striking syringeal diversity of piprids and other suboscines requires some general explanation. The oscine passerines are more than four times as diverse as the suboscines in numbers of biological species (Bock and Farrand, 1980), yet the oscine syrinx is comparatively stereotyped. There are few known variations in oscine supporting elements and musculature even though the oscine syrinx is muscularly more complex (Ames, 1971, 1975, 1987; Warner, 1972). This difference in diversity of syringeal morphology between oscines and suboscines is associated with another major difference in their vocal behavior. Oscines generally learn their songs (Kroodsma, 1982), whereas the limited available evidence indicates that suboscine vocalizations are innate (Kroodsma, 1982, 1984). If there is any correlation between syringeal structure and function, then selection on innate vocalizations will produce correlated evolution in syringeal structure. In contrast, selection on learned vocalizations will not lead to evolution of sound-producing organs but to social evolution of culturally transmitted behaviors. Syringeal morphology should be less subject to selection when interindividual vocal variation is the result of learning. This general model is congruent with the differences in syringeal diversity of the oscine and suboscine passerines, and could be further tested with comparisons of syringeal diversity in closely related clades that differ in vocal learning ability.

There are several potential sources of selection on vocalizations. For example, vocalizations could be selected for efficiency of acoustic transmission (Wiley and Richards, 1982). Vocalizations that are part of breeding behavior could also be subject to sexual selection (Payne, 1983; West-Eberhard, 1983).

Sexual selection based on female preference for heritable variation in male traits should produce more rapid evolution of male traits than natural selection (West-Eberhard, 1983; Lande, 1981). If the intensity of sexual selection on song varies in related clades in which vocalizations are innate, then this model further predicts that syringeal diversification will be more rapid and more extensive in clades that have undergone significantly higher levels of sexual selection. It is difficult to quantify syringeal variation in a clade or compare unique morphological novelties of separate clades, but it would be interesting to pursue this possibility with comparative tests of syringeal diversity in clades which differ in breeding system and therefore in the intensity of sexual selection.

An intriguing preliminary association between syringeal morphology and breeding behavior is also apparent in this investigation. Many male piprids produce mechanical wing noises as part of their courtship displays; however, one exploded lek species, *Machaeropterus deliciosus,* uses mechanical wing noises exclusively as territorial advertisement calls (Willis, 1966; Prum, personal observ.); male vocalizations are simple and infrequent (Prum, personal observ.). *Machaeropterus deliciosus* differs strikingly from all other piprids, including its congeners *M. regulus* and *pyrocephalus,* in that the syringeal musculature of both adult males and females is largely undeveloped. Further, all other known manakins, including *Machaeropterus regulus* (Prum, personal observ.), vocalize frequently on their display territories. This unique secondary loss of developed syringeal musculature in *M. deliciosus* is associated with the evolution of obligate mechanical wing noise production and the reduction of male vocalization. The correlation of these two unique factors indicates that replacement of vocal behavior by other means of acoustic communication can lead to a degeneration of syringeal morphology and reduction in vocal ability.

The extraordinary behavior of *M. deliciosus* has few, if any, parallels in other birds that might permit us to test this intriguing hypothesis. Likewise, the differences between *Pipra serena* and *P. suavissima* described

above may be a unique example of especially rapid syringeal evolution. But both findings underscore the conclusion that syringeal evolution in piprids has been very dynamic. Future models of syringeal evolution and function must take into account the diversity and plasticity of the syrinx in suboscine birds. Detailed, comparative investigations of syringeal morphology and vocalizations in piprids and other suboscines should lead to advances in our understanding of the relationship between syringeal evolution, vocal complexity, and avian natural history.

PHYLOGENETIC CLASSIFICATION OF THE PIPRIDS

The currently accepted classification of the Pipridae (Snow, 1975, 1979) is based almost entirely on Hellmayr's (1910, 1929) diagnoses of piprid genera using male plumage characters. Snow (1975, 1979) subsequently lumped some monotypic genera and rearranged the order of the genera to reflect the degree of development of polygynous display behavior within the family. Although the syringeal hypothesis of phylogeny may be altered by future investigations of other morphological or molecular character systems, a phylogenetic classification of the piprids is proposed here as an advance over the current, eclectic classification that is based solely on overall plumage and behavioral similarity (Snow, 1975, 1979).

The proposed phylogenetic classification reflects the syringeal hypothesis of phylogeny (figs. 24, 25) by recognizing monophyletic taxa. To simplify the number of named groups, I use a phylogenetic ranking convention by which subcategories of equal rank are each the sister group to the remaining taxa of the same level within that higher category (Raikow, 1985). Areas of ambiguity in the consensus tree are indicated by the placement of a taxon as sedis mutabilis (s.m.) within a monophyletic higher taxon; a taxon labeled sedis mutabilis has unresolved phylogenetic relationships to the other taxa of that level in the same higher category (Raikow, 1985).

In order to conform to these phylogenetic classification criteria, several paraphyletic or polyphyletic traditional generic groups are changed, and four new tribes are named. In figure 26, I present the syringeal hypothesis of phylogeny that incorporates the taxonomic changes which are described fully below.

The genera *Chloropipo* and *Xenopipo* form a clade, but *Chloropipo* is paraphyletic. *Chloropipo uniformis* shares several unique syringeal synapomorphies with *Xenopipo atronitens*. Additional syringeal and plumage characters indicate that *Chloropipo unicolor* and *flavicapilla* are the sister group to this clade (Prum, in prep.). The paraphyletic genus *Chloropipo* should be combined with *Xenopipo* in a single monophyletic genus. The name *Xenopipo* Cabanis 1847 has priority over *Chloropipo* Cabanis and Heine 1859, so all five species in this clade are placed in the genus *Xenopipo* in the proposed classification.

The genus *Pipra* is polyphyletic. *Heterocercus* is more closely related to the *Pipra aureola* and *erythrocephala* clades than is *Pipra pipra*. Although the syringeal characters do not completely resolve the relationships of the *serena* group, they strongly indicate that the *serena* group is unrelated to other species currently placed in *Pipra*, and more closely related to *Manacus*, *Chiroxiphia*, and *Antilophia*. The monophyly of the *serena* species group is accepted here based on plumage characters discussed above. The three clades currently placed in the polyphyletic genus *Pipra*—the *aureola-erythrocephala* clade, the species *pipra*, and the *serena* group—should each be recognized as separate genera.

The type of the genus *Pipra* Linnaeus is *Parus aureola* Linnaeus (by subsequent designation; Gray, 1840: 33). The *Pipra aureola-erythrocephala* clade should retain this genus name. Within this restricted genus *Pipra*, I recognize two subgenera: the subgenus *Pipra* with the type species *aureola* Linnaeus to include *aureola*, *filicauda*, and *fasciicauda*; and the subgenus *Ceratopipra* with the type species *cornuta* Spix to include *cornuta*, *mentalis*, *chloromeros*, *rubrocapilla*, and *erythrocephala*. *Ceratopipra* is an available junior synonym of *Pipra*, and its type species is *Pipra cornuta* Spix.

The generic names *Dixiphia* Reichenbach

1850, *Lepidothrix* Bonaparte 1854, and *Dasyncetopa* Bonaparte 1854 are available for *pipra* and the *serena* species group. *Dixiphia* has priority over the other two names, which both date from the same publication (Bonaparte, 1854). The type species of *Dixiphia* is *leucocilla* Linnaeus (= *pipra* Linnaeus), so *Dixiphia* should be applied to the species *pipra*. The type species of *Lepidothrix* is *cyanocapilla* Hahn (= *coronata*; type by subsequent designation, Gray, 1855). The type species of *Dasyncetopa* is *serena* (by monotypy). Both *coronata* and *serena* are in the *serena* clade, so either name is available. Priority among available names which date from the same publication should be set by the first reviser (International Code of Zoological Nomenclature, 1985). *Lepidothrix* is here recommended to have priority over *Dasyncetopa* because its etymology is more appropriate, and it appears first in the original publication (Bonaparte, 1854). *Lepidothrix* is apparently derived from the Latin *lepidus* (pretty) and the Greek *thrix* (hair). I could not determine an obvious etymology for *Dasyncetopa*, but it may be derived from the Latin *dasys* (hairy) and the Greek *ceo* (split) and *topos* (place). In the proposed phylogenetic classification, the *serena* clade is placed in *Lepidothrix*.

Alternatively, it would also be possible to recognize a reconstituted genus *Pipra* to include the *aureola-erythrocephala* clade, *Heterocercus*, and the species *pipra*, but this would eliminate the informative monophyletic genus *Heterocercus* from the classification. Likewise, it would be possible to recognize a more restricted genus *Pipra* to include only the three species of the *aureola* clade, and to place the five species of the *erythrocephala* clade in separate genus, for which the name *Ceratopipra* Bonaparte is available. I have chosen the proposed limits to the genus *Pipra* to emphasize the monophyly of these eight species. The monophyly of the *aureola* and *erythrocephala* clades themselves is more widely appreciated because of their recognition as species groups in recent classifications and biogeographic analyses (Haffer, 1974; Snow, 1975, 1979). However, the monophyly of the combined *aureola* and *erythrocephala*

clades is a novel hypothesis that is well corroborated here by syringeal synapomorphies and elsewhere by derived behavioral traits (Prum, 1990a).

Traditional systematists may see this application of genus group names as overly restrictive or narrow. For example, Sibley (1957) maintained that the piprids were "oversplit" at the generic level because of the reliance on male secondary sexual plumage characters for generic diagnoses. However, 33 of the 40 species in the family were originally described as members of the genus *Pipra* and were eventually moved into seven other genera (Hellmayr, 1910, 1929; Snow, 1979). The history of the classification of the piprids has been the gradual restriction of the genus *Pipra* and the recognition of smaller distinct genera. Most of these genera have been corroborated as monophyletic in this investigation. This proposed classification extends the dismantling of the polyphyletic genus *Pipra* to include the last taxa in the genus whose generic relationships have never been critically evaluated. Recognition of a restricted, monophyletic *Pipra*, a monotypic *Dixiphia*, and novel, monophyletic *Lepidothrix* will reflect more accurately the phylogenetic history of these species and expedite explicit evolutionary analyses based on taxonomy.

Four new tribes of piprid genera are created to reflect the higher-level structure in the syringeal hypothesis of phylogeny. Each tribe name is based on the oldest generic name in that tribe. The tribe Ilicurini is created to include *Ilicura, Masius,* and *Corapipo*. It is placed first in the sequence to indicate that it is the sister group to all other piprids. The tribe Machaeropterini includes *Machaeropterus* only and is labeled sedis mutabilis to indicate that it has unresolved relationships to the two remaining, monophyletic piprid tribes. The tribe Manacini includes *Lepidothrix* sedis mutabilis, *Manacus, Antilophia,* and *Chiroxiphia*. The last tribe Piprini contains *Xenopipo, Dixiphia, Heterocercus,* and *Pipra*. Within tribes, the order of genera follows the ranking convention, so that *Xenopipo* is the sister group to the rest of the Piprini, etc.
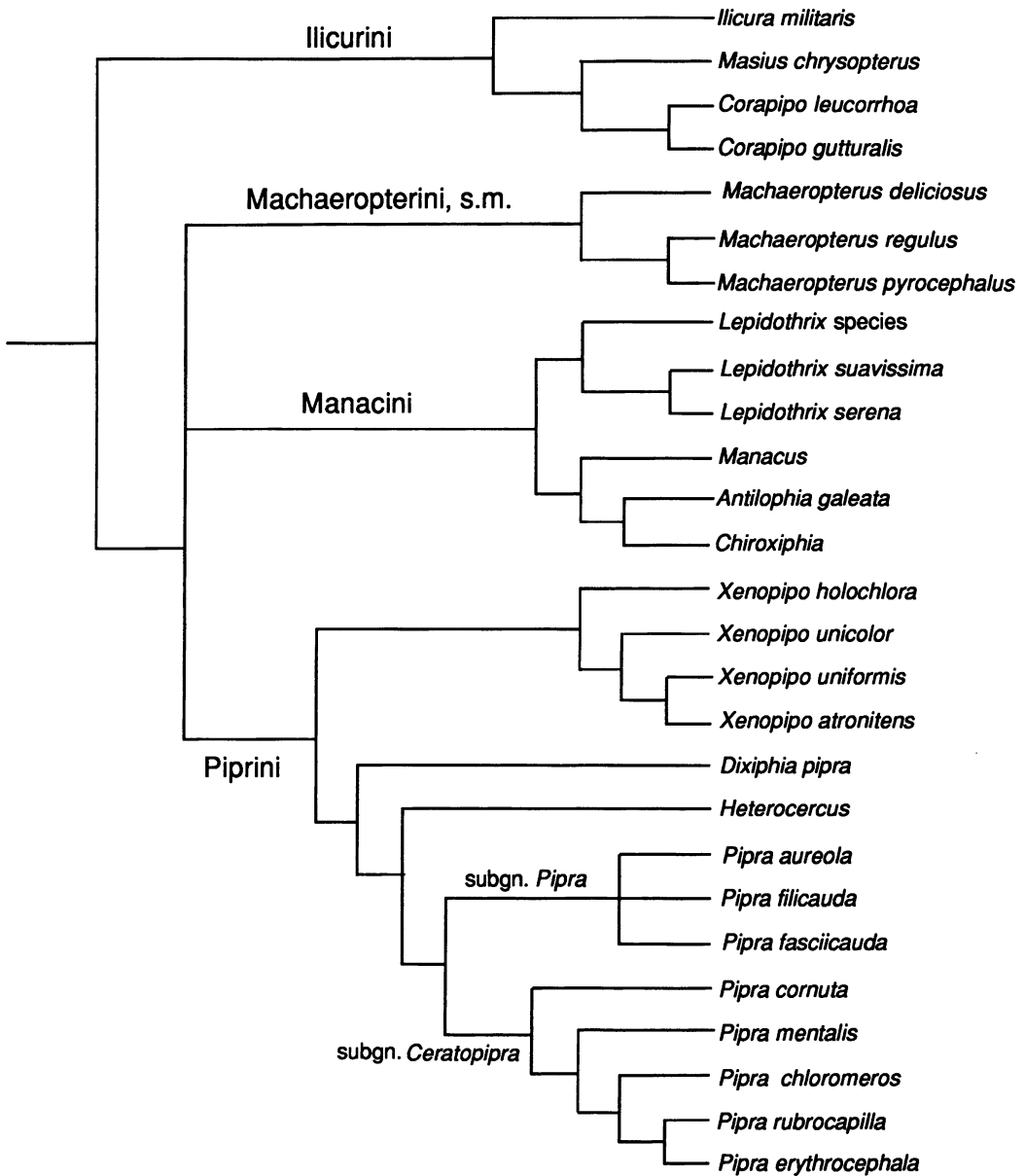
Fig. 26. A phylogenetic hypothesis for the piprids incorporating taxonomic changes of the proposed phylogenetic classification of the family. The four new tribes are: Ilicurini; Machaeropterini, s.m.; Manacini; and Piprini. The genera *Chloropipo* and *Xenopipo* are combined into the single senior generic group name *Xenopipo*. The polyphyletic genus *Pipra* is split. The *aureola* and *erythrocephala* clades remain in *Pipra,* in the separate subgenera *Pipra* and *Ceratopipra*. The species *pipra* is placed in the monotypic genus *Dixiphia*. The *serena* species group is placed in the available generic name *Lepidothrix*. See text for details and classification.

Family PIPRIDAE

Tribe Ilicurini, new; type—*Ilicura* Reichenbach
 Genus *Ilicura* Reichenbach
  Ilicura militaris (Shaw and Nodder)
 Genus *Masius* Bonaparte
  Masius chrysopterus (Lafresnaye)
 Genus *Corapipo* Bonaparte
  Corapipo leucorrhoa (Sclater)
  Corapipo gutturalis (Linnaeus)
Tribe Machaeropterini, new, s.m.; type—*Machaeropterus* Bonaparte
 Genus *Machaeropterus* Bonaparte
  Machaeropterus deliciosus (Sclater)
  Machaeropterus regulus (Hahn)
  Machaeropterus pyrocephalus (Sclater)
Tribe Manacini, new; type—*Manacus* Brisson
 Genus *Lepidothrix* Bonaparte, s.m.
  Lepidothrix coronata (Spix), s.m.
  Lepidothrix isidorei (Sclater), s.m.
  Lepidothrix coeruleocapilla (Tschudi), s.m.
  Lepidothrix nattereri (Sclater), s.m.
  Lepidothrix vilasboasi (Sick), s.m.
  Lepidothrix iris (Schinz), s.m.
  Lepidothrix suavissima (Salvin and Godman)
  Lepidothrix serena (Linnaeus)
 Genus *Manacus* Brisson
  Manacus manacus (Linnaeus), s.m.
  Manacus vitellinus (Gould), s.m.
  Manacus candei (Parzudaki), s.m.
 Genus *Antilophia* Reichenbach
  Antilophia galeata (Lichtenstein)
 Genus *Chiroxiphia* Cabanis
  Chiroxiphia caudata (Shaw and Nodder), s.m.
  Chiroxiphia linearis (Bonaparte), s.m.
  Chiroxiphia lanceolata (Wagler), s.m.
  Chiroxiphia pareola (Linnaeus), s.m.
Tribe Piprini, new; type—*Pipra* Linnaeus
 Genus *Xenopipo* Cabanis
  Xenopipo holochlora (Sclater)
  Xenopipo unicolor (Taczanowski), s.m.
  Xenopipo flavicapilla (Sclater), s.m.
  Xenopipo uniformis (Salvin and Godman)
  Xenopipo atronitens Cabanis
 Genus *Dixiphia* Reichenbach
  Dixiphia pipra (Linnaeus)

 Genus *Heterocercus* Sclater
  Heterocercus aurantiivertex Sclater and Salvin, s.m.
  Heterocercus flavivertex Pelzeln, s.m.
  Heterocercus linteatus (Strickland), s.m.
 Genus *Pipra* Linnaeus
  Subgenus *Pipra*, new; type—*Pipra aureola* (Linnaeus)
  Pipra aureola (Linnaeus), s.m.
  Pipra fasciicauda Hellmayr, s.m.
  Pipra filicauda Spix, s.m.
  Subgenus *Ceratopipra*, new; type—*Pipra cornuta* Spix
  Pipra cornuta Spix
  Pipra mentalis Sclater
  Pipra chloromeros Tschudi
  Pipra rubrocapilla Temminck
  Pipra erythrocephala (Linnaeus)

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APPENDIX

List of piprid syringeal specimens observed. Syringeal specimens were either cleared and double stained (C&S) for cartilage and bone (Dingerkus and Uhler, 1977) or stained with reversible iodine stain (IS) for observation of muscle fibers (Bock and Shear, 1972). Specimens were borrowed from various institutions, and abbreviations are given in the introduction. Uncataloged specimens are identified by the original collector's number in parentheses.

Corapipo leucorrhoa — C&S: LSUMZ 102429, 108441. IS: LSUMZ 104779, 108683; MVZ 4801, 4802, 4804; USNM 510718, 510719; UMMZ 226607, 226608, 226609, 226610.

Corapipo gutturalis — C&S: AMNH 2256, BM 1968.46.17.

Masius chrysopterus — C&S: CM 1161, LSUMZ 117121. IS: BM A/1968-3-12; LSUMZ 83866, 89470; UMMZ 225059, 226604, 226605, 226606.

Ilicura militaris — C&S: FMNH 107023, 107029. IS: FMNH 107028, 107030; MZUSP uncat.

Manacus candei — C&S: AMNH 6654.

Manacus vitellinus — C&S: AMNH 8084; LSUMZ 108418, 108423.

Manacus manacus — C&S: AMNH 7707, 7710, 8147. IS: LSUMZ 35355, 112833, 112834, 114482, 114483; ROM 107498, 113119, 127649; USNM 515118, 515119.

Chiroxiphia linearis — C&S: AMNH 3671, 3672. IS: USNM 541043, 541044, 541045, 541046, 541048.

Chiroxiphia lanceolata — C&S: CM 373.

Chiroxiphia pareola — C&S: AMNH 8080, LSUMZ 95546. IS: LSUMZ 95548, 123335, 131837; MPEG 5701; MZUSP uncat.; UMMZ 225060, 225061, 225062.

Chiroxiphia caudata — C&S: AMNH 2447, 2525, 2526. IS: FMNH 107322, 107323, 107334.

Antilophia galeata — C&S: BM 1968.66.-205. IS: MPEG 7296, 7297; ZUB 88008, 88015, MAM-1988.

Machaeropterus regulus — C&S: LSUMZ 85980, 85981, 115836, KU 66684. IS: LSUMZ 111081, 114486, 120584; UMMZ 225052.

Machaeropterus pyrocephalus — C&S:

FMNH 289998. IS: FMNH 290401, 322567; LSUMZ 79589, 131842, 131844, 131845; MPEG 4080, 5860, 5861, 5863.

Machaeropterus deliciosus — C&S: AMNH 8713. IS: BM A/1986-3-1; UMMZ 225054, 225055, 225056, 225057.

Chloropipo holochlora — C&S: LSUMZ 112837; KU 60693, 65552. IS: UMMZ 225045, 225046, 225047, 225048, 225049, 225050, 225051, 226601.

Chloropipo flavicapilla — no specimens observed.

Chloropipo uniformis — C&S: AMNH 7680. IS: AMNH 10378, 10379, 10407; USNM 504508, 504509, 504510.

Chloropipo unicolor — C&S: LSUMZ 71544, 89472. IS: LSUMZ 70637, 71541, 71543, 89471, 89474.

Xenopipo atronitens — C&S: AMNH 8083, 8152. IS: AMNH 18118; MPEG 4099, 4619, 5849, 5850.

Heterocercus flavivertex — C&S: AMNH 9840, 15203, 15204; USNM 504517. IS: AMNH 9374; COP ML-1983, ML-1987.

Heterocercus linteatus — C&S: FMNH 330655. IS: MPEG 4129, 5836.

Heterocercus aurantiivertex — no specimens observed.

Pipra coronata — C&S: AMNH 2257, 9838, 15194, 15199; LSUMZ 102412, 102419. IS: UMMZ 225063, 225064, 225065, 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; MPEG 1979, 1980, 1981, 1983, 3739, 3740, CG-1105.

Pipra vilasboasi — no specimens observed.

Pipra iris — C&S: AMNH 9892. IS: AMNH 17691; MPEG 4590, 4784, 5838, 5840.

Pipra suavissima — C&S: AMNH 9366, 9368, 816768. IS: BM A/1968-46-19; AMNH 10326, 10327.

Pipra serena — C&S: ROM 127643, 127657.

Pipra pipra — C&S: AMNH 2259, 8145, 9358. IS: CM 1395, 1442, 1446; LSUMZ 118022, 118027, 118028, 118030; ROM 107489, 107637, 112440; UMMZ 226613; USNM 515095, 515100, 515101.

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; KU 66660. IS: UMMZ 225067, 225068, 225069, 225070, 226603.

Pipra mentalis — C&S: LSUMZ 95070; UMMZ 226611. IS: UMMZ 226612; USNM 510741, 510743, 510746, 510747.

Pipra erythrocephala — C&S: AMNH 8081, 9839, 15178; LSUMZ 108388, 108390, 110345, (SWC-1412). IS: BM A/1970-34-1; UMMZ 225071, 225073, 225074, 225075.

Pipra rubrocapilla — C&S: AMNH 2517, 2520; BM 1933.2.4.1. 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: AMNH 10484, 10485, 10486, 10487, 10488, 10489, 10490, 10491; USNM 504506, 504507.