A Phylogeny of the Thirty-Two Genera in the *Elaenia* Assemblage of Tyrant Flycatchers

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ABSTRACT

Shared derived characters from cranial and syringeal morphology are the basis for the development of a phylogeny for those genera of tyrant flycatchers that make up the bulk of two of Hellmayr's (1927) subfamilies, the Serpophaginae and Elaeniinae, along with a few genera at the end of his Euscarthminae. Monophyly of this assemblage is established solely on the basis of a derived configuration of the nasal septum in which the trabecular plate is described as being within the septum. Putative relatives that do not share this derived condition are excluded from this assem-

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blage: *Phyllomyias* (sensu stricto), *Tachuris, Xenopsaris, Culicivora,* the "tody-tyrants," and the "flatbills."

Generic limits and relationships of the 32 genera admitted to the *Elaenia* assemblage are determined primarily by the morphology of the syrinx, and secondarily by cranial characters, nesting behavior, and external morphology. Variation in the basic configuration of the tracheobronchial junction of the syrinx and in the support for each bronchus provides the basis for defining five primary lineages within the assemblage.

The largest of these lineages, in which there is fusion of the A elements to form a drum and a uniquely shaped pessulus, is dominated numerically by *Elaenia, Tyranniscus, Myiopagis, Serpophaga,* and *Anairetes,* and in addition includes *Tyrannulus, Ornithion, Camptostoma, Mecocerculus,* two groups of species formerly in *Mecocerculus, Uromyias, Suiriri, Pseudocolopteryx, Polystictus, Capsiempis, Phaeomyias,* and *Nesotriccus.*

The next largest lineage, in which one A element forms a complete ring around each bronchus, is dominated numerically by *Phylloscartes, Zim-*

merius, Mionectes, and *Leptopogon,* and in addition includes *Inezia, Sublegatus, Myiotriccus,* and two groups of species formerly in *Myiophobus.*

Three smaller lineages, in which there is no complete A ring around either bronchus, have unresolved relationships with each other and the two larger groups. One of these consists of *Stigmatura* and *Pseudelaenia,* a new genus for *leucospodia* Taczanowski, 1877, both of which have the dorsal ends of three pairs of A elements connected by a cartilaginous bronchial plate to which are attached large internal cartilages. A second consists of *Pseudotriccus* and *Corythopis,* which possess a uniquely shaped pessulus. The enigmatic *Euscarthmus* belongs in this assemblage but has no obvious close relatives; the tracheobronchial junction is unlike that of the other lineages.

The fact that most of these groups, as defined by shared derived syringeal morphology unique among tyrant flycatchers, heretofore have not been considered monophyletic illustrates the difficulties in identifying natural groups of flycatchers on the basis of external morphology, the classical methodology.

RESUMEN

Características compartidas y derivadas de la morfología del cráneo y de la siringe son la base para el diseño de una filogenia de los géneros de atrapamoscas tiránidos que constituyen el grueso de dos de las subfamilias de Hellmayr (1927), Serpophaginae y Elaeniinae, junto con unos pocos géneros al final de su Euscarthminae. Se establece la monofilia de este conjunto basándose solamente en la configuración derivada del septum nasal en el cual la placa trabecular se describe como presente dentro del septum. Los géneros putativos que no comparten esta condición derivada están excluidos de dicho conjunto: *Phyllomyias* (sensu stricto), *Tachuris, Xenopsaris, Culicivora,* los "tody tiranos," y los "pico-plano."

Los límites genéricos y las relaciones de los 32 géneros aceptados en el conjunto de *Elaenia* son determinados principalmente por la morfología de la siringe, y en segundo lugar, por las características craniales, el comportamiento de anidación y morfología externa. Variación en la configuración básica de la confluencia traqueobranquial de la siringe y en el soporte para cada bronquio proveen las bases para definir cinco linajes primarios dentro de este conjunto.

El linaje más grande, en la cual existe fusión de los elementos A para formar un tambor y un "pessulus" de forma única, está dominado numéricamente por *Elaenia, Tyranniscus, Myiopagis, Serpophaga,* y *Anairetes,* en adición, se incluyen

Tyrannulus, Ornithion, Camptostoma, Mecocerculus, los dos grupos de especies antes incluidos en *Mecocerculus, Uromyias, Suiriri, Pseudocolopteryx, Polystictus, Capsiempis, Phaeomyias,* y *Nesotriccus.*

El siguiente mayor linaje, en el cual un elemento A forma un anillo completo alrededor de cada bronquio, está dominado numéricamente por *Phylloscartes, Zimmerius, Mionectes,* y *Leptopogon*; en adición, se incluye *Inexia, Sublegatus, Myiotriccus,* y dos grupos de especies antes incluidos en *Myiophobus.*

Tres linajes menores, en las cuales no existe un anillo A alrededor de los dos bronquios, no tienen relaciones definidas uno con el otro ni con los grupos mayores. Uno de estos linajes consiste de *Stigmatura* y *Pseudelaenia,* un nuevo género para *leucospodia* Taczanowski, 1877. Estos dos últimos tienen la parte dorsal terminal de tres pares de elementos A conectados por una placa cartilaginosa bronquial a la cual están adheridos grandes cartílagos internos. El segundo linaje consiste de *Pseudotriccus* y *Corythopis* que posee un "pessulus" de forma peculiar. El enigmático *Euscarthmus* pertenece a este conjunto pero no tiene relativos cercanos obvios. Su confluencia tráqueobranquial es diferente de la de los otros linajes.

El hecho de que la mayoría de estos grupos comparten la morfología siringeal derivada, única en-

tre los atrapamoscas tiránidos, no haya sido tratada monofiléticamente, ilustra la dificultad para la determinación de grupos naturales de atrapamoscas basándose en la morfología externa que es la metodología clásica.

INTRODUCTION

Shared derived characters from cranial and syringeal morphology have proven effective in reconstructing phylogenies for a number of assemblages of genera of tyrant flycatchers (Tyrannidae): the kingbirds and their allies (Lanyon, 1984b), the myiarchines (Lanyon, 1985), the 33 genera in the *Empidonax* assemblage (Lanyon, 1986), and the tody-tyrants (Lanyon, MS). The assemblage for which a phylogeny is developed in this report consists of genera that, with few exceptions, make up the bulk of two of Hellmayr's (1927) subfamilies, the Serpophaginae and Elaeniinae, along with a few genera at the end of his Euscarthminae (presumably thought to be transitional to the Serpophaginae). Warter (1965), working with cranial characters, acknowledged the difficulty in recognizing boundaries between these subfamilies of "smaller flycatchers" and suggested reducing two of them to tribal rank (the Elaeniini and Serpophagini). Traylor (1977) concluded that all of Warter's tribes of small flycatchers "seem to merge into each other so insensibly that no divisions can be recognized," and he adopted a classification for Peters' Check-list in which these taxa were brought together in a single subfamily, the Elaeniinae. It is this latter group, modified by the addition of a few genera and by the exclusion of the "tody-tyrants" and the "flatbills" (best considered as separate assemblages, to be discussed elsewhere) and given the working name of the *Elaenia* assemblage, that is the subject of this report.

METHODS

In developing my concepts of relationships among the tyrant flycatchers, I have been greatly influenced by landmark studies of the tyrannoid skull by Warter (1965) and of the suboscine syrinx by Ames (1971), and I follow the terminology of those authors. Each of these morphological complexes has its greatest utility at a different hierarchical level, and I have benefited from acquiring personal familiarity with the clues to genealogy that each provides. Syringeal morphology supplies information for determining the limits of genera and for clustering related genera, but, with few exceptions, is not useful at the higher taxonomic levels. Cranial characters, on the other hand, can provide data that enable us to establish relationships *between* clusters of genera, leading to recognition of large assemblages and subfamilies. Warter (1965) and Ames (1971), working independently, each with his own character complex, had insufficient information for establishing phylogenies.

Historically, students of tyrant flycatchers have not concerned themselves with the necessity of establishing monophyletic groups within the family. Following the practice of the time, genera were clustered almost exclusively on general considerations of external morphology (form of the bill, shape of the wing and tail, color and pattern of plumage), on habitat and distribution, and to a lesser degree on similarities in nesting behavior.

Monophyly of each of my assemblages of tyrant flycatchers rests on the evidence for shared derived states of the nasal septum. As Warter (1965) reported, the septum in most birds is essentially unossified; little remains for study in the cleaned skull maintained in museum collections. The widespread occurrence of this unossified state in birds in general suggests that it is the primitive condition, and the ontogenetic transformation from membrane, through cartilage, to bone could also be interpreted as support for the hypothesis that the primitive state is the unossified septum. Among the tyrant flycatchers there is an array of character states of the nasal capsule, from the presumed primitive condition in "flatbills" and "tody-tyrants," through the fully ossified but unmodified or unspecialized septum of the kingbirds and their allies, to the septum of the *Empidonax* assemblage in which there is a transverse trabecular plate located basally. The very different appearing nasal septum of *Elaenia* and

its allies, with its trabecular plate located within the septum, is discussed in detail in my argument for monophyly of this assemblage.

The syrinx is less conservative than the skull and variability in its morphology is my principal basis for determining the primary lineages within the assemblage, and for clustering and defining the limits of genera. Unfortunately, from the standpoint of establishing polarity of character states, we do not as yet have a clear understanding of the "ancestral form of the syrinx." It is unclear whether it will be possible to establish with great confidence transformation series for the character states in the morphology of the tyrannid syrinx. At the present state of knowledge, the uniqueness of distribution of the character state indicates the derived condition. Study of the number, shape, and position of the bony and cartilaginous supporting elements in the syrinx was facilitated by double-staining with alcian blue for cartilage and alizarin red for ossified bone (after Dingerkus and Uhler, 1977).

After monophyly is established based on syringeal characters, relationships within clusters of genera are established by considering derived states in three areas: (1) other cranial characters, (2) nesting behavior, and (3) external morphology. Other derived cranial characters include the obliteration (through ossification) of the superior fenestra of the interorbital septum, and ossification of the alinasal turbinals and walls. The derived pattern of nesting behavior in this assemblage is the construction of an enclosed nest, with side entrance, which has apparently evolved independently in two different lineages. External morphological characters that have some utility, once monophyly has been established for a group of genera, are the shape and pattern of the tail and the presence of a concealed crown patch or other specialization of the feathering of the crown. There is no sexual dimorphism in plumage coloration and pattern sufficient enough to make identity of the sexes apparent in the field, as there is in the *Empidonax* assemblage and in some of the tody-tyrants.

Character states are identified which separate a genus or cluster of genera; their assigned numbers in the text correspond to the numbers in the phylogenetic diagrams and their corresponding tables.

It would be premature and presumptuous for me, at this early stage, to use formal subfamily names to identify my assemblages of tyrant genera. But some designation is necessary and I prefer to use the oldest generic name available, particularly if it is a large genus and representative of the entire group. Thus, *Myiarchus* was available for the myiarchine flycatchers, and *Tyrannus* for the kingbirds and their allies. In the absence of a suitable older name, I selected the largest genus, *Empidonax,* as the basis for a working name for its assemblage. In the present study, I chose *Elaenia,* the oldest name among several large, representative genera.

I consider the tyrant flycatchers (Tyrannidae) to be a monophyletic group on the basis of the internal cartilages of the syrinx, structures uniquely derived within all suboscine birds. The exact limits of the Tyrannidae, particularly with respect to *Oxyruncus* and certain genera of manakins (Pipridae), have yet to be determined (Ames, 1971; Lanyon, unpubl.; McKitrick, 1985). For my outgroup comparisons I have examined the skulls of 143 and the syringes of 146 of the 151 genera of New World Tyrannoidea (Tyrannidae, Pipridae, and Cotingidae). Within the Tyrannidae (sensu Traylor, 1979), I have examined over 900 skulls of 89 of the 90 genera, over 850 syringes of all 90 genera, and have data on nesting behavior for 81 of these genera.

In addition to the anatomical collections at the American Museum of Natural History (AMNH), New York, I borrowed specimens from the Academy of Natural Sciences, Philadelphia; the British Museum (Natural History) (BMNH), Tring; the Carnegie Museum of Natural History (CMNH), Pittsburgh; the Charles R. Conner Museum at Washington State University (CCM), Pullman; the Delaware Museum of Natural History (DM), Greenville; the Field Museum of Natural History (FMNH), Chicago; the Los Angeles County Museum of Natural History (LACM), Los Angeles; the Museu de Ciências Naturais (MCN), Porto Alegre, Brazil; the Museu Parense Emilio Goeldi (MG), Belém, Brazil; the Museum of Natural History at the University of Kansas (UK), Lawrence; the

Museum of Zoology at Louisiana State University (LSU), Baton Rouge; the Museum of Zoology at the University of Michigan (UMMZ), Ann Arbor; the Museum of Vertebrate Zoology at the University of California (MVZ), Berkeley; the National Museum of Natural History, Smithsonian Institution (USNM), Washington, D.C.; the Peabody Museum of Natural History at Yale University (PMNH), New Haven; the collection of Peter L. Ames (PA); the collection of Pierce Brodkorb (PB); the Rijksmuseum van Natuurlijke Histoire (RNH), Leiden; the Royal Ontario Museum (ROM) in Toronto, Canada; and the Western Foundation of Vertebrate Zoology (WFVZ) in Los Angeles. Specimens cited in the text, in figure captions, and in the Appendix are identified to collection by the abbreviations given above.

MONOPHYLY OF THE ASSEMBLAGE

Monophyly of the *Elaenia* assemblage rests on a derived configuration of the nasal septum that is shared by all the constituent genera and found in only one other group of flycatchers (discussed below). The nasal septum possesses a transverse trabecular plate that is elevated somewhat above the ventral edge of the septum, creating the appearance of a sagittal ridge when viewed from below, and there is no "anterior notch" (character A; labeled in fig. 4: 1–3). This configuration of the trabecular plate is equivalent to Warter's (1965) "type 5," in which the plate is described as being "within the septum." The septum itself generally is fully ossified, though there is much variation and sections of the septum (with its trabecular plate) may be missing in preserved skulls.

The presence of the transverse trabecular plate within the nasal septum distinguishes the genera in the *Elaenia* assemblage from those genera in the myiarchine assemblage and the kingbirds and their allies, which lack any type of plate associated with the septum (Lanyon, 1984b, 1985), and from the genera in the *Empidonax* assemblage, which possess a plate that bases the nasal septum (Lanyon, 1986).

In roughly half of the genera within the *Elaenia* assemblage there is only a single trabecular plate, located anterior to the ventral end of the internal supporting rod, as illustrated in figure 4: 1–4. This plate is extremely variable in size and shape, however, ranging from the very broad, well-developed plate in *Sublegatus* (fig. 8: 1) to the very narrow, poorly developed plate in *Myiopagis* (fig. 21: 1). The other half of the *Elaenia* assemblage possesses an additional plate located beneath and/or posterior to the ventral end of the internal supporting rod. This posterior plate also varies greatly in size, as illustrated in the sample of *Elaenia* skulls in figure 17; in some species it appears merely as a bulbous swelling beneath the internal supporting rod (fig. 12: 1).

These variations in size, shape, and location of the trabecular plate provide useful characters in diagnosing genera and clusters of genera within the assemblage, and these will be described in greater detail as the groups of genera are discussed.

Elsewhere within the family of tyrant flycatchers I have found this type of trabecular plate (located within the septum) only in the occasional specimen (not consistent within species or genera) of tody-tyrant (Lanyon, MS).

In most tody-tyrant skulls there is little os-sification of the nasal septum and no sugges-tion of a laterally projecting or transverse tra-becular plate. It is quite possible that further study, perhaps augmented by biochemical data, will warrant recognition of the tody-tyrants as an early derivative from the *Elae-nia* assemblage. At present it seems best to treat them as a distinct assemblage, having their own uniquely derived syringeal mor-phology.

PHYLOGENETIC RELATIONSHIPS WITHIN THE ASSEMBLAGE

As in my previous analyses of other assem-blages of tyrant flycatchers, variation in the basic configuration of the tracheobronchial junction of the syrinx and in the degree to which the A elements provide support for each bronchus is interpreted as evidence for defining primary lineages within the *Elaenia* assemblage. These variations in morphology are more conservative than other aspects of syringeal evolution (e.g., size, form, and po-sition of internal cartilages), and are illus-trated in figure 1 and listed in table 1.

The five basic variants in syringeal mor-phology are used as the principal diagnoses for five different clusters of genera within the assemblage; i.e., I have made the assumption that each variant arose but once and indicates monophyly. I know of no morphological characters that will resolve the polychoto-mous relationship between these five groups,

as illustrated in figure 2. Evolutionary rela-tionships within each group are discernible, however, using a combination of characters from cranial, syringeal, and external mor-phology, as well as from nesting biology, and these will be discussed in detail.

The *Phylloscartes* Group
(Figure 3 and table 2)

My *Phylloscartes* group is dominated nu-merically by *Phylloscartes, Zimmerius, Mio-nectes,* and *Leptopogon,* and in addition in-cludes *Inezia, Sublegatus, Myiotriccus,* and two groups of two species each, formerly con-tained in *Myiophobus,* whose generic status remains uncertain. I have examined skulls and syringes from all nine genera, but was unable to examine any anatomical material of "*Myiophobus*" *lintoni* and of 6 of the 18 species of *Phylloscartes.*

There is no tradition for considering these taxa as constituting a monophyletic group. Hellmayr (1927) distributed them among four subfamilies (Euscarthminae, Elaeniinae, Serpophaginae, and Myiarchinae). Traylor (1977) recognized the arbitrariness of some of Hellmayr's subfamilies and brought most of these taxa into an enlarged Elaeniinae. He acknowledged the probable relatedness of *Phylloscartes, Leptopogon,* and *Mionectes,* but scattered *Zimmerius, Inezia,* and *Sublegatus* in other parts of this subfamily, and placed *Myiotriccus* and the four species of "*Myio-phobus*" in another subfamily, Fluvicolinae.

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Fig. 1. **1.** Drawings and photographs of the five basic types of syringes in the *Elaenia* assemblage (dorsal aspect; magnification ×8 in 1–4 and 9 and 10, and ×15 in 5–8). **(1, 2)** Characters B, C—one A element (A2–A4) forms a complete ring around each bronchus; calcified pessulus formed from extensions from the A3, A4, or A5 elements (*Zimmerius bolivianus,* LSU 70641); **(3, 4)** Character E—no complete A ring around either bronchus; A1–A5 incomplete, with at least three pairs of these elements connected by a cartilaginous plate to which large internal cartilages are attached (*Stigmatura budytoides,* PMNH 4537); **(5, 6)** Character F—no complete A ring around either bronchus, no cartilaginous plate, and no drum; A1–A3 incomplete; narrow, calcified pessulus (independent of A elements) to which large internal cartilages are attached (*Euscarthmus meloryphus,* AMNH 8866); **(7, 8)** Character H—pessulus unusually large, calcified, and concave when viewed dorsally (*Pseudotriccus pelzelni,* UK 6900); **(9, 10)** Character I—fusion of dorsal A3–A5 elements with the pessulus, as well as fusion of other A elements in varying degrees, to form a drum; internal cartilages attach to dorsomedial positions on drum; pessulus well-developed, calcified, broad dorsally and narrow ventrally (*Elaenia mesoleuca,* AMNH 9093). Dotted areas represent calcified tissue, lined areas represent cartilaginous tissue; A elements as numbered; B elements omitted from drawings; tbj = tracheobronchial junction; ic = internal cartilage; itm = internal tympaniform membrane; p = pessulus; cp = cartilaginous plate; d = drum.
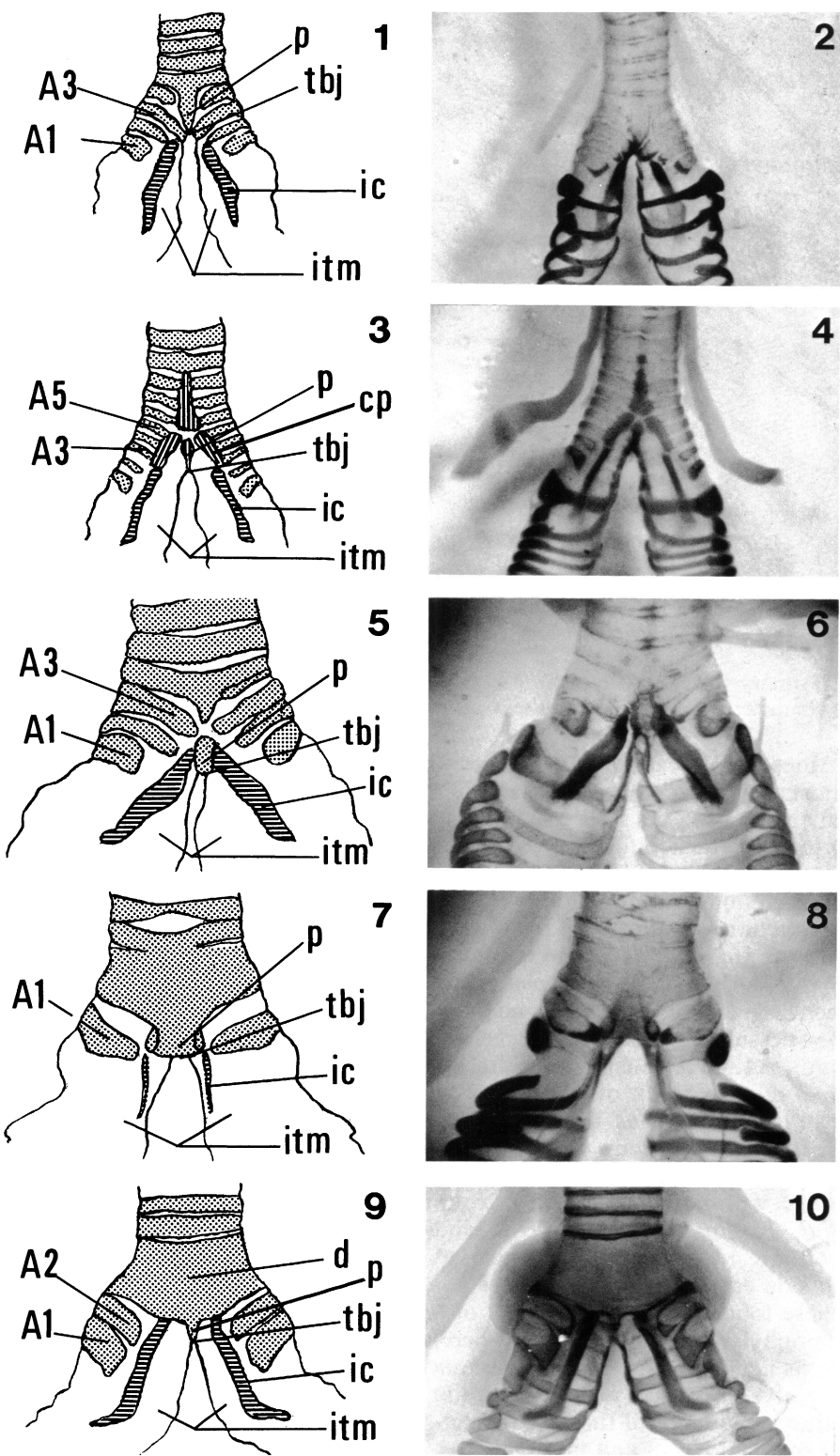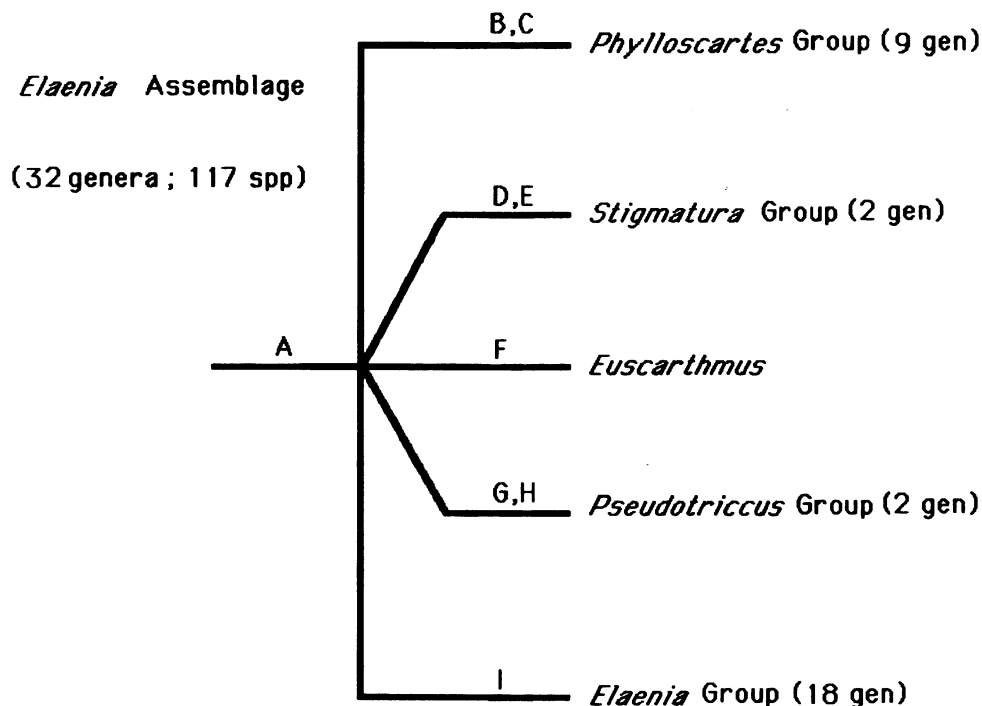
Fig. 2. Primary lineages within the *Elaenia* assemblage (32 genera; 117 species). Letters identify diagnostic character states described in text and in table 1.

Though Ames (1971) examined representatives of most of the genera, he refrained from placing any of them in his syringeal groups.

The syringeal evidence for the close relationship of the taxa in my *Phylloscartes* group is in the basic configuration of the tracheo-bronchial junction, which is unique within the assemblage (fig. 1: 1, 2). One of the A elements (A2–A4) forms a complete ring around each bronchus (character B), and there is a calcified pessulus formed from extensions from the A3, A4, or A5 elements (character C). There is no suggestion of a fusion of A elements into a "drum" as in my *Elaenia* group, the other major group within the assemblage.

Four genera within the *Phylloscartes* group (*Zimmerius, Phylloscartes, Mionectes,* and *Leptopogon*) are reported to build enclosed nests with side entrances (see references below). If these four genera are members of a larger monophyletic group, as argued here, then it seems likely that this unusual nesting behavior evolved but once within the group and constitutes evidence of their close relatedness (character 1; fig. 3 and table 2). Elsewhere within the *Elaenia* assemblage, this unusual nesting behavior has been reported in only one other genus, *Camptostoma,* where it must have evolved independently (see discussion for the *Elaenia* group).

Among the four genera having enclosed nests there is a dichotomy with respect to the location of the nest, which suggests possible relationships. The nest of three species of *Zimmerius* (*gracilipes* — Snethlage, 1935; Hilty and Brown, 1986; *vilissimus* — Skutch, 1960; *viridiflavus* — Hilty and Brown, 1986) and for one species of *Phylloscartes* (*ventralis* — AMNH coll.; Ihering, 1904; Dinelli, 1918; Belton, 1985; Sick, 1985) typically are located within a mass of vegetation such as moss or dead leaves (character 2), rather than being suspended by narrow strands of nest material as in the sister-group (*Mionectes* and *Leptopogon,* discussed below) and in the tody-tyrant assemblage (Lanyon, MS).

Traylor (1977) proposed the name *Zimmerius* for five species (*vilissimus, bolivianus, cinereicapillus, gracilipes,* and *viridiflavus*) formerly in *Tyranniscus* (Hellmayr, 1927; Zimmer, MS), in part because of differences in external morphology, but also due to earlier findings by Ames (1971) and Warter

TABLE 1

Characters Used for Primary Lineages in the *Elaenia* Assemblage

A. Nasal septum possesses a transverse trabecular plate elevated somewhat above the ventral edge of the septum, creating the appearance of a sagittal ridge when viewed from below, and lacks an anterior notch

B. One A element (A2–A4) forms a complete ring around each bronchus

C. Calcified pessulus formed from extensions from the A3, A4, or A5

D. Two trabecular plates, both small bulbous swellings; one anterior to the internal supporting rod, and one at the base of that rod

E. No complete A ring around either bronchus; A1 through A5 incomplete, with at least three pairs of these A elements connected by a cartilaginous plate to which large internal cartilages are attached

F. No complete A ring around either bronchus, no cartilaginous plate, and no drum; A1 through A3 incomplete; narrow, calcified pessulus (independent of A elements) to which large internal cartilages are attached

G. Nasal septum poorly ossified; small trabecular plate within anterior section of septum, when retained in museum specimens, and no plate posteriorly

H. Pessulus unusually large, calcified, and concave when viewed dorsally

I. Fusion of dorsal A3–A5 elements with the pessulus, as well as fusion of other A elements in varying degrees, to form a drum; internal cartilages attach to dorsomedial positions on drum; pessulus well-developed, calcified, broad dorsally and narrow ventrally

TABLE 2

Characters Used for *Phylloscartes* Group

B. One A element (A2–A4) forms a complete ring around each bronchus

C. Calcified pessulus formed from extensions from the A3, A4, or A5

1. Nest enclosed, with side entrance

2. Nest located within a mass of vegetation such as moss or dead leaves

3. Internal cartilages broad and straight, with diffusely staining terminal segment

4. Dorsal ends of the B3–B4 elements are club-shaped

5. Internal cartilages are narrow, straight, and pointed distally

6. Transpalatine processes are narrow, rather long, and pointed

7. Superior fenestra in the interorbital septum obliterated, or nearly so, through ossification

8. Narrow, often bulbous swelling (trabecular plate) basal to internal supporting rod and/or just posterior to the rod

9. Nests suspended in a dark cleft or recess, often over water

10. B1 elements of the syrinx partly calcified

11. Internal cartilages are ring-shaped

12. B2 elements greatly swollen

13. B3 elements forked dorsally

14. Anterior segment of nasal septum poorly ossified or missing, and no conspicuous trabecular plate anterior to the rod; trabecular plate reduced to bulbous swelling beneath and sometimes posterior to internal supporting rod

15. Plumage olive-green above, whitish to yellowish below, with white wing bars and white supraloral

16. Internal cartilages very broad basally, more or less pointed distally, and attached to cartilaginous medial sections of A2s

17. Inferior and superior fenestrae of the interorbital septum are obliterated, or nearly so, through ossification

18. Internal cartilages as broad distally as basally, and attached to A2s and A3s

19. Plumage with concealed crown patch

20. Internal cartilages rather narrow, straight, as broad distally as basally, and attached to A2s

21. Internal cartilages broad basally, more or less pointed distally, and attached to A2s and A3s

22. B2s partially calcified

23. Nasal capsule fully ossified, including alinasal walls and turbinals

24. Internal cartilages broad, slightly J-shaped, and attached to A2s

(1965). Zimmer (1955) had acknowledged variability in the external morphology of *Tyranniscus* and identified two species groups according to bill shape and wing pattern, but concluded subdivision of the genus to be "undesirable." Ames (1971) reported that the two species of *Tyranniscus* he examined (*viridiflavus* and *nigrocapillus*) "differ so strikingly in syringeal morphology that I felt it necessary to verify the identity of the specimens through comparison with skins. One cannot help wondering if a thorough analysis of structural and behavioral characters of these and other species of *Tyranniscus* would not result in dividing the genus." Warter (1965) interpreted the skulls of his specimens of *gracilipes, viridiflavus,* and *vilissimus* as having a nasal septum like that of Hellmayr's Fluvicolinae and unlike all other members of the Elaeniinae and Serpophaginae that he ex-

amined. Traylor had *Zimmerius* follow the other species of *Tyranniscus* in his lineal list
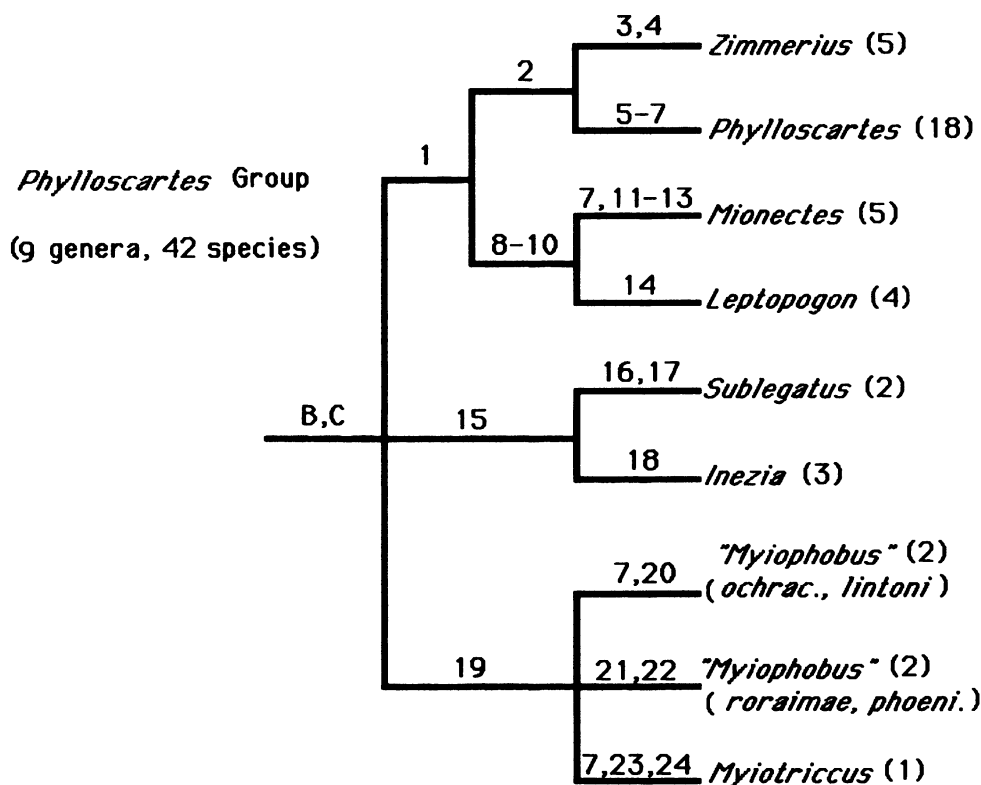
Fig. 3. Phylogenetic relationships within the *Phylloscartes* group (9 genera; 42 species). Numbers identify diagnostic character states described in text and in table 2. Numbers in parentheses indicate number of species per genus.

though he was "not convinced they are closely related. There is, however, no other genus to which they seem more nearly related."

The nasal septum of *Zimmerius* (10 specimens examined, representing all 5 species) is not like that of the Fluvicolinae (my *Empidonax* assemblage; see Lanyon, 1986), contrary to the findings of Warter, but instead has a trabecular plate that is within the septum and lacks an "anterior notch" (character A). All of my specimens have a trabecular plate that is well-developed, rather broad, and deflected laterally so that it appears slightly concave in cross section, and the nasal capsule is well-ossified, including portions of the alinasal walls and turbinals (fig. 4: 1).

I have examined the syringes (nine specimens) of all five species of *Zimmerius*; they have characters B and C, the criteria for my *Phylloscartes* group (figs. 1–3), and are very different from the syringes of *Tyranniscus* (discussed with the *Elaenia* group), thus confirming the earlier findings of Ames (1971) and supporting the separation from *Tyranniscus* (Traylor, 1977). The syrinx of *Zimmerius,* though like those of other genera in the *Phylloscartes* group with respect to characters B and C, differs in that the internal cartilages are broad and straight, and have a diffusely staining terminal segment (character 3; fig. 5: 1, 2). In addition, the dorsal ends of the B3–B4 elements are club-shaped (character 4; fig. 5: 1, 2), a character state that is unique within the entire assemblage.

Syringeal morphology confirms most of the changes that Traylor (1977) made in Hellmayr's (1927) treatment of *Phylloscartes* and its close relatives. Unfortunately the only syringes available from traditional *Phylloscartes* are from *ventralis* (fig. 5: 3) and *chapmani,* hence I have had to make the assumption that these species are representative of those whose syringes I lack (*flavovirens, virescens, paulistus, oustaleti, difficilis,* and *roquettei*). The syringes of *Pogonotriccus* (five of seven species examined, see fig.
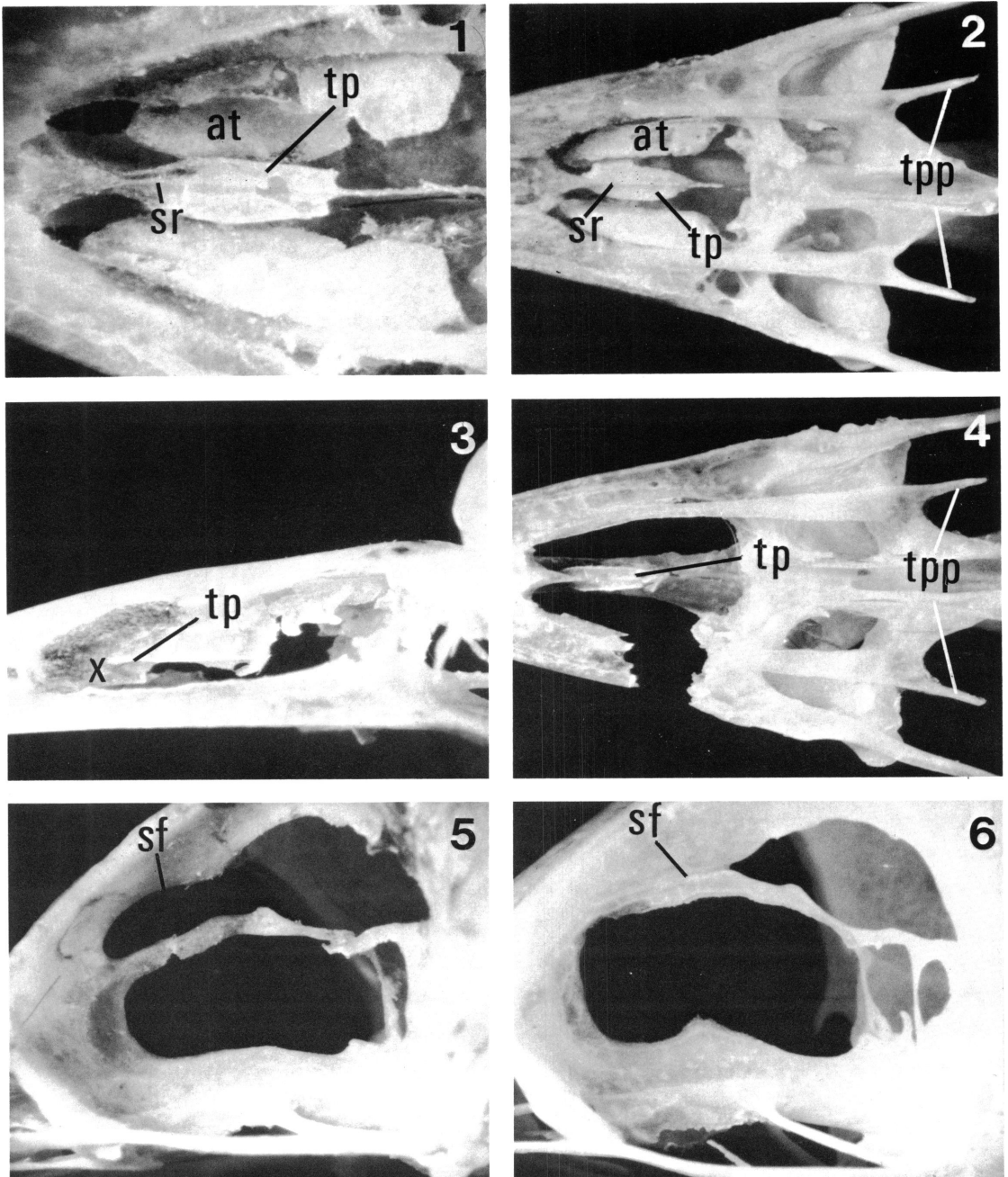
Fig. 4. Cranial characters in *Zimmerius* and *Phylloscartes,* two genera in the *Phylloscartes* group (anterior end of skull to left; ventral views in 1, 2, 4, and lateral in 3, 5, 6; magnification ×8 in 2, 4–6, ×12 in 3, and ×18 in 1). (**1**) *Zimmerius vilissimus,* AMNH 14553; (**2**) *Phylloscartes orbitalis,* FMNH 323141; (**3, 4**) *P. eximius,* PMNH 6431; (**5**) *Zimmerius viridiflavus,* MVZ 141808; (**6**) *Phylloscartes orbitalis,* FMNH 323141. at = alinsal turbinal; sf = superior fenestra; sr = sagittal ridge; tp = trabecular plate; tpp = transpalatine process; x = absence of anterior notch.

5: 4; *venezuelanus* and *flaviventris* lacking) and of *Leptotriccus sylviolus* (fig. 5: 5) do not

differ significantly from those of *ventralis* and *chapmani*; consequently, I agree with Traylor
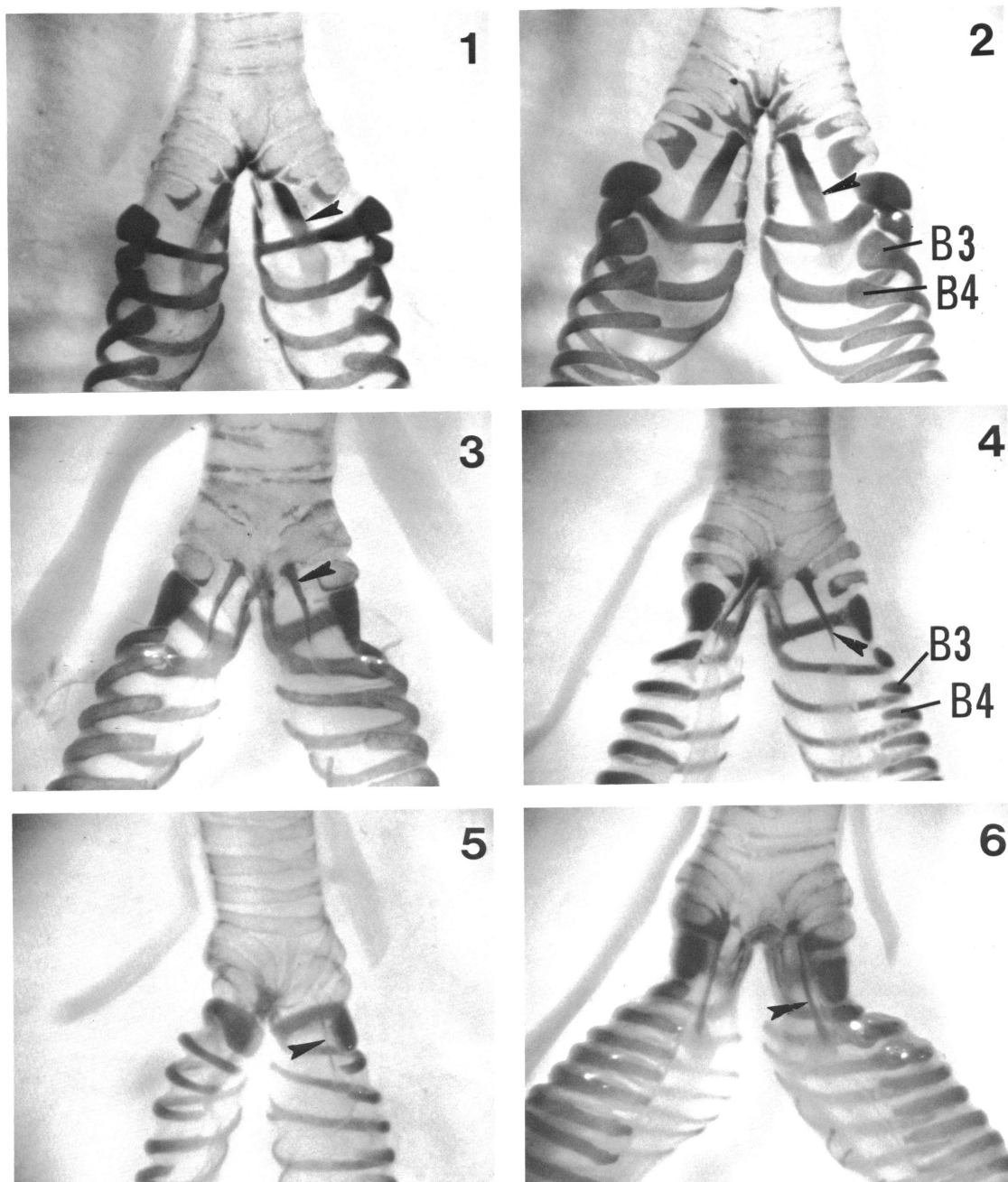
Fig. 5.   Syringes of *Zimmerius* and *Phylloscartes,* two genera in the *Phylloscartes* group (dorsal aspect; magnification ×15 in 1, 2, and ×18 in 3–6). (1) *Zimmerius bolivianus,* LSU 70641; (2) *Z. gracilipes,* AMNH 7703; (3) *Phylloscartes ventralis,* PMNH 2754; (4) *P. eximius,* PMNH 2764; (5) *P. sylviolus,* PMNH 2691; (6) *P. superciliaris,* USNM 510881. Arrows indicate internal cartilages; B elements as numbered.

that *Pogonotriccus* and *Leptotriccus* should be merged with *Phylloscartes.* I also agree with Traylor (1979) and Zimmer (1940) that *nigrifrons* belongs in *Phylloscartes*; its syrinx

is very different from those of *Leptopogon* (see discussion below) and of *Mecocerculus* (Chapman, 1929) (see the *Elaenia* group). Similarly I agree with these authors that *superciliaris* Sclater and Salvin (fig. 5: 6) belongs with *Phylloscartes* and not with *Mecocerculus* as provisionally recommended by Hellmayr (1927); the syringes of *Mecocerculus* are very different (as discussed with the *Elaenia* group).

I disagree with Traylor (1977) only in his merger of *Capsiempis flaveola* with *Phylloscartes*. Traylor (1977) admitted that "the one species that is out of place on ecological grounds is *Capsiempis flaveolus* [sic] . . . . Eisenmann (in litt.) says that where *Capsiempis* overlaps the range of *Phylloscartes flavovirens* in Panama, the two are unlike in habits and do not appear closely related . . . . I keep it in the enlarged *Phylloscartes* on morphological grounds." Cranial and syringeal morphology suggest that *Capsiempis* is most closely related to *Phaeomyias* and *Nesotriccus* in the *Elaenia* group.

The syrinx of *Phylloscartes* (18 specimens examined, representing 10 of 18 species) differs from that of *Zimmerius* principally in the shape of the internal cartilages, which in the former genus are narrow, straight, and pointed distally (character 5; fig. 5: 3–6). The nasal capsule of *Phylloscartes* (15 specimens examined, representing 8 of 18 species) is quite variable with respect to the shape and size of the trabecular plate and to the degree of ossification of the alinasal turbinals and walls. In most of the specimens the plate is smaller than in *Zimmerius* and not deflected laterally, but one specimen of *orbitalis* has a plate that is indistinguishable from that of *Zimmerius* and the capsule is as fully ossified as in that genus (fig. 4: 2). However, all of the skulls of *Phylloscartes* are separable from those of *Zimmerius* by the shape of the transpalatine processes, which are narrow, rather long, and pointed in *Phylloscartes* (character 6; fig. 4: 2, 4), not short, broad, and blunt as in *Zimmerius*; and in *Phylloscartes* the superior fenestra in the interorbital septum is obliterated, or nearly so, through ossification (character 7; fig. 4: 6).

Mionectes and *Leptopogon* are sister taxa by virtue of a shared derived state of the trabecular plate, which is poorly developed, narrow, and without any obvious deflection laterally: all specimens have a narrow plate, often simply a bulbous swelling, located either at the base of the internal supporting rod and/ or just posterior to that rod (character 8; fig. 6: 1–6). In addition, the reports of nests of four species of *Mionectes* (Ihering, 1904; Snethlage, 1935; Dickey and Van Rossem, 1938; Skutch, 1960; Herklots, 1961; Smithe, 1966; ffrench, 1976; Willis et al., 1978; Wetmore, 1972; Snow, 1979) and of two species of *Leptopogon* (AMNH coll.; Ihering, 1900; Moore, 1944; Herklots, 1961; Smithe, 1966; Skutch, 1967; Wetmore, 1972; ffrench, 1976) suggest that these may be sister taxa, for the enclosed nests, with side entrances, are suspended (as in the tody-tyrants) in a dark cleft or recess, often over water (character 9). Furthermore, the B1 elements of the syrinx of *Mionectes* and *Leptopogon* are partly calcified (character 10), a derived character state within the Tyrannidae.

Syringeal morphology supports Traylor's (1977) reunion of *Pipromorpha* with *Mionectes*; the syringes are indistinguishable. The syrinx of *Mionectes* (18 specimens examined, representing all 5 species; fig. 7: 1, 2) is unique among tyrant flycatchers in having the internal cartilages ring-shaped (character 11), the B2 elements greatly swollen (character 12), and the B3 elements forked dorsally (character 13).

The nasal septum of *Mionectes* (23 specimens examined, representing all 5 species; fig. 6: 1–3) is fully ossified and complete with narrow trabecular plate; all specimens have a smaller, sometimes bulbous plate beneath or just posterior to the internal supporting rod (character 8). *Mionectes* skulls are separable from those of *Leptopogon* by having the superior fenestra in the interorbital septum obliterated, or nearly so, through ossification (character 7; fig. 6: 7). In my series of *Leptopogon* skulls (17 specimens examined, representing all 4 species; fig. 6: 4–6), the anterior segment of the nasal septum is poorly ossified or missing all together; the trabecular plate is reduced to a bulbous swelling beneath and sometimes posterior to the internal supporting rod; there is no conspicuous plate anterior to the rod (character 14).

My series of *Leptopogon* syringes (23 specimens examined, representing all 4 species) reveals two types of syringeal morphology:
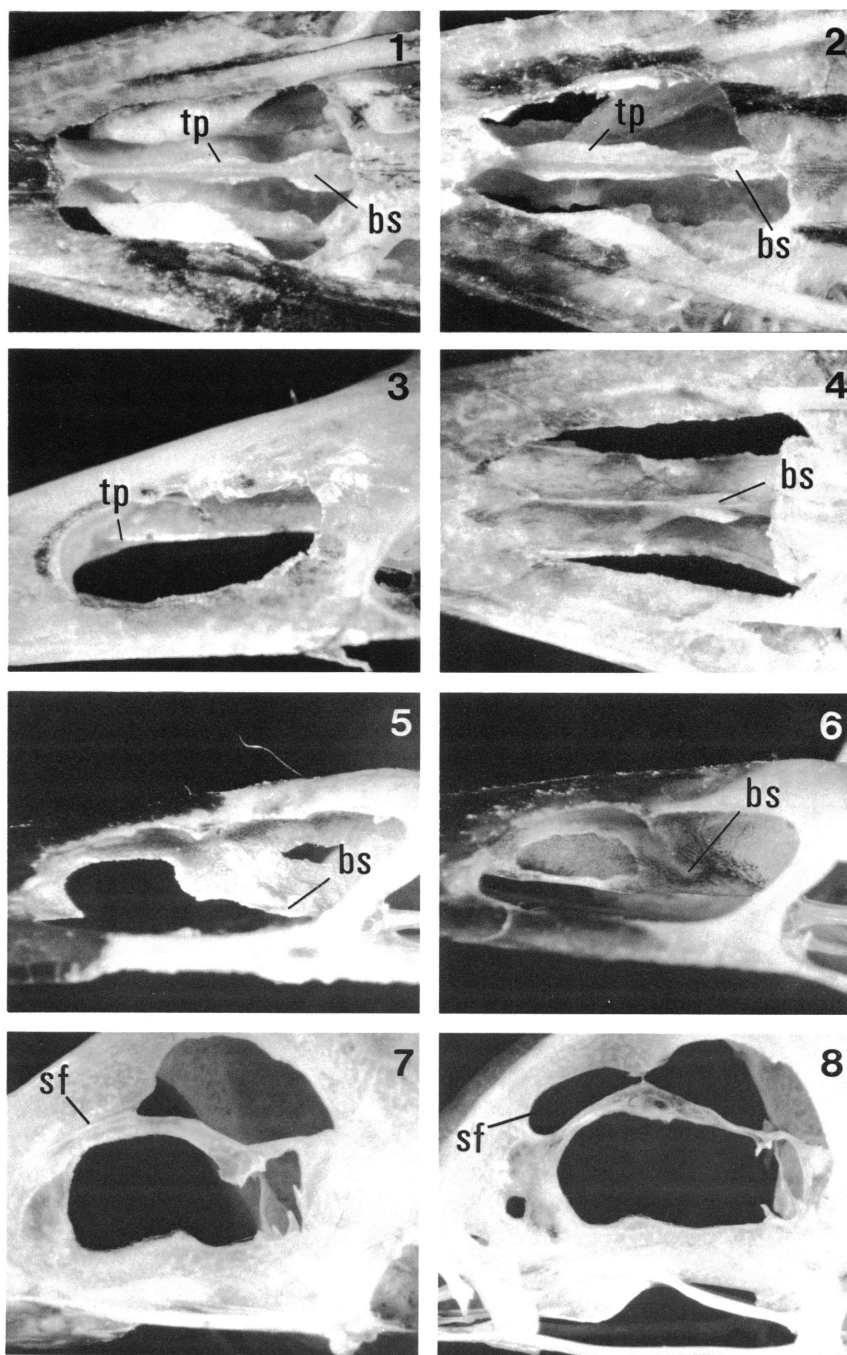
Fig. 6.   Cranial characters in *Mionectes* and *Leptopogon*, two genera in the *Phylloscartes* group (anterior end of skull to left; ventral views in 1, 2, 4, and lateral in 3, 5–8; magnification ×10 in 1–6, and ×5 in 7, 8). **(1)** *Mionectes macconnelli*, FMNH 315934; **(2)** *M. striaticollis*, PMNH 11710; **(3)** *M. rufiventris*, UMMZ 200882; **(4, 5)** *Leptopogon superciliaris*, AMNH 14153; **(6)** *L. taczanowski*, LSU 79834; **(7)** *Mionectes striaticollis*, PMNH 11710; **(8)** *Leptopogon superciliaris*, AMNH 14153. bs = bulbous swelling; sf = superior fenestra; tp = trabecular plate.
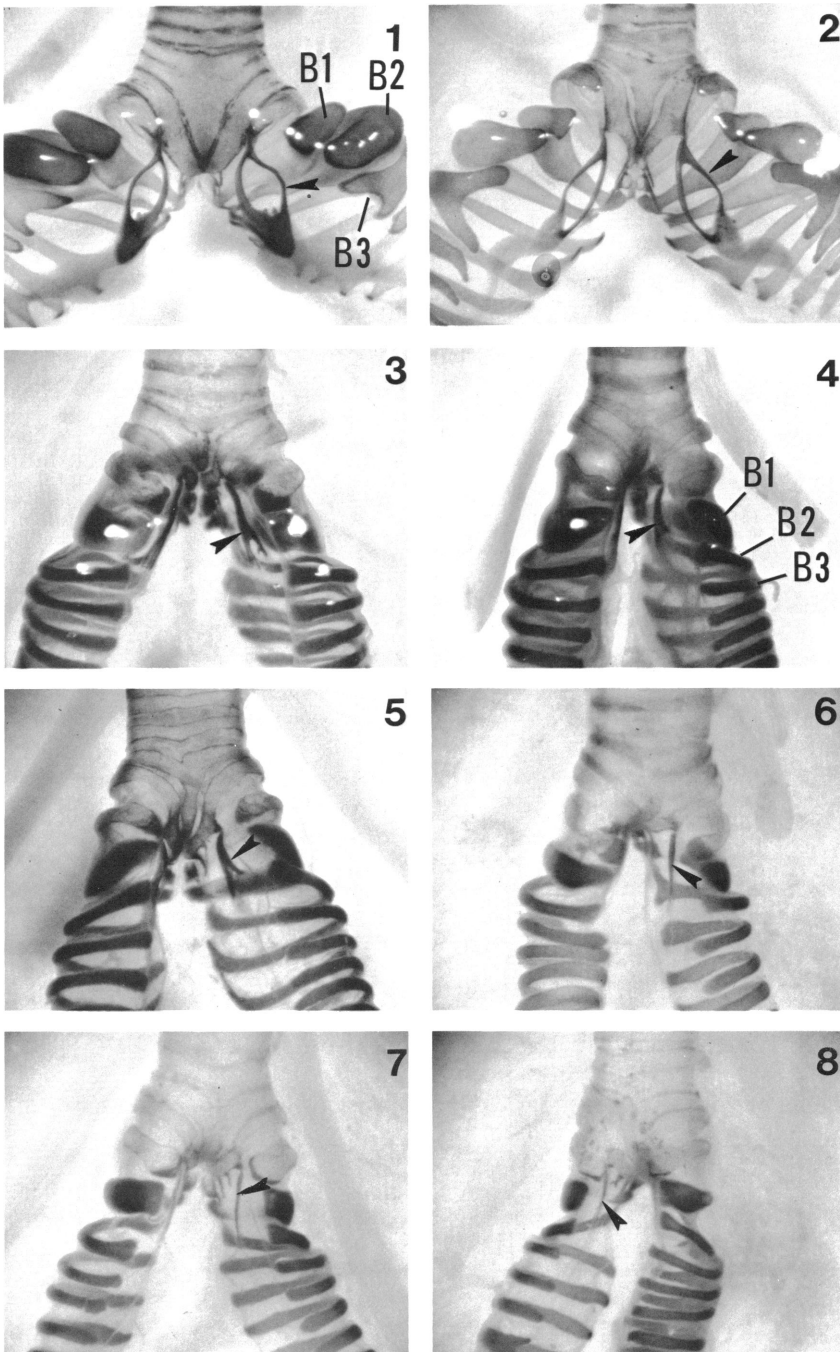
Fig. 7.   Syringes of *Mionectes* and *Leptopogon*, two genera in the *Phylloscartes* group (dorsal aspect; magnification ×11 in 1–4, and ×14 in 5–8). (1) *Mionectes olivaceus*, LSU 108515; (2) *M. macconnelli*, AMNH 8085; (3) *Leptopogon amaurocephalus*, AMNH 2509; (4) *L. superciliaris albidiventer*, LSU 91224; (5) *L. s. superciliaris*, USNM 512061; (6) *L. superciliaris transandinus*, LSU 108509; (7) *L. rufipectus*, LSU 97549; (8) *L. taczanowski*, LSU 107670. Arrows indicate internal cartilages; B elements as numbered.

(1) the internal cartilages are broad distally and usually strongly forked, and the B1 elements are greatly swollen (fig. 7: 3–5); (2) the internal cartilages are slender and pointed distally, and the B1 elements are not greatly swollen (fig. 7: 6–8). Type (1) syrinx is found in all of my specimens of *L. amaurocephalus,* from Nicaragua to Argentina, and from two subspecies of *L. superciliaris* (the nominate form and *albidiventer*) from Peru and Bolivia. I cannot, with certainty, identify syringes to one or the other of these forms. Type (2) syrinx is found in Peruvian specimens of *L. rufipectus* and *L. taczanowski* and my only specimen of *L. superciliaris transandinus* from Panama (LSU 108509). As Zimmer (MS) has noted, study skins of *transandinus* are not nearly as distinguishable from those of nominate *superciliaris* as are skins of *albidiventer,* hence this great similarity of the *transandinus* syrinx to the distinctive syringes of *L. rufipectus* and *L. taczanowski* is quite unexpected. Syringeal morphology suggests, at the very least, that there are two species groups within the genus (this kind of variability exceeds normal intrageneric variability) and, more importantly, that there may be a problem of specific limits worthy of investigation with appropriate field techniques.

Sibley and Ahlquist (1985), using DNA–DNA hybridization, have argued that *Mionectes* and *Leptopogon* (and a number of "related" genera) are part of a lineage that "branched from the rest of the tyrannoids before the radiation of the typical tyrants, becards, cotingas, and manakins began." To argue thus implies that syringeal internal cartilages must have evolved independently in *Mionectes, Leptopogon,* and "relatives," on the one hand, and in all other tyrant flycatchers, on the other, or that these cartilages are primitive for all tyrannoids and subsequently were lost in all cotingas and true manakins. Also included among related genera, according to Sibley and Ahlquist, are *Pseudotriccus* and *Corythopis,* two other genera in my *Elaenia* assemblage (see the *Pseudotriccus* group). Most unsettling in this report is the fact that *Hemitriccus* and *Todirostrum* were designated members of this early radiation, while the DNA data were found "equivocal" on such clearly related genera as *Lophotriccus* and *Atalotriccus* (Lanyon, MS). Until there is

additional support for this novel hypothesis, I favor the more parsimonious interpretation that the internal cartilages shared by all tyrant flycatchers are indeed evidence for common ancestry, and that *Mionectes* and *Leptopogon* are bona fide members of the tyrant lineage.

The remaining genera in the group appear to sort into two clusters on the basis of external morphology. The interrelationships between the clusters are unclear, hence the trichotomy in figure 3. Nests have been reported only for *Sublegatus* (AMNH coll.; Cherrie, 1916; Herklots, 1961; Wetmore, 1972; ffrench, 1976) and *Inezia* (Snethlage, 1935; Haverschmidt, 1968), and these were simple, open cups—the presumed primitive nest construction for tyrant flycatchers.

Sublegatus traditionally has been considered a close relative of *Elaenia* (Hellmayr, 1927; Traylor and Fitzpatrick, 1982); Traylor (1977) remarked that "there is little besides intuition that leads me to keep *Sublegatus* out of *Elaenia.*" Ames (1971) had access to a single syrinx of *Sublegatus modestus* but refrained from assigning it to any of his species groups. *Inezia* historically has been considered a close relative of *Serpophaga* (Hellmayr, 1927; Zimmer, MS; Traylor, 1977), and Smith (1971) recommended that these genera be merged because of similarities in behavior and external morphology. Ames (1971) reported that his single syrinx of *Inezia subflava* was unlike that of *Serpophaga,* but refrained from assigning it to any of his species groups. Hellmayr's (1927) *Inezia* consisted solely of *subflava,* but Zimmer (1955) added *inornata* (formerly in *Serpophaga*) and *tenuirostris* (formerly in *Phaeomyias*).

A sister-group relationship between *Sublegatus* and *Inezia* has not been suggested heretofore. Having determined (see discussion below) that *Sublegatus* and *Inezia* share derived character states of the syrinx (B, C), placing them in the *Phylloscartes* group, the similarity in the plumage coloration and pattern of these two genera takes on greater significance and reliability as an indicator of their relationship. Both genera are olive-green above, whitish to yellowish below, and have white wing bars and a white supraloral (character 15).

I stained Ames' (1971) specimen of *Sublegatus modestus,* along with two other spec-
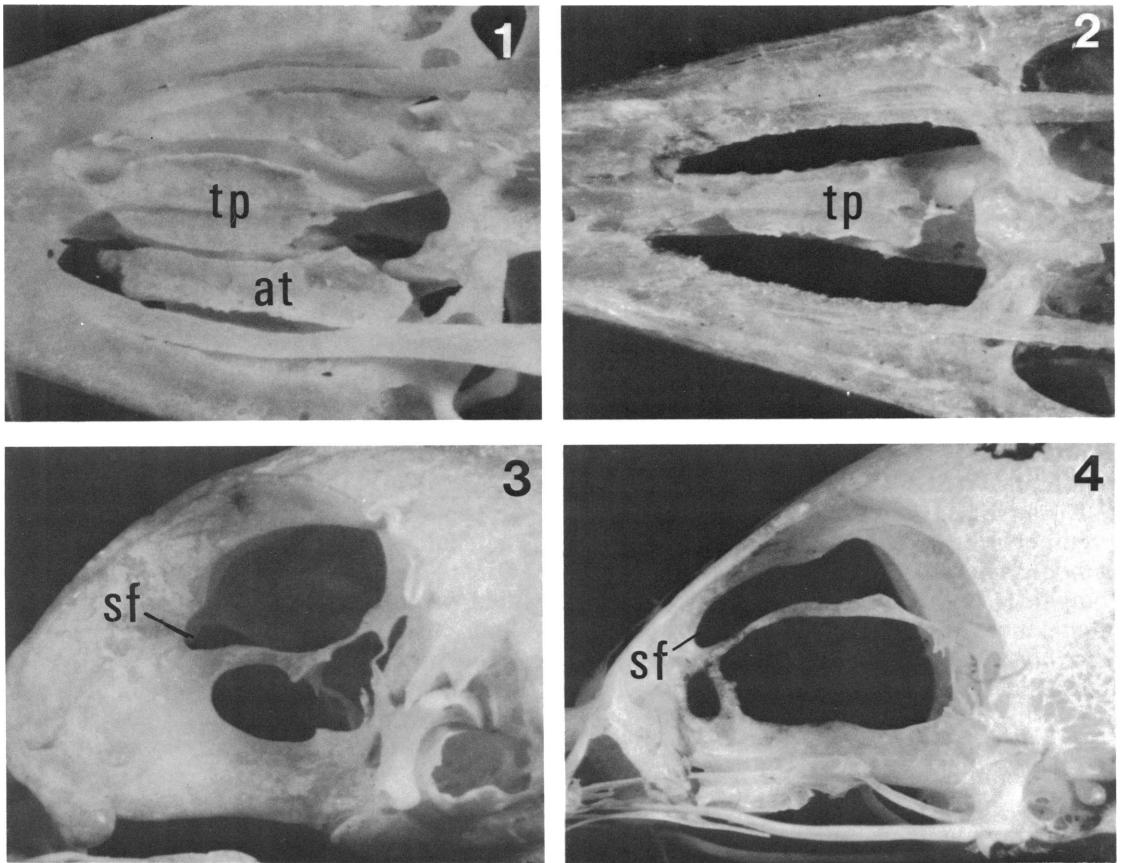
Fig. 8.   Cranial characters in *Sublegatus* and *Inezia,* two genera in the *Phylloscartes* group (anterior end of skull to left; ventral views in 1, 2, and lateral in 3, 4; magnification ×12 in 1, 2, and ×7 in 3, 4); (**1, 3**) *Sublegatus modestus,* USNM 346034; (**2**) *Inezia tenuirostris,* FMNH 313436; (**4**) *I. inornata,* LSU 95240. at = alinasal turbinal; sf = superior fenestra; tp = trabecular plate.

imens of *S. modestus* and two of *S. arenarum*; none of these syringes has the A elements fused into the derived state ("drum") that characterizes the members of my *Elaenia* group, and all have one complete A ring around each bronchus (character B), the shared derived character that serves to cluster this *Phylloscartes* group. The internal cartilages of *Sublegatus* are very broad basally, more or less pointed distally, and attached to cartilaginous medial sections of the A2s (character 16; fig. 10: 1). In *Sublegatus* skulls (one *modestus* and one *arenarum* examined) the nasal capsule is nearly fully ossified, including the alinasal walls and turbinals, and there is a well-developed, rather broad, trabecular plate within the anterior segment of

the anterior septum (fig. 8: 1). The distinctive feature of these *Sublegatus* skulls, however, is that both the superior and inferior fenestrae in the interorbital septum are obliterated, or nearly so, through ossification (character 17), as seen in figure 8: 3.

My series of *Inezia* syringes includes two specimens of *inornata* and one of *subflava.* None of these specimens has the A elements fused into a "drum," the derived character shared by *Serpophaga, Phaeomyias,* and the other members of my *Elaenia* group. The internal cartilages of *Inezia* differ from those of *Sublegatus* in being as broad distally as they are basally and being attached to the A2s and A3s (character 18; fig. 10: 2). Though I lack a syrinx of *tenuirostris,* my two skulls of

that species are similar to the three skulls that I have of *subflava* and *inornata* (fig. 8: 2) and to the skulls of most of the members of this *Phylloscartes* group, and they lack a highly derived character that is diagnostic of *Phaeomyias* skulls. Consequently I concur with Zimmer and Traylor that *inornata* and *tenuirostris* belong in *Inezia*.

The remaining taxa ("*Myiophobus*" and *Myiotriccus*) in my *Phylloscartes* group were placed in the nonmyiarchine portion of Hellmayr's (1927) Myiarchinae and at the beginning of Traylor's (1977) Fluvicolinae; no one had suggested that they might be more closely related to *Elaenia* and its allies. Neither Warter (1965) nor Ames (1971) examined anatomical material of these taxa.

I (Lanyon, 1986) have already presented argument for considering the genus *Myiophobus* as visualized by Hellmayr (1927) and Traylor (1979) to be polyphyletic. One segment, including at least *fasciatus, flavicans,* and *inornatus,* possesses a nasal septum characteristic of my *Empidonax* assemblage, in which the closest relatives appear to be *Pyrrhomyias* and *Hirundinea.* The other segment, including *phoenicomitra, roraimae,* and *ochraceiventris* (and presumably *lintoni,* but skeleton unavailable; see Remsen, 1984, and Parker et al., 1985), does not share the derived character states of the nasal septum unique to my *Empidonax* assemblage. The anterior portion of the septum is completely ossified (no anterior notch), and the trabecular plate is elevated above the ventral edge of the septum (fig. 9: 1–3); this is the derived character (A) shared by all members of my *Elaenia* assemblage.

These four species of "*Myiophobus*" cluster with the monotypic *Myiotriccus* by virture of their plumage having a concealed crown patch (character 19), a unique character within the *Phylloscartes* group. All five species have a well-developed, broad, trabecular plate that is deflected laterally so that it appears slightly concave in cross section (fig. 9: 1–4). I am unable to determine unequivocal relationships among them, however, hence the unresolved trichotomy in figure 3.

The syrinx of *ochraceiventris* (three specimens examined) has internal cartilages that are rather narrow, straight, as broad distally as they are basally, and that attach to the A2 elements (character 20; fig. 10: 3), while the

skull of this species (three specimens examined) has the superior fenestra of the interorbital septum obliterated, or nearly so, through ossification (character 7; fig. 9: 6). My five syringes of *roraimae* and one of *phoenicomitra* have internal cartilages that are broad basally, more or less pointed distally, and that attach to the A2 and the A3 elements (character 21; fig. 10: 4, 5). In addition, they differ from the syringes of *ochraceiventris* in having the B2 elements partly calcified (character 22). I refrain from proposing new generic names for these two species groups of "*Myiophobus*" until we know more about their comparative behavior (no nests have been reported for these "*Myiophobus*" or for *Myiotriccus*) and until the trichotomy in figure 3 can be resolved. The skull of *Myiotriccus* (12 specimens examined) has the nasal capsule more fully ossified, including the alinasal walls and turbinals, than in any other genus within the *Phylloscartes* group (character 23; fig. 9: 4, 5). The superior fenestra of the interorbital septum is obliterated, or nearly so, through ossification (character 7; fig. 9: 8), as in *ochraceiventris.* The syrinx of *Myiotriccus* (three specimens examined) has internal cartilages that are broad, slightly J-shaped, and attach to the A2 elements (character 24; fig. 10: 6).

The *Stigmatura* Group
(Figure 11 and table 3)

This small group consists only of the two species in the genus *Stigmatura,* and *leucospodia* Taczanowski, 1877. I have examined skulls and syringes of all three species.

Hellmayr (1927) placed *Stigmatura* in his Serpophaginae, next to *Serpophaga,* but revealed some uncertainty by noting that "in general appearance, [it] bears close resemblance to certain Formicariidae and possibly belongs to that family." Earlier, Ridgway (1907) had placed the genus in Formicariidae on the basis of its resemblance to the antbird genus *Formicivora,* and Wetmore (1926) agreed. Smith (1971) felt that the extant behavioral information on *Stigmatura* supported its current position within a "closely coherent group" consisting of *Serpophaga* (including *Inezia*), *Anairetes,* and *Mecocerculus.* Traylor (1977) acknowledged a close resemblance between *Inezia* and *Stigmatura*
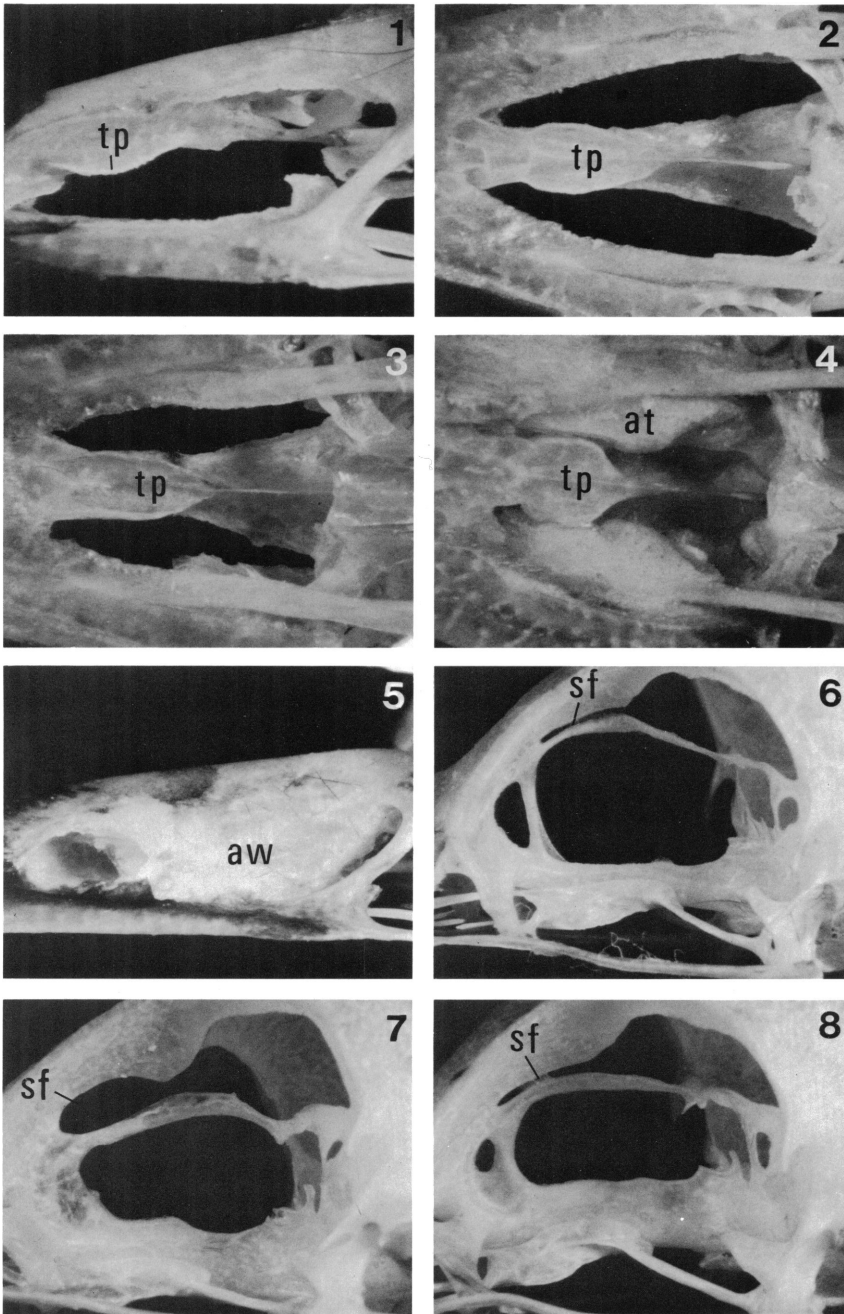
Fig. 9. Cranial characters in "*Myiophobus*" and *Myiotriccus*, two genera in the *Phylloscartes* group (anterior end of skull to left; lateral views in 1, 5–8, and ventral in 2–4; magnification ×9 in 1–4, ×7 in 5, and ×5 in 6–8); (1, 2) "*Myiophobus*" *ochraceiventris*, LSU 113683; (3) "*M.*" *phoenicomitra*, LSU 86568; (4, 5) *Myiotriccus ornatus*, FMNH 323253; (6) "*Myiophobus*" *ochraceiventris*, LSU 113683; (7) "*M.*" *phoenicomitra*, LSU 86568; (8) *Myiotriccus ornatus*, LSU 86414. at = alinasal turbinal; aw = alinasal wall; sf = superior fenestra; tp = trabecular plate.

and placed both genera between *Serpophaga* and *Anairetes*.

As Ames (1971) reported, *Stigmatura* is typically tyrannid in its syrinx, with no re-
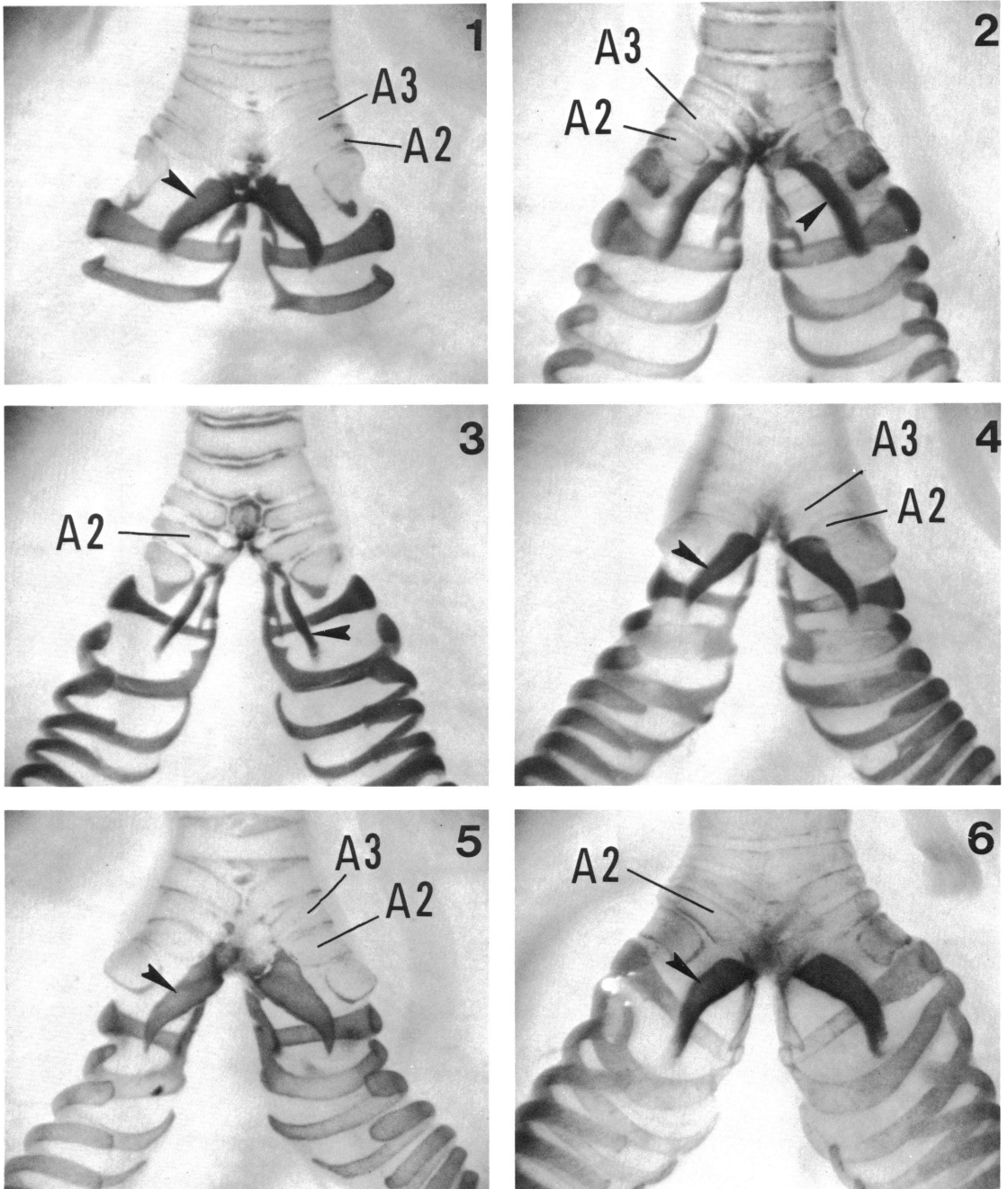
Fig. 10. Syringes of *Sublegatus, Inezia, "Myiophobus,"* and *Myiotriccus,* four genera in the *Phyllos-cartes* group (dorsal aspect; magnification ×18). (**1**) *Sublegatus modestus,* FMNH 322863; (**2**) *Inezia inornata,* AMNH 6784; (**3**) *"Myiophobus" ochraceiventris,* LSU 113743; (**4**) *"M." phoenicomitra,* LSU 85982; (**5**) *"M." roraimae,* LSU 118050; (**6**) *Myiotriccus ornatus,* LSU 85984. Arrows indicate internal cartilages; A elements as numbered.

semblance to formicariids as suggested by Ridgway and Wetmore. Ames remarked that

the syrinx of *Stigmatura* is unlike those of eight other genera in Hellmayr's Serpopha-

Stigmatura Group

(2 genera, 3 species)
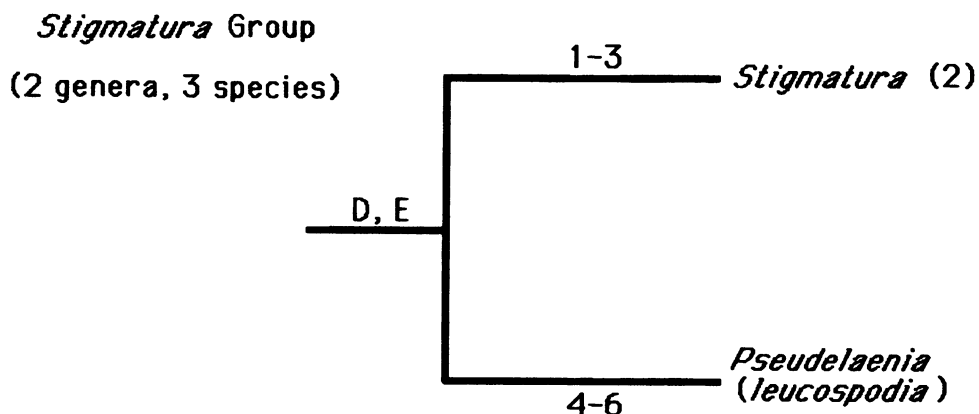
Fig. 11. Composition of the *Stigmatura* group (two genera; three species). Numbers identify diagnostic character states described in text and in table 3. Number in parentheses indicates number of species in genus.

ginae, but was unable to assign the genus to any of his species groups.

Warter (1965) reported that the nasal septum of his single skull of *Stigmatura* lacked a trabecular plate, unlike the other members of the Serpophaginae that he examined. That portion of the septum anterior to the internal supporting rod tends to be poorly ossified and is easily lost in museum preparation. If lost, the small bulbouslike trabecular plate that lies within this segment of the septum is lost as well. Two of the nine specimens that I examined were lacking this anterior portion of the septum; two others retained this segment, with its small trabecular plate, but the septum surrounding the plate was so thin and transparent as to transmit light from the microscope illuminator. All nine skulls possessed another bulbous swelling at the ventral end of the internal supporting rod; it follows, then, that in those specimens that retain the anterior segment of the septum, there are actually two small trabecular plates, one within the septum anteriorly, and one near the base of the internal supporting rod posteriorly (character D; fig. 12: 1).

Taczanowski's *leucospodia* has had a checkered taxonomic history. It was originally assigned to *Elaenia* (Taczanowski, 1877) and retained there by Sclater (1888) and Hellmayr (1927), but the latter remarked that it is "a rather aberrant species, recalling, in some respects, certain members of the genus *Serpophaga*." Zimmer (1941) acknowledged that the "closest point of resemblance between

leucospodia and the members of the genus *Elaenia* or *Myiopagis* is found in the presence of a white crest and this is hardly a generic character, being absent in some *Elaenia*." Because of similarities in the concealed crown patch (lacking "all trace of white in the center of the crown") and in the scutellation of the tarsus, Zimmer placed *leucospodia* in *Phaeomyias* but admitted it "is not typical" of that genus. Traylor (1977) argued that *leucospodia* "should not be placed in a crestless genus without more substantial evidence," and shifted it to *Myiopagis*.

TABLE 3
Characters Used for *Stigmatura* Group

D. Two trabecular plates, both small bulbous swellings; one anterior to the internal supporting rod, and one at the base of that rod

E. No complete A ring around either bronchus; A1 through A5 incomplete, with at least three pairs of these A elements connected by a cartilaginous plate to which large internal cartilages are attached

1. Cartilaginous pessulus and dorsomedial plate extending anteriorly between incomplete A elements of lower trachea

2. Superior fenestra of interorbital septum much reduced through ossification

3. Tail rounded, with conspicuous white medial and distal patches

4. Calcified pessulus projecting posteriorly from A6 element

5. Some fusion of A6–A9 elements

6. Plumage with concealed crown patch
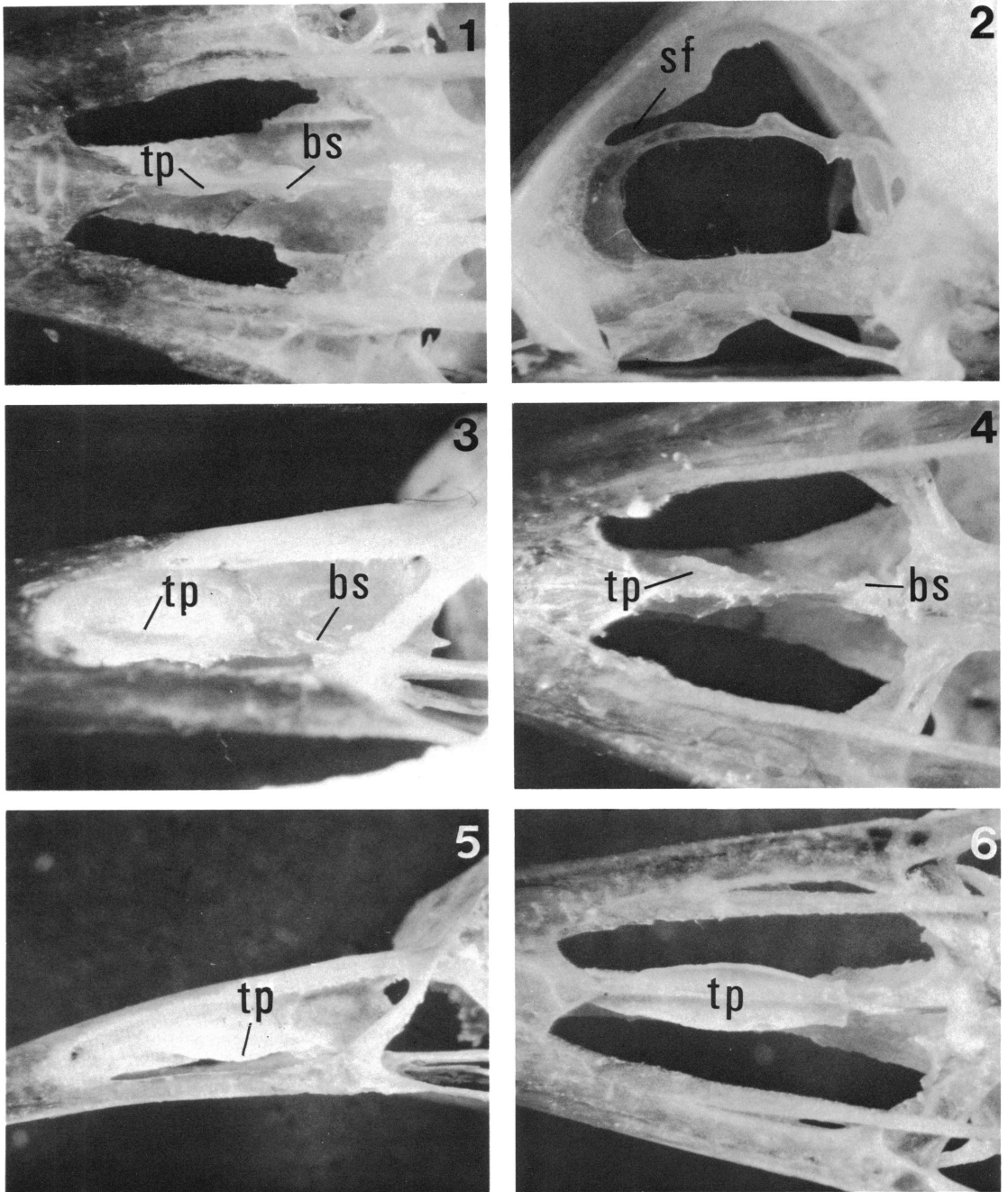
Fig. 12. Cranial characters in the *Stigmatura* group and in *Euscarthmus* (anterior end of skull to left; ventral views in 1, 4, 6, and lateral in 2, 3, 5; magnification ×12 in 1, 3, 4, 6, ×7 in 2, and ×8 in 5). (1, 2) *Stigmatura napensis,* LSU 111583; (3, 4) *Pseudelaenia leucospodia,* LSU 86587; (5, 6) *Euscarthmus meloryphus,* AMNH 7183. bs = bulbous swelling; sf = superior fenestra; tp = trabecular plate.

In view of this taxonomic history, I was totally unprepared for the close relationship between *Stigmatura* and *leucospodia* suggested by my examination of skulls and sy-

ringes. The skull of *leucospodia* (two specimens examined) is unlike that of *Elaenia, Myiopagis,* or of *Phaeomyias murina,* and is very similar to that of *Stigmatura* as described above. There is a small trabecular plate within the anterior segment of the nasal septum, and a still smaller enlargement (bulbous swelling) at the base of the internal supporting rod, in the manner of *Stigmatura* (character D; fig. 12: 3, 4). In addition, the syringes of *leucospodia* (three specimens) and of *Stigmatura* (four specimens) share a suite of derived character states that are probably interrelated: there is no complete A ring around each of the bronchi, but instead A1 through A4 or A5 elements are incomplete, and the dorsal ends of three pairs of these elements (usually 2 through 4) are connected by a cartilaginous bronchial plate to which a pair of large internal cartilages is attached (character E; fig. 13: 1, 2). This syringeal morphology places both taxa well outside my *Elaenia* group, and is congruent with the cranial morphology. Collectively these characters argue for considering them to be sister taxa.

That *leucospodia* should not be merged with *Stigmatura* is suggested by differences in syringeal, cranial, and external morphology. In *Stigmatura* the pessulus is cartilaginous and is not fused with any A elements, and there is a cartilaginous tracheal plate that extends anteriorly between the incomplete A elements of the lower dorsomedial trachea (character 1; fig. 13: 1); the superior fenestra of the interorbital septum is much reduced in size due to ossification (character 2; fig. 12: 2); and the tail is rounded and bears conspicuous white patches medially and distally (character 3). In *leucospodia* the pessulus is calcified and projects posteriorly from the A5 or A6 element (character 4; fig. 13: 2); there is considerable fusion of the A5 or A6–A9 elements, above the syrinx proper (character 5; fig. 13: 2); and the plumage has a concealed crown patch (character 6). In view of these differences, a new genus is described below for *leucospodia*.

Pseudelaenia, new genus

TYPE SPECIES: *Elaenia leucospodia* Taczanowski, 1877: 325; Tumbes, Peru.

INCLUDED SPECIES: The type species only.

DISTRIBUTION: Arid littoral of southwestern Ecuador and northwestern Peru (Traylor, 1979).

ETYMOLOGY: From the Greek *pseudo* meaning false, alluding to the mistaken placement of this species in *Elaenia.*

DIAGNOSIS: The morphology of the nasal septum and the syrinx is closest to that of *Stigmatura* (characters D and E); differs from *Stigmatura* in syringeal characters 4 and 5, and in the possession of the concealed crown patch (character 6). *Pseudelaenia* lacks the conspicuous white tail pattern of *Stigmatura.*

The nest of *Stigmatura* is a shallow cup, and the eggs are white marked with cinnamon or brownish spots (AMNH coll.; Dinelli, 1918; Smith, 1971); that of *Pseudelaenia leucospodia* has been described as a deep, "barrel-shaped" cup, and the creamy-buff eggs are unmarked (Marchant, 1960).

It is tempting to regard *Pseudelaenia* as a vicariant Pacific coastal relict of a formerly widespread form ancestral to both genera. *Stigmatura* is now found throughout much of South America east of the Andes.

Euscarthmus
(Figure 2 and table 1)

The taxonomic position of the two species of *Euscarthmus* has been an enigma. Since Berlepsch (1907), they have usually been placed at the end of the Euscarthminae with *Pseudocolopteryx, Habrura* (=*Polystictus*), and *Culicivora.* Hellmayr (1927) acknowledged that "the systematic position of the genus is quite uncertain. Its taxaspidean tarsus would seem to exclude it from the Tyrannidae, but color pattern, particularly the rufous crown patch points to relationships in this family . . . . Mr. Ridgway suggests Formicariinae affinities. Without anatomical investigations it will be difficult to satisfactorily decide the question." Wetmore (1926) stated that it was "certainly not a true flycatcher," and placed the genus tentatively in the antbirds. Zimmer (MS) thought the tarsi might show relationship to one of several tyrant genera (*Muscigralla, Stigmatura, Polystictus,* or *Culicivora*), but refrained from moving the genus from its historical sequence. Traylor (1977) followed tradition; he noted that the
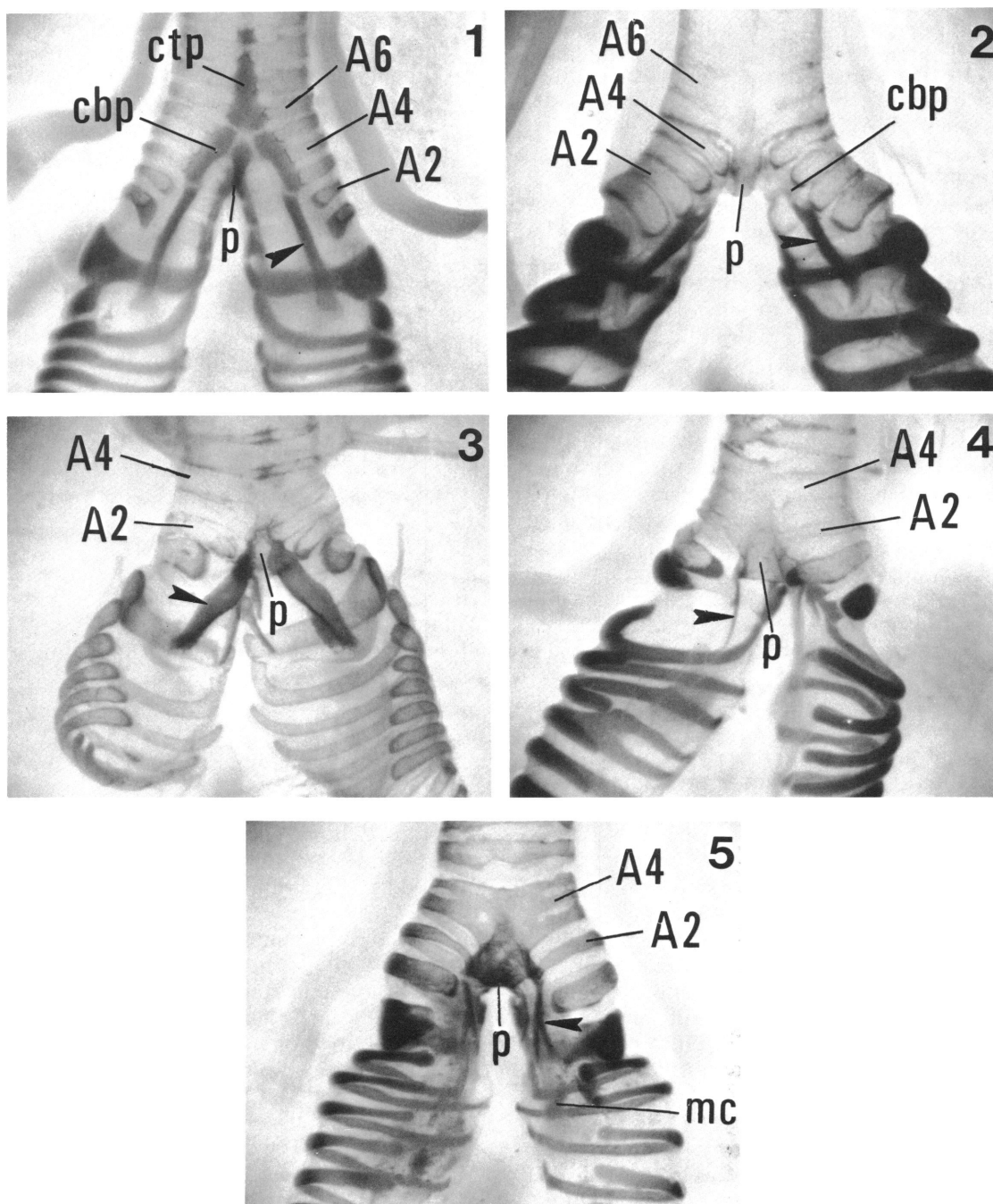
Fig. 13.   Syringes of the *Stigmatura* group, *Euscarthmus,* and the *Pseudotriccus* group (dorsal aspect; magnification ×15 in 1, 5, and ×18 in 2–4). (**1**) *Stigmatura budytoides,* PMNH 4537; (**2**) *Pseudelaenia leucospodia,* LSU 114008; (**3**) *Euscarthmus meloryphus,* AMNH 8866; (**4**) *Pseudotriccus pelzelni,* UK 69000; (**5**) *Corythopis torquata,* AMNH 816755. Arrows indicate internal cartilages; A elements as numbered; cbp = cartilaginous bronchial plate; ctp = cartilaginous tracheal plate; mc = mass of cartilage; p = pessulus.

two species "have frequently been allied to *Pseudocolopteryx,* but I hesitate to unite them because the latter is so uniform without *Euscarthmus.*"

There is no question that *Euscarthmus* is a tyrant flycatcher. Ames (1971) noted internal cartilages in his single specimen but was unable to place it any of his species groups. I have examined five syringes of *meloryphus* (*rufomarginatus* lacking); they contain none of the shared derived characters of the Formicariidae and do possess large internal cartilages (fig. 13: 3).

The nasal septum of *Euscarthmus* (five specimens of *meloryphus* examined; *rufomarginatus* lacking) has the shared derived character (A) that defines my *Elaenia* assemblage; it is fully ossified and has a large trabecular plate, located within the septum and deflected laterally so that it appears conspicuously concave in cross section (fig. 12: 5, 6). This configuration of the nasal septum is not helpful in placing *Euscarthmus* within the assemblage, however, for several genera in different lineages have evolved similar septa (*Inezia, Polystictus, Serpophaga*). There are no derived cranial characters to link *Euscarthmus* with other genera in the assemblage.

Since there is no complete A ring around either bronchus, no cartilaginous plate as in my *Stigmatura* group, and no fusion of A elements into a drum, the syrinx of *Euscarthmus* also is an equivocal factor for placement of this genus within the *Elaenia* assemblage. One conclusion is apparent, however: it does not belong with my *Elaenia* group. Ames (1971) reported that his single specimen of *Euscarthmus* had a well-developed drum, and illustrated it accordingly. I have examined and stained this specimen (USNM 227325) and, though badly damaged, find it similar to the rest of my series, i.e., lacking any suggestion of a fusion of the A elements. There is a narrow, calcified pessulus that is more or less independent of the A elements, and it is to this pessulus that the large internal cartilages are attached (character F; fig. 13: 3). This syringeal morphology is sufficiently distinct from those that characterize the other primary lineages in my *Elaenia* assemblage that I have no recourse but to treat *Euscarthmus* as part of the unresolved polychotomy in figure 2.

Both species of *Euscarthmus* have concealed crown patches; such patches have evolved independently in three of the four other primary lineages within the assemblage (and, of course, in other assemblages of tyrants). The nest of *Euscarthmus* has been reported to be a rather frail and shallow cup (Euler, 1900; Ihering, 1904; Marchant, 1960), presumably the primitive state for all tyrant flycatchers. The eggs have been described as being white or creamy white, either unmarked (Ihering, 1904; Smyth, 1928) or spotted with brown (Euler, 1900; Marchant, 1960).

The *Pseudotriccus* Group
(Figure 14 and table 4)

This is another small group consisting only of two genera, *Pseudotriccus* and *Corythopis.* I have examined the skulls of all five species and the syringes of all but *Corythopis delalandi.*

Historically *Pseudotriccus* (including *Caenotriccus*) has been placed with *Hemitriccus, Myiornis,* and the other tody-tyrants (Sclater, 1888; Berlepsch, 1907; Hellmayr, 1927; Zimmer, MS; Meyer de Schauensee, 1966). Traylor (1977) was the first to question this alliance, remarking that this genus "seems to have no close relatives . . . . It has generally been associated with *Hemitriccus* at the end of the *Todirostrum* group, but there is little real resemblance . . . . The one genus to which *Pseudotriccus* may be allied is *Corythopis,* which has only recently been admitted to the Tyrannidae and which is without obvious relatives. The two genera share a proportionately long tarsus . . . the scutes of the tarsi are almost obsolete, giving a smooth booted effect . . . . Fitzpatrick (in conversation) says they share similar feeding habits, walking along the ground and leaping up to pick insects from the under sides of leaves. I place *Corythopis* and *Pseudotriccus* together, and leave them between the *Phylloscartes* and the *Todirostrum* group of genera, not because I am convinced that that is where they belong, but because I know of no better place."

Corythopis had been assigned to the family

Pseudotriccus Group

(2 genera; 5 spp.)

```
                                    4,5
                          ┌──────────────── Pseudotriccus (3)
                          │
            6,H,1-3       │
        ──────────────────┤
                          │
                          │    6,7
                          └──────────────── Corythopis (2)
```
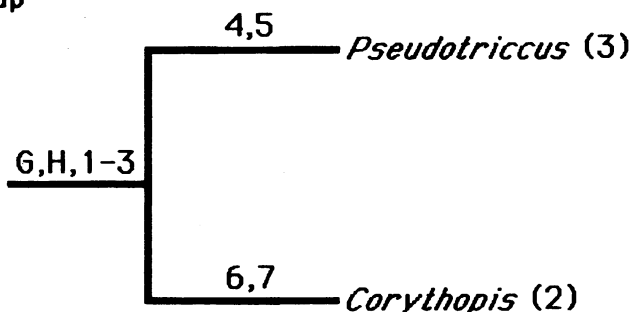
Fig. 14. Composition of the *Pseudotriccus* group (two genera; five species). Numbers identify diagnostic character states described in text and in table 4. Numbers in parentheses indicate number of species per genus.

Conopophagidae, within the antbird–ovenbird complex, until Ames et al. (1968) presented conclusive evidence (from syringeal morphology, antorbital osteology, and dorsal pterylosis) that is should be transferred to the Tyrannidae. Ames (1971) noted "the peculiar shape of the internal cartilages [in the syrinx of his *Corythopis*], which are not far from those of *Leptotriccus* [=*Phylloscartes*] *sylviolus*. There is little in the external anatomy to suggest a relationship between the two genera, so one may probably assume the slight similarity of internal cartilages to be convergent." However, in his appendix of specimens examined, Ames listed his *Corythopis* specimens between *Euscarthmus* and *Pseudocolopteryx*; he did not examine a syrinx of *Pseudotriccus*.

The possibility of *Pseudotriccus* as a member of the tody-tyrants has been dismissed in my analysis of the phylogeny of that assemblage; it does not share the derived syringeal characters common to all tody-tyrants (Lanyon, MS). Cranial and syringeal morphology support the contention (Traylor, 1977; Traylor and Fitzpatrick, 1982) that *Pseudotriccus* and *Corythopis* are sister taxa based on external morphology and behavior. The nasal septum (six specimens of *Pseudotriccus* examined, representing all three species; five specimens of *Corythopis* examined, representing both species) is poorly ossified and may be missing altogether in some specimens. In those specimens in which some of the anterior section of the septum is retained in museum preparation, there is a small trabecular plate within the anterior septum, and

there is no plate posteriorly (character G; fig. 15: 1, 2, 4). In both genera the superior fenestra of the interorbital septum is much reduced through ossification (character 1; fig. 15: 3). The syringes of the two genera (eight specimens of *Pseudotriccus* examined, representing all three species; four specimens of *Corythopis torquata* examined; *delalandi* lacking) show no well-developed drum, though there may be some slight fusion of A elements in the vicinity of the pessulus, and there is no complete A ring around either bronchus, and no cartilaginous plate as in my *Stigmatura* group. The pessulus is unusually large, calcified, and uniquely shaped in both genera, in that the greatest breadth of the pessulus is at that point where the internal cartilages attach, and the pessulus is concave when viewed dorsally (character H; fig. 13:

TABLE 4
Characters Used for the *Pseudotriccus* Group

G. Nasal septum poorly ossified; small trabecular plate within anterior section of septum, when retained in museum specimens, and no plate posteriorly

H. Pessulus unusually large, calcified, and concave when viewed dorsally

1. Superior fenestra in the interorbital septum much reduced through ossification
2. Internal cartilages forked and connected with poorly stained club-shaped mass of cartilage
3. B1 elements partly calcified .
4. A1 elements are L-shaped dorsally
5. A2 elements are fused with the A3s
6. B1 elements are very broad throughout their length
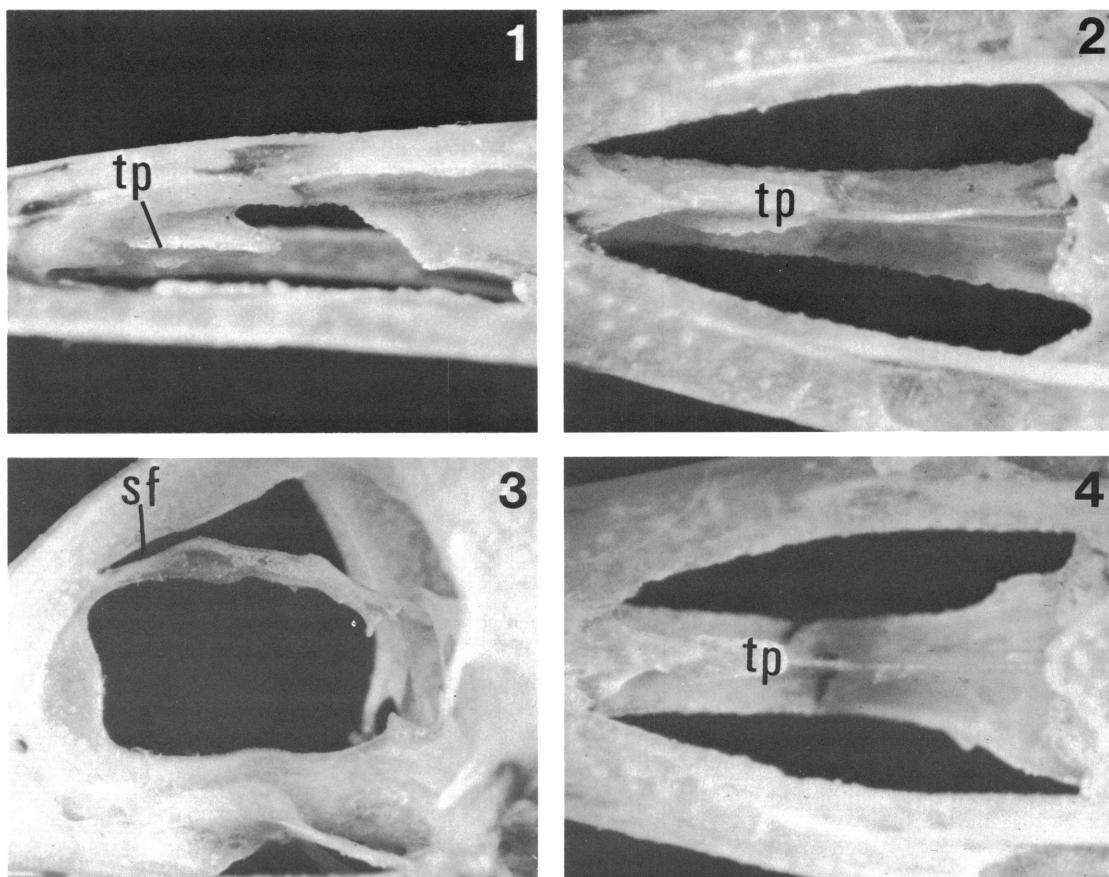7. Internal cartilages are much more deeply forked

Fig. 15. Cranial characters in the *Pseudotriccus* group (anterior end of skull to left; lateral views in 1, 3, and ventral in 2, 4; magnification ×12 except ×7 in 3). (**1, 2**) *Pseudotriccus ruficeps,* AMNH 6937; (**3, 4**) *Corythopis delalandi,* AMNH 14476. sf = superior fenestra; tp = trabecular plate.

4, 5). The internal cartilages are forked (more strongly so in *Corythopis*), with the ventral segment being attached via a poorly staining cartilaginous filament to an equally poorly staining club-shaped mass of cartilage lying farther posteriorly within the internal tympaniform membrane (character 2; fig. 13: 5). In addition, the B1 elements in both genera are partly calcified (character 3).

The cranial and syringeal evidence for the relatedness of *Pseudotriccus* and *Corythopis* is impressive. That the two genera should be kept distinct seems equally clear, based on a number of external morphological characters and on differences in syringeal morphology: in *Pseudotriccus* the A1 elements are L-shaped dorsally (character 4; fig. 13: 4) and the A2s are fused with the A3s (character 5), while in *Corythopis* the B1 elements are very broad

throughout their length (character 6) and the internal cartilages are more deeply forked (character 7; fig. 13: 5). I cannot appreciate the similarity reported (see quotation from Ames, above) between the syringes of *Corythopis* and *Phylloscartes* (compare fig. 13: 5 with fig. 5: 3–6). What remains unclear is the relationship of the group to the rest of the *Elaenia* assemblage, hence the contribution to the polychotomy in figure 2.

Sibley and Ahlquist (1985) reported that DNA comparisons suggest that *Pseudotriccus* and *Corythopis* belong to an early radiation that occurred independent of that of the true flycatchers (along with *Mionectes* and *Leptopogon*). As explained earlier in my discussion of the *Phylloscartes* group, until there is more supporting evidence I reject this novel hypothesis in favor of the more parsimonious

view that internal cartilages evolved but once and truly reflect monophyly for all tyrant flycatchers.

The nest of *Corythopis* is unique for the assemblage, so far as is known, having been reported as being an oven-shaped structure (with side entrance) located on the ground (character 1; Oniki and Willis, 1980). The nest of *Pseudotriccus* is unreported.

The *Elaenia* Group
(Figure 16 and table 5)

My *Elaenia* group, the largest in the assemblage, is dominated numerically by *Elaenia, Tyranniscus, Myiopagis, Serpophaga,* and *Anairetes,* and in addition includes *Tyrannulus, Ornithion, Camptostoma, Mecocerculus, "Mecocerculus"* spp. (two groups of species formerly in *Mecocerculus*), *Uromyias, Suiriri, Pseudocolopteryx, Polystictus, Capsiempis, Phaeomyias,* and *Nesotriccus.* I have examined skulls and syringes from all 18 genera, but lack skulls of 14 of the 65 species and syringes of 14.

Once again, there is no tradition for considering these taxa as constituting a monophyletic group. The species are those that made up the bulk of Hellmayr's (1927) Elaeniinae (10 of 16 genera in that subfamily), plus nearly half of his Serpophaginae (four of nine genera), four genera that he placed at the end of his Euscarthminae, and one genus in his Myiarchinae. The fact that my group, defined by a shared derived syringeal morphology that is unique among tyrant flycatchers, includes some genera (but not all) from four of Hellmayr's subfamilies illustrates the difficulties in identifying natural (i.e., monophyletic) groups on the basis of external morphology, the classical methodology. In the broad sense, the discreteness of these particular subfamilies of Hellmayr had been questioned. Warter (1965) doubted that separation of the Serpophaginae from the Elaeniinae "is justifiable at the level of the subfamily," and Traylor (1977) concurred: "There seems little question that the former subfamilies or tribes were artifacts."

Traylor's (1977) treatment more nearly corresponds to the one proposed here. My *Elaenia* group corresponds to the first half of his Elaeniinae, with the following exceptions. Traylor included *Sublegatus, Inezia,* and *Stigmatura* within his sequence, whereas I place these genera elsewhere within the *Elaenia* assemblage since they do not share the syringeal morphology unique to my *Elaenia* group. Traylor also included *Tachuris* and *Culicivora;* these genera do not share the characters of the *Elaenia* group, and they remain incertae sedis until their relationships can be determined. I believe Traylor's enlarged genus *Phyllomyias* to be polyphyletic (discussed in greater detail on p. 37): *Tyranniscus* (including *Xanthomyias, Oreotriccus,* and *Acrochordopus*) is an appropriate member of my *Elaenia* group; Traylor's new genus *Zimmerius* belongs with *Sublegatus* and *Inezia* in my *Phylloscartes* group; and *Phyllomyias,* sensu stricto, does not share the uniquely derived syringeal characters of the *Elaenia* group, is itself polyphyletic, and must remain incertae sedis until more material clarifies the affinities of its three species. Two species included in my *Elaenia* group were omitted from Traylor's sequence: *Capsiempis flaveola* was merged with *Phylloscartes* in the second half of his Elaeniinae, and *Nesotriccus ridgwayi* was placed near *Empidonax* in his Fluvicolinae (see Lanyon, 1984a).

Among several groups of genera distinguished by their syringeal homogeneity, Ames (1971) recognized an *Elaenia* group, consisting of representatives of *Elaenia* (including *Myiopagis*), *Suiriri, Camptostoma, Tyrannulus, Phaeomyias, Microtriccus (=Ornithion),* and *Tyranniscus.* In addition, Ames reported that the syringes of *Mecocerculus, Serpophaga, Anairetes, Pseudocolopteryx, Capsiempis,* and *Habrura (Polystictus)* have fused A elements as in *Elaenia,* but did not assign these genera to any of his taxonomic groups. The other genera in my *Elaenia* group were unavailable to Ames.

The 18 genera in my *Elaenia* group have a configuration and structure of the tracheobronchial junction that is unique among all tyrant flycatchers. There is extensive if not complete fusion of the dorsal A3 through A5 elements with the pessulus, as well as fusion of other A elements in varying degrees, to form a "drum." Consequently, the pessulus is extremely well-developed, calcified, and broad dorsally and narrow ventrally. The internal cartilages are attached to dorsomedial points on the drum. Undoubtedly the above

Elaenia (17)
Myiopagis (6)
Tyrannulus (1)
Tyranniscus (7)
"Mecocerculus" (*calopterus, minor*)
Ornithion (3)
Camptostoma (2)
"Mecocerculus" (*stictop., poecil., hell.*)
Suiriri (1)
Pseudocolopteryx (4)
Polystictus (2)
Mecocerculus (1)
Uromyias (2)
Capsiempis (1)
Phaeomyias (1)
Nesotriccus (1)
Serpophaga (6)
Anairetes (5)

Elaenia Group
(18 gen., 65 spp.)
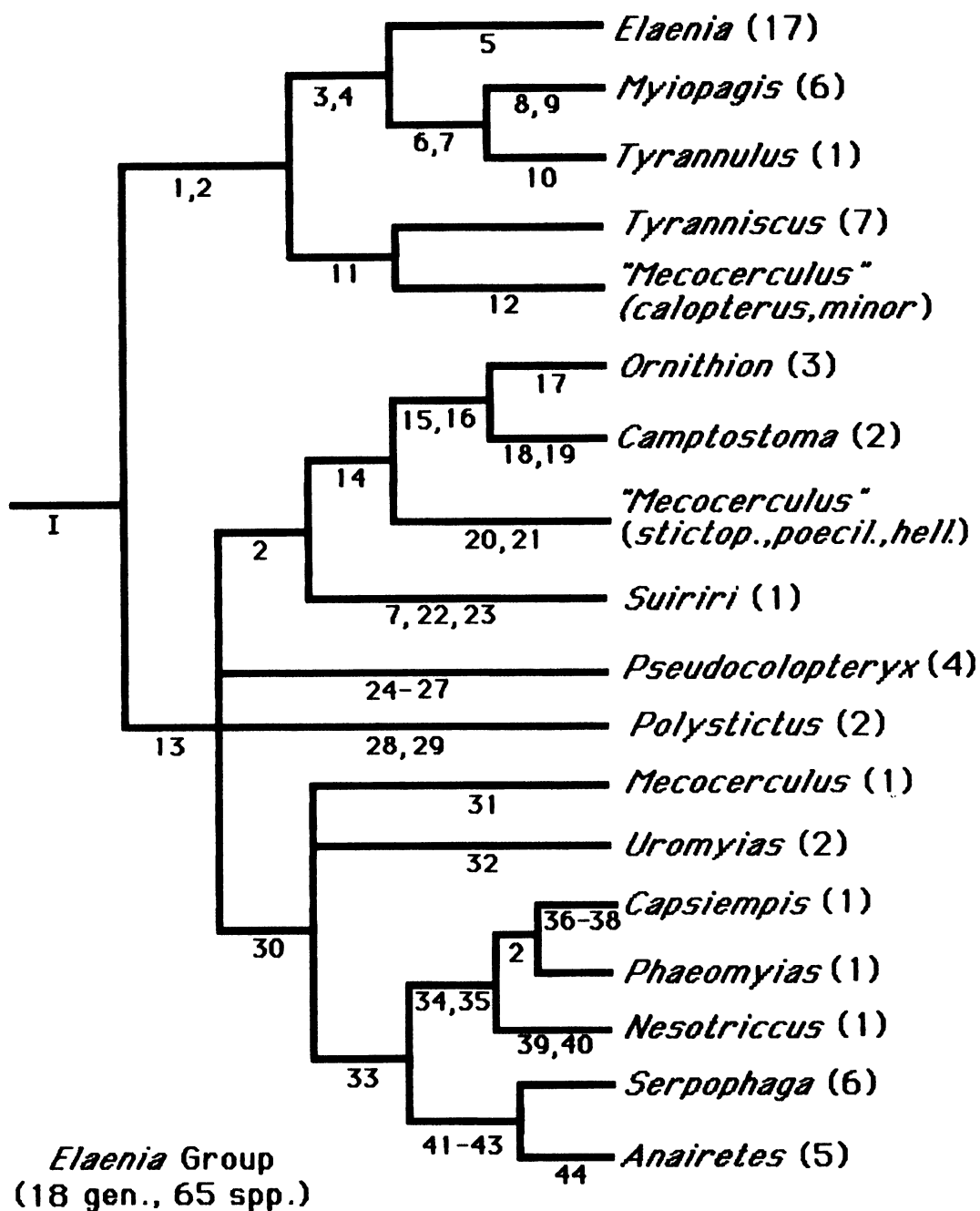
Fig. 16. Phylogenetic relationships within the *Elaenia* group (18 genera; 65 species). Numbers identify diagnostic character states described in text and in table 5. Numbers in parentheses indicate number of species per genus.

structures are interrelated and I regard them as part of a single complex (character I; fig. 1: 9, 10).

In five genera within the *Elaenia* group (*Elaenia, Myiopagis, Tyrannulus, Tyranniscus,* and *"Mecocerculus"* spp.), the syringeal drum excludes the A2 elements, i.e., there is no evidence that the A2s have fused into the

TABLE 5
Characters Used for *Elaenia* Group

I. Fusion of dorsal A3–A5 elements with the pessulus, as well as fusion of other A elements in varying degrees, to form a drum; internal cartilages attach to dorsomedial positions on drum; pessulus well-developed, calcified, broad dorsally and narrow ventrally

1. Syringeal drum excludes A2 elements (not fused into drum)
2. Intrinsic muscles of the syrinx well-developed (bulging masses of tissue)
3. A1 elements terminate dorsally in large, cartilaginous segments
4. Plumage with concealed crown patch
5. Some species have a trabecular plate that bases the septum and a nasal septum that has an anterior notch
6. Internal cartilages conspicuously attached to dorsal ends of A2 elements as well as to the drum, and with amorphous segment projecting ventrally from their posterior third
7. Nasal capsule more fully ossified, including alinasal walls and turbinals
8. Nasal septum poorly ossified in most specimens; some specimens have nasal septum fully ossified, with a very narrow and obscure trabecular plate located within the anterior section
9. Internal cartilages more slender and more gracefully curved into a shallow S-shape
10. Small but well-developed ovate trabecular plate within the nasal septum
11. Internal cartilages are narrow basally, broad distally, and have an amorphous distal segment
12. More prominent posterior trabecular plate
13. Syringeal drum includes the A2 elements (fused into drum)
14. Internal cartilages are straight and broad, and have ventral extension from distal half of cartilage
15. Ventral extension from distal half of internal cartilage is poorly staining and amorphous
16. Dorsal ends of the A1 elements are broad
17. Nasal septum has a small, ovate trabecular plate located within the septum at the base of the internal supporting rod
18. Long, narrow trabecular plate within and for most of the length of the anterior section of the nasal septum
19. Nest is enclosed, with side entrance, and generally located within a clump of vegetation
20. Ventral extension from distal half of internal cartilage stains well and is well-formed, in the shape of a fully extended and nearly square flag
21. Anterior section of nasal septum has a long, narrow plate located within it; a similar but shorter, less prominent plate located just posterior to the internal supporting rod
22. Internal cartilages stain very poorly, except distally

TABLE 5—(*Continued*)

23. B1 elements very broad throughout their length
24. Dorsal ends of the B1 elements slightly forked
25. A1 elements comparatively narrow dorsally and terminate in small cartilaginous knobs
26. Trabecular plate well-developed, widens somewhat in region beneath the internal supporting rod and is deeply forked posteriorly
27. Plumage of underparts bright yellow, unstreaked
28. Trabecular plate is quite broad, slightly deflected ventrally along the lateral margins, and is just barely forked posteriorly
29. Internal cartilages straight, wider basally than distally, and have a peculiar nonstaining centrum in the basal segment
30. Internal cartilages relatively narrow and slightly curved
31. Internal cartilages somewhat larger and more robust, and terminating in a poorly staining, amorphous segment
32. Tail long and graduated
33. Trabecular plate conspicuously forked posteriorly in the shape of a slender tuning fork
34. Anterior segment of nasal septum poorly ossified, sometimes missing; if present, there may be a narrow, inconspicuous trabecular plate within that region
35. Internal cartilages attached to dorsal ends of A1s as well as to the drum
36. Long, cartilaginous extensions from the dorsal ends of the A1s
37. Internal cartilages attached closer together on the drum
38. Ventral ends of the B1s are broader
39. Internal cartilages much broader, more robust
40. Bill much longer than in the sister taxa
41. Anterior segment of nasal septum fully ossified, with a conspicuous, well-developed trabecular plate within that segment
42. Crown with streaks and/or concealed patch of white or cream color
43. Drum more poorly developed, on average, than in other genera in the group
44. Plumage of crown with elongate black feathers (prominently crested); all but *alpinus* have throat and chest heavily streaked with black

drum (character 1; figs. 16, 19, 20, 22); I regard this as a shared derived character and evidence of monophyly. In addition, the intrinsic muscles of the syrinx are better developed than in many of the other genera within the assemblage, and can be seen as conspicuous masses of tissue bulging from the sides of the syrinx (character 2; labeled

in figs. 19: 2 and 22: 2). This particular character has apparently evolved three times within this group (see fig. 16), for this would appear to be a more parsimonious explanation than hypothesizing multiple changes in the more conservative basic configuration of the tracheobronchial junction (e.g., character 13 in fig. 16). This cluster of genera agrees well with the treatment by Traylor (1977), except that he merged *Tyranniscus* (sensu stricto) with an enlarged *Phyllomyias,* which he placed at the beginning of his Elaeniinae.

If these five genera have had a common ancestry, as hypothesized here, then it is reasonable to argue that *Elaenia, Myiopagis,* and *Tyrannulus* form a cluster within this subgroup, on the basis of their having the A1 elements terminating dorsally in large, cartilaginous segments (character 3; figs. 19, 20, 22), and in their having concealed crown patches in their plumage (character 4). Among genera of tyrant flycatchers, *Elaenia* is one of the most widespread geographically, and one of the four most speciose (with *Hemitriccus, Myiarchus,* and *Phylloscartes*). The nasal septum of *Elaenia* shows significant variation not heretofore reported and worthy of documentation in some detail. I have examined skulls of 15 of the 17 species (*strepera* and *dayi* lacking). Of these 15 species, 9 (32 specimens) have character A that I use as argument for monophyly of the assemblage, i.e., there is a trabecular plate elevated somewhat above the ventral edge of the septum, and there is no anterior notch in the septum (fig. 17). This is the type of septum (number five) reported for *Elaenia* by Warter (1965). In addition, these nine species also have a second trabecular plate, usually very narrow to the point of being obscure, and located along the ventral edge of the septum (i.e., basal to it) posterior to the internal supporting rod. Three specimens illustrate variation in this configuration of the nasal septum: the two *flavogaster* skulls (fig. 17: 3, 4) illustrate intraspecific variation in the prominence of the sagittal ridge on the anterior trabecular plate and in the size of the posterior plate; the *mesoleuca* skull illustrates the maximum size of the posterior plate in this sample (fig. 17: 8).

In the remaining six species for which I have skulls (31 specimens of *frantzii, martinica, parvirostris, pallatangae, albiceps,* and *fallax*), the trabecular plate *bases the septum* (i.e., there is no sagittal ridge when viewed from below) and the septum has an anterior notch (character 5; fig. 18). Warter (1965), working with only eight species (but including *frantzii, parvirostris, pallatangae, albiceps,* and *fallax*), did not report this type (his number 6) of septum in *Elaenia.* Possession of a trabecular plate that bases the septum is the diagnostic character state of the *Empidonax* assemblage (Lanyon, 1986), but these six species of *Elaenia* have a trabecular plate that is not conspicuously forked posteriorly (as in *Empidonax* and allies), and they also have a smaller plate located posterior to the internal supporting rod (as in the sample of nine species of *Elaenia* mentioned above), which is quite variable in shape and size (and absent in *Empidonax* and allies). Three specimens (fig. 18: 2, 3, 5) illustrate variation in configuration in this type of nasal septum and particularly in the size of the posterior plate. Exceptions to the above generalization were two of five skulls of *fallax* (fig. 18: 4) in which the larger anterior plate was conspicuously forked posteriorly, in the manner of *Empidonax* and its allies; however, even these specimens had very small posterior plates, which are lacking in all members of the *Empidonax* assemblage.

The variation in the degree to which the superior and inferior fenestrae of the interorbital septum are ossified in *Elaenia* skulls matches that observed in all of the other genera within the assemblage. On average this septum in *Elaenia* is somewhat more ossified than in the *Phylloscartes* group, but the extremes (fig. 18: 7, 8) are close to the extremes recorded for that group (fig. 4: 5, 6).

The monophyly of the 17 species admitted to *Elaenia* (Traylor, 1979) has not been challenged and they have an extremely uniform external morphology, in addition to the uniformity in syringeal morphology demonstrated below. That a segment of the genus should have evolved a configuration of the nasal septum similar to that reported for the *Empidonax* assemblage is unexpected indeed; a trabecular plate that bases a septum with an anterior notch, in a genus that otherwise has all the appropriate characters for my *Elaenia* group in the *Elaenia* assemblage, can only be interpreted as a derived condition convergent upon the similar condition found within the

Fig. 17. Intrageneric variation in cranial characters in *Elaenia*; these species have a nasal capsule typical of the assemblage (anterior end of skull to left; ventral views, except lateral in 1; magnification × 10). (1, 2) *Elaenia ruficeps,* AMNH 11451; (3) *E. flavogaster,* AMNH 10320; (4) *E. flavogaster,* AMNH 12069; (5) *E. obscura,* LSU 84041; (6) *E. chiriquensis,* DM 57483; (7) *E. spectabilis,* UMMZ 158834; (8) *E. mesoleuca,* FMNH 105689. ptp = posterior trabecular plate; sr = sagittal ridge on trabecular plate; tp = trabecular plate; x = absence of anterior notch.
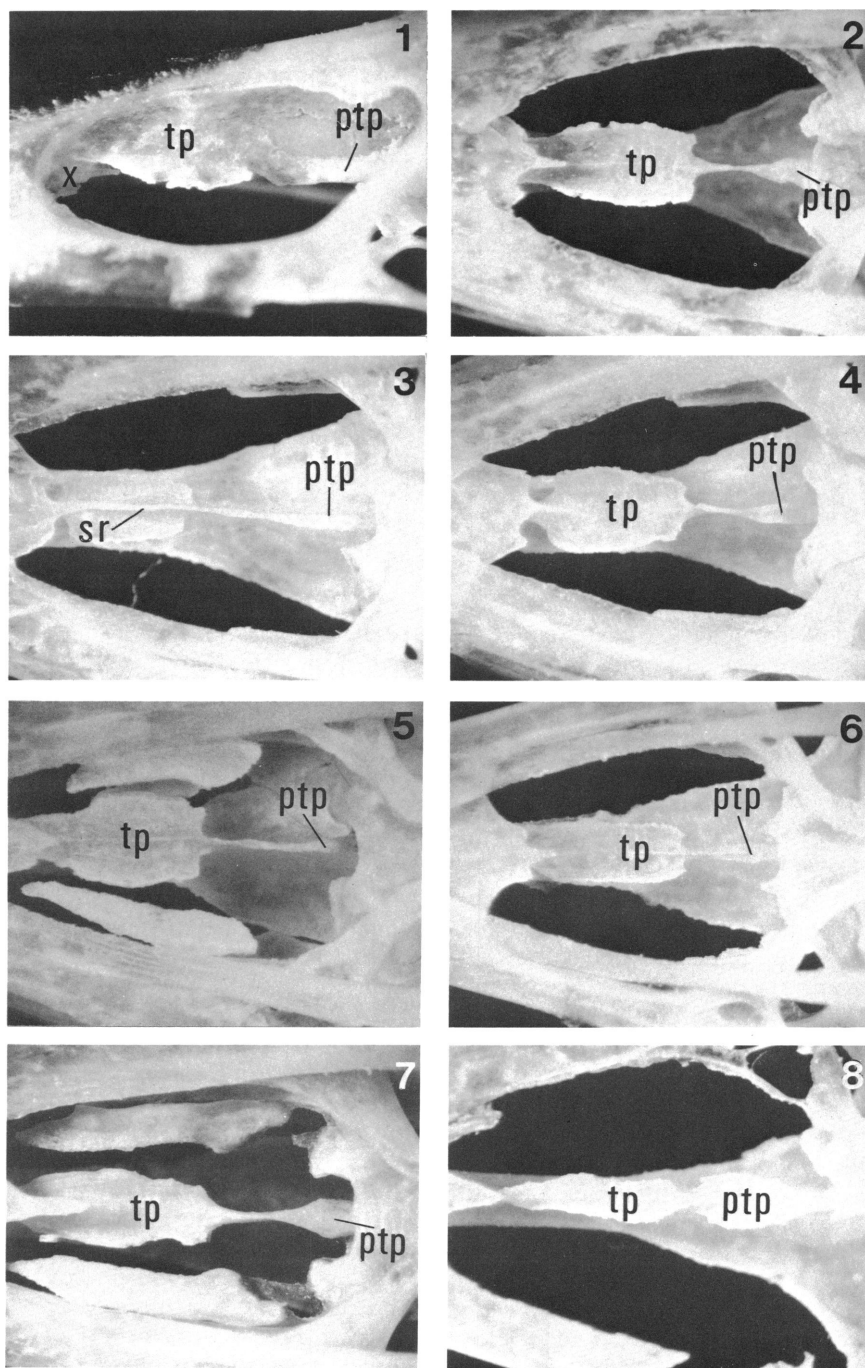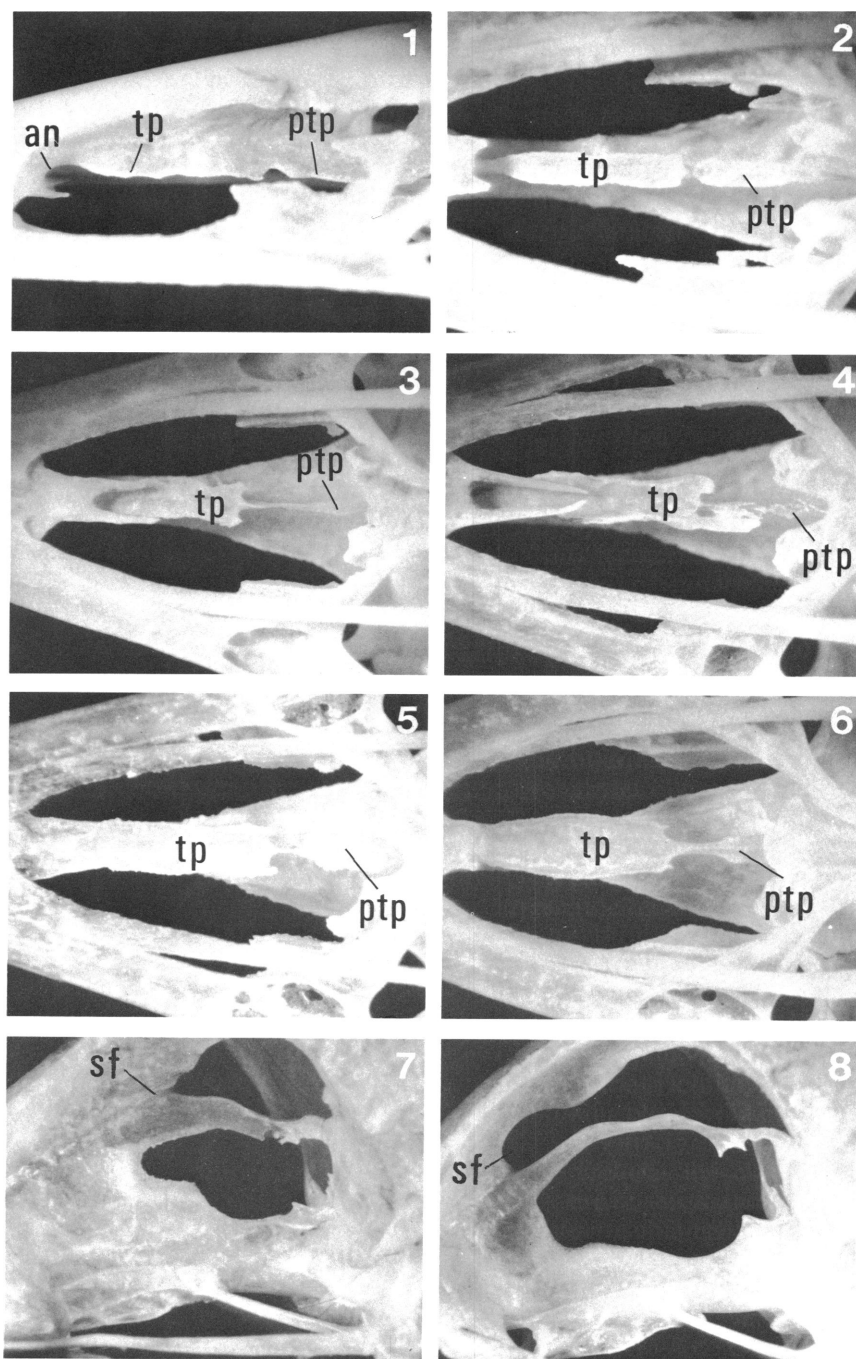
Fig. 18.   Intrageneric variation in cranial characters in *Elaenia*; all but *E. cristata* have a nasal capsule unique in the assemblage (anterior end of skull in left; ventral views, except lateral in 1, 7, 8; magnification ×10, except ×5 in 7, 8). (**1, 2**) *Elaenia martinica,* USNM 488003; (**3**) *E. fallax,* USNM 555840; (**4**) *E. fallax,* PMNH 7432; (**5**) *E. albiceps,* AMNH 6709; (**6**) *E. frantzii,* DM 62988; (**7**) *E. cristata,* AMNH 11929; (**8**) *E. pallatangae,* AMNH 15224. an = anterior notch; ptp = posterior trabecular plate; sf = superior fenestra; tp = trabecular plate.

Empidonax assemblage. From a practical standpoint, in terms of identifying skulls, it is fortunate indeed for the taxonomist that those *Elaenia* specimens having this convergent basal plate also have the small posterior plate, which is absent in all members of the *Empidonax* assemblage. I can find no correlation between the division of the genus (perhaps best treated as two species groups, or subgenera) on the basis of type of nasal septum and the distributional patterns of the species in the respective species groups.

There is a remarkable uniformity in the morphology of the *Elaenia* syringes examined (37 specimens of 15 species; *strepera* and *dayi* lacking). Though there are no evident differences between the two subgenera as defined by significant differences in the nasal septum, I have arranged the photographs of the syringes according to these two groups, to facilitate comparison (figs. 19, 20). The drum is formed by varying degrees of fusion of the A3 through A6 elements; in no specimen are the A2s fused with the drum (character 1). The internal cartilages are large, rather broad, basically straight or slightly J-shaped, and often have a poorly staining, somewhat amorphous terminal segment; they attach to a cartilaginous knob on the drum (the position of the dorsal ends of the fused A3s).

I have seen reports on nests of 13 of the 17 species of *Elaenia* (*gigas, pelzelni, ruficeps,* and *dayi* lacking). All records are of a rather compact, open cup, placed on a horizontal branch, fork, or upright crotch; the eggs are white, with reddish-brown blotches and markings, mainly around the large end (AMNH coll.; Barrows, 1883; Taczanowski, 1884; Cherrie, 1890, 1916; Ihering, 1900, 1904; Berlepsch and Hartert, 1902; Oates and Reid, 1903; Carriker, 1910; Todd and Carriker, 1922; Smyth, 1928; Hellmayr, 1932; Dickey and Van Rossem, 1938; Bond, 1943, 1971; Blake, 1956; Skutch, 1960, 1967; Allen, 1961; Herklots, 1961; Miller, 1963; Johnson, 1967; Haverschmidt, 1968; Humphrey, 1970; Wetmore, 1972; Gep, 1973; ffrench, 1976; Belton, 1985).

I have already discussed the placement of Taczanowski's *leucospodia* (cf. p. 23), formerly assigned to *Elaenia* (Taczanowski, 1877; Sclater, 1888; Hellmayr, 1927), *Phaeo-*

myias (Zimmer, 1941), and *Myiopagis* (Traylor, 1977). *Myiopagis* formerly was merged with *Elaenia* (Sclater, 1888; Berlepsch, 1907; Hellmayr, 1927), but Zimmer (1941) considered them distinct genera on the basis of differences in tarsal scutellation and in the color of the concealed crown patch. Traylor (1977) recognized *Myiopagis*, "but with the knowledge that further anatomical research may suggest either merging it with *Elaenia,* or transferring species between them." As will be noted below, *Myiopagis* differs significantly from *Elaenia* with respect to a number of cranial and syringeal characters and these genera should not be merged.

A sister-group relationship between *Myiopagis* and *Tyrannulus* had not been suggested until Traylor (1977) commented on the monotypic *Tyrannulus*: "[it] is almost a miniature of *Myiopagis gaimardii,* and I believe that is where its relationships lie .... *Tyrannulus* should be placed next to but not in *Myiopagis.*" Two anatomical characters support this relationship suggested by external morphology. The internal cartilages in syringes of the two genera are basically similar, but very different from those of *Elaenia*; they are conspicuously attached to the dorsal ends of the A2 elements as well as to the drum (solely to the drum in *Elaenia*), and have a more poorly staining, somewhat amorphous segment projecting ventrally from their posterior third (character 6; fig. 22: 1, 2). The nasal capsule in *Myiopagis* and *Tyrannulus* is more fully ossified than in *Elaenia,* including the alinasal walls and turbinals (character 7; fig. 21: 1, 2).

In *Myiopagis* the nasal septum is poorly ossified and most of the specimens in my sample (nine specimens of five species; *flavivertex* lacking) had no evidence of a trabecular plate; in two specimens of *M. gaimardii* (USNM 344217, UMMZ 208538) the septum is fully ossified and there is a very narrow and obscure trabecular plate located within the anterior section (character 8; fig. 21: 1). The syrinx of *Myiopagis* (nine specimens of five species examined; *cotta* lacking) is basically like that of *Tyrannulus,* but the internal cartilages are gracefully curved into a shallow S-shape (character 9) and more slender than in *Tyrannulus* (fig. 22: 1). In the skull of the monotypic *Tyrannulus* (two spec-
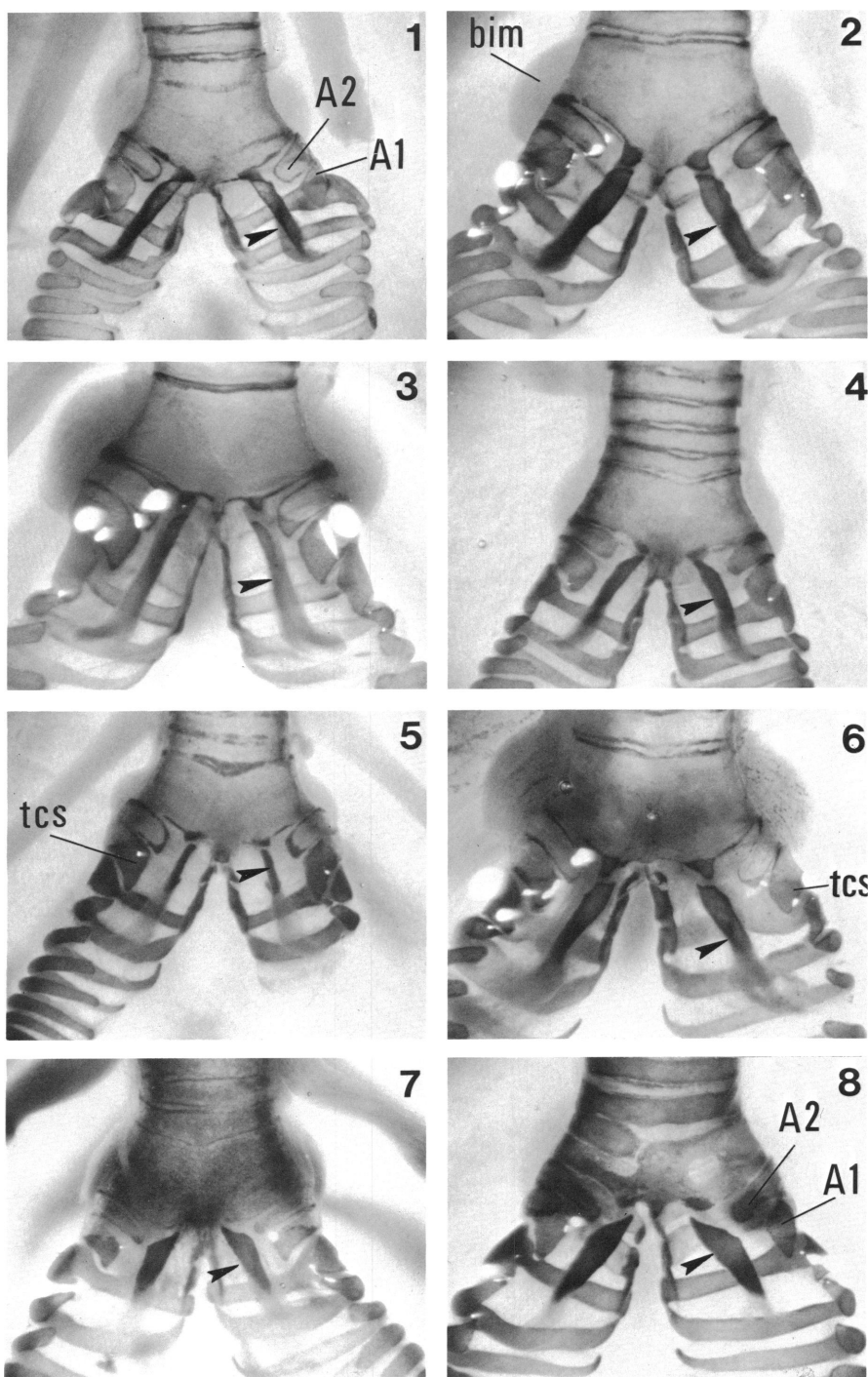
Fig. 19.   Intrageneric variation in syringeal morphology in *Elaenia* (dorsal aspect; magnification ×12). **(1)** *Elaenia cristata,* AMNH 8091; **(2)** *E. flavogaster,* AMNH 8094; **(3)** *E. mesoleuca,* AMNH 9093; **(4)** *E. ruficeps,* AMNH 8095; **(5)** *E. chiriquensis,* PMNH 4691; **(6)** *E. gigas,* FMNH 291669; **(7)** *E. spectabilis,* USNM 512631; **(8)** *E. pelzelni,* LSU 114510. Arrows indicate internal cartilages; bim = bulging intrinsic muscle; tcs = terminal cartilaginous segment on A1 element; A elements as numbered.

Fig. 20. Intrageneric variation in syringeal morphology in *Elaenia* (dorsal aspect; magnification ×15). **(1)** *Elaenia fallax,* PMNH 8889; **(2)** *E. martinica,* CM 1065; **(3)** *E. albiceps,* AMNH 2464; **(4)** *E. pallatangae,* LSU 103311; **(5)** *E. parvirostris,* USNM 504593; **(6)** *E. frantzii,* CM 392. Arrows indicate internal cartilages; tcs = terminal cartilaginous segment on A1 element; A elements as numbered.
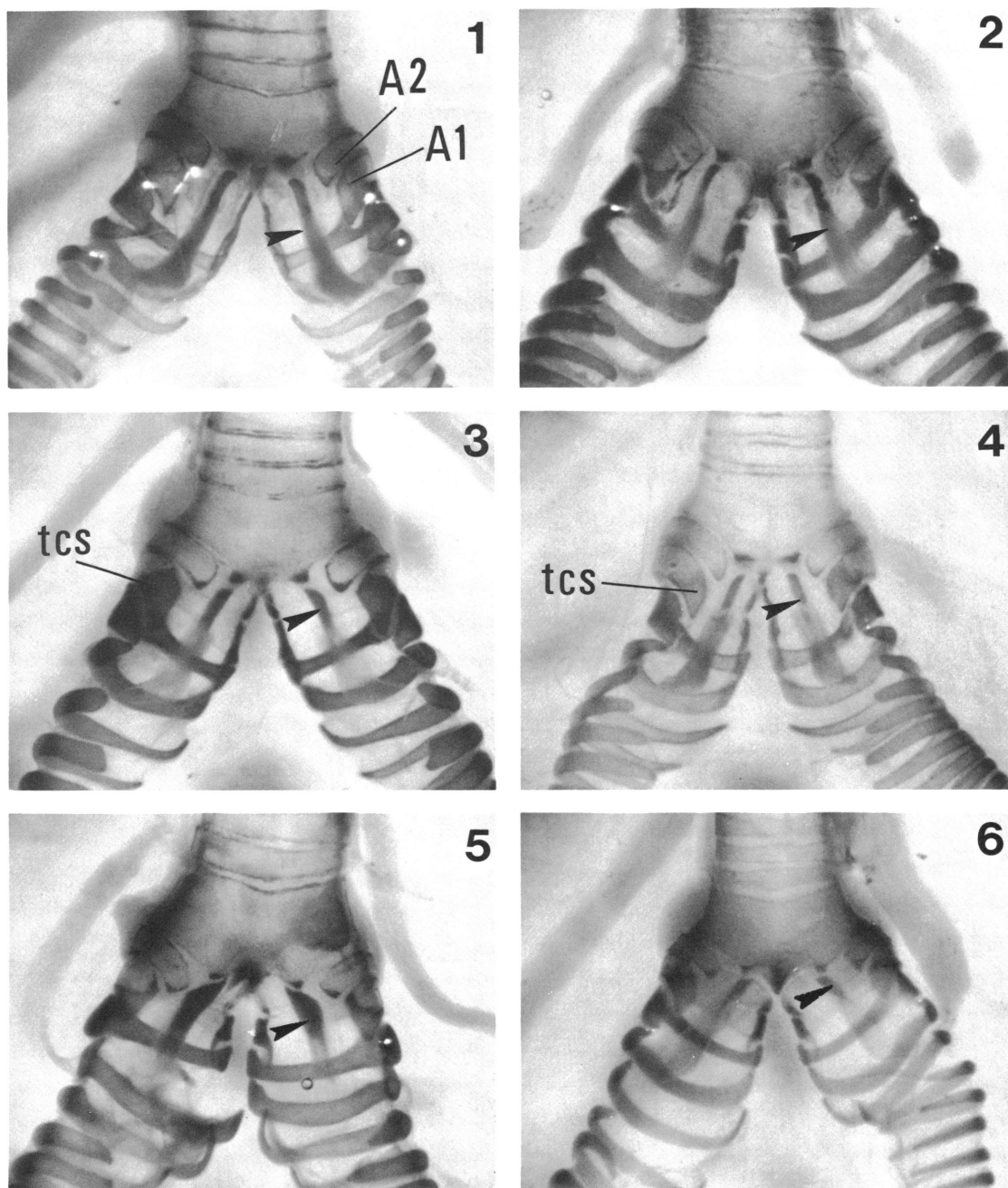
imens examined), there is a small but well-developed ovate trabecular plate, located within the nasal septum (character 10; fig. 21: 2). In the *Tyrannulus* syrinx (two specimens
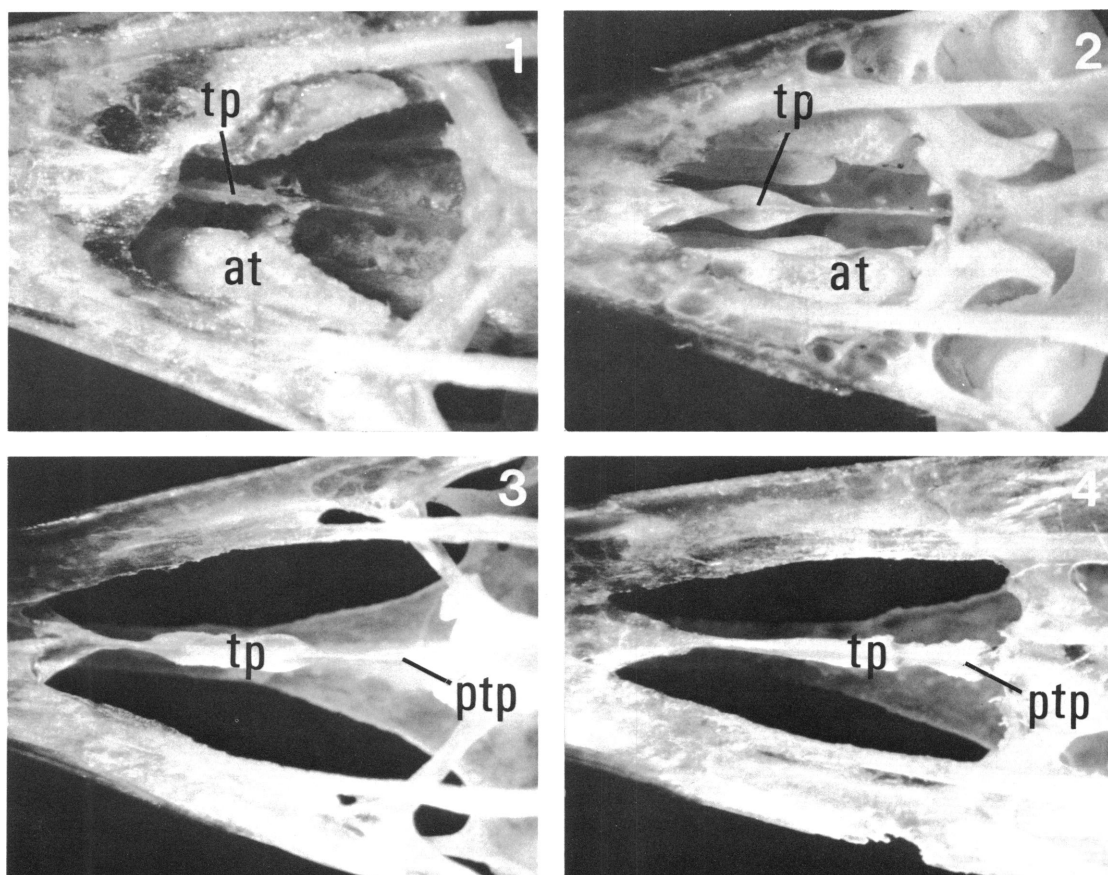
Fig. 21. Cranial characters in four genera in the *Elaenia* group (anterior end of skull to left; ventral views; magnification ×12). (**1**) *Myiopagis gaimardii*, UMMZ 208538; (**2**) *Tyrannulus elatus*, AMNH 11930; (**3**) *Tyranniscus uropygialis*, AMNH 14154; (**4**) *"Mecocerculus" calopterus*, LSU 94087. at = alinasal turbinal; ptp = posterior trabecular plate; tp = trabecular plate.

examined) the internal cartilages are somewhat more robust than in *Myiopagis,* and less curved (fig. 22: 2).

The nests of *Myiopagis* and *Tyrannulus* are reported to be small, shallow, open cups; the eggs of *Myiopagis* are white, marked with reddish-brown, as in *Elaenia,* whereas the eggs of *Tyrannulus* are clear white (Snethlage, 1935; Rowley, 1962; Wetmore, 1972; ffrench, 1976).

My concept of the remaining two genera within the cluster that contains *Elaenia* and its closest allies (fig. 16) is substantially different from the historical treatment of these taxa. Traylor (1977) subdivided the *Tyranniscus* of Hellmayr (1927) and Zimmer (MS) and assigned five of the species to a new ge-

nus, *Zimmerius*. I have already discussed the appropriateness of this move in recognizing *Zimmerius* as a member of my *Phylloscartes* group. Traylor merged the remaining three species of *Tyranniscus* (*nigrocapillus, uropygialis,* and *cinereiceps*) with four small genera (*Phyllomyias, Xanthomyias, Oreotriccus,* and *Acrochordopus*) that Hellmayr (1927) and Zimmer (MS) had acknowledged might be closely related to *Tyranniscus;* Traylor selected *Phyllomyias* as the name for the enlarged genus. Cranial and syringeal morphology support the merger of these taxa with the exception of the three species of *Phyllomyias*. The single skull available (*P. fasciatus,* AMNH 13712) does not have the well-developed trabecular plate within the anterior
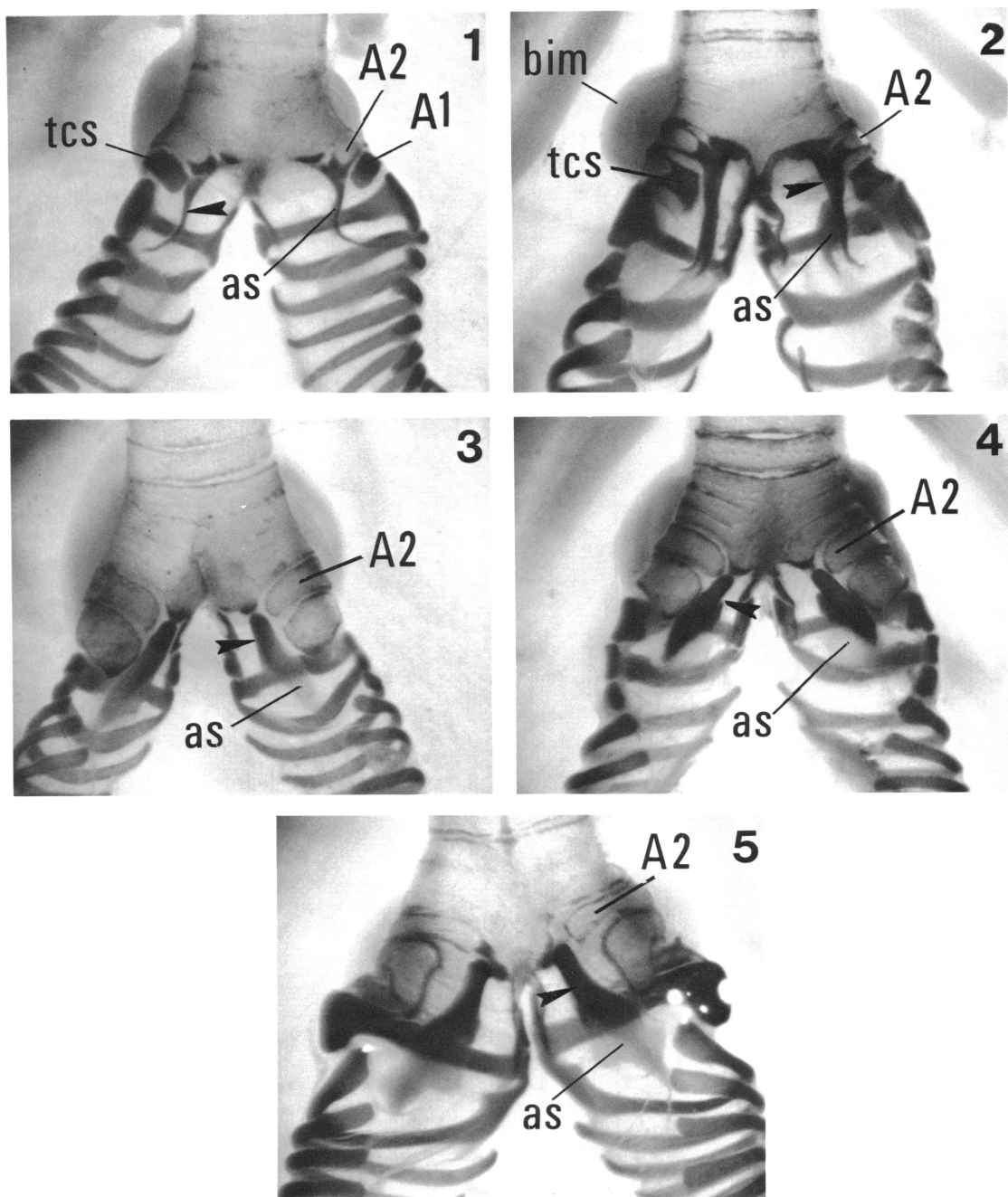
Fig. 22.   Syringes of four genera in the *Elaenia* group (dorsal aspect; magnification ×18). **(1)** *Myiopagis caniceps,* PMNH 2720; **(2)** *Tyrannulus elatus,* AMNH 7718; **(3)** *Tyranniscus burmeisteri,* FMNH 322860; **(4)** *T. nigrocapillus,* LSU 107668; **(5)** "*Mecocerculus*" *minor,* LSU 91532. Arrows indicate internal cartilages; as = amorphous segment; bim = bulging intrinsic muscle; tcs = terminal cartilaginous segment; A elements as numbered.

portion of the nasal septum that characterizes the skulls of the three species of *Tyranniscus*

and of *Xanthomyias virescens,* and the inter-orbital septum is more fully ossified than in

those specimens. I have examined syringes of *Phyllomyias fasciatus* and *P. griseiceps* (*griseocapilla* lacking) and find them to be very different from each other and from *Tyranniscus* and its allies. The nest of *griseiceps* is reported to be a small lichen-encrusted cup (Hilty and Brown, 1986); the nests of the other two species are unknown. It is clear that *Phyllomyias* does not belong with *Tyranniscus*, and may well be polyphyletic. Until we have more information about the morphology and nesting behavior of these three species (*fasciatus, griseiceps,* and *griseocapilla*), I reserve judgment on their relationships and maintain *Phyllomyias* as incertae sedis. I recognize the congeneric status of the remaining seven species in Traylor's enlarged *Phyllomyias*, and retain them under *Tyranniscus*, the oldest available name.

The nasal septa of the available *Tyranniscus* (four specimens of four species; *burmeisteri, sclateri,* and *plumbeiceps* lacking) are fully ossified and have a rather long but narrow trabecular plate located within the septum (fig. 21: 3). In two specimens there is a suggestion of a second plate posterior to the internal supporting rod and basal to the septum, but these are easily overlooked. There are no uniquely derived cranial characters in *Tyranniscus*.

The only reports of nesting behavior in this enlarged *Tyranniscus* are actually from species in two of the merged genera: "*Acrochordopus*" *burmeisteri* (Ihering, 1900, 1902, 1904) and "*Xanthomyias*" *sclateri* (Dinelli, 1918). Their nests were described as being open cups, and the eggs cream-colored and unmarked.

Historically the genus *Mecocerculus* has been something of a "wastebasket" for a number of unrelated taxa. Berlepsch (1907) acknowledged the problem in labeling the genus incertae sedis and suggesting possible "affinities with *Serpophaga, Ochthoeca,* and with *Tyranniscus.*" Hellmayr (1927) provisionally assigned Sclater and Salvin's *superciliaris* to *Mecocerculus*. As discussed in my *Phylloscartes* group, I agree with Zimmer (1940) and Traylor (1979) that *superciliaris* belongs with *Phylloscartes* and not with *Mecocerculus*. Likewise, Chapman (1929) assigned his new species, *nigrifrons*, to *Mecocerculus*; again, I agree with Zimmer and Traylor that *nigrifrons* belongs with *Phyllos-*

cartes, as discussed in that group. Even the genus as conceived by Zimmer (MS) and Traylor (1979) appears to be polyphyletic, according to syringeal morphology, though all three divisions recognized in this study are appropriate members of my *Elaenia* group within the *Elaenia* assemblage, and not "closely allied to *Ochthoeca*" as maintained by Sclater (1888) (and see Lanyon, 1986). "*Mecocerculus*" *calopterus* and *minor* constitute the first of these three divisions, and they have syringes (three specimens examined) that are not significantly different from those available for *Tyranniscus* (seven specimens of five species; *virescens* and *sclateri* lacking): the basic morphology is that of *Elaenia, Myiopagis,* and *Tyrannulus,* but the internal cartilages are narrow basally, broad distally, and have an amorphous distal segment (character 11; fig. 22: 3–5). I refrain from merging these two species of "*Mecocerculus*" with *Tyranniscus* or from proposing a new generic name for them until we have more information about their morphology and behavior. The nests of *calopterus* and *minor* are unknown. The nasal septum in the only skull available (*calopterus,* LSU 94087) has a long, very narrow trabecular plate in the anterior section, similar to that of *Tyranniscus,* but there is a much more prominent posterior plate as well (character 12; fig. 21: 4).

The remaining genera within the *Elaenia* group form a monophyletic cluster by virtue of their having the A2 elements included within the drum (character 13; figs. 24, 26). My assumption is that this unusual configuration of the tracheobronchial junction (unique among all tyrant flycatchers), being a conservative character complex, evolved but once within the assemblage.

Within the cluster of genera having a syrinx with character 13, there is a polychotomy that I am unable to resolve at present (fig. 16). There appear to be two major lineages: one in which the intrinsic muscles of the syrinx have undergone great development (character 2, as already seen in the *Elaenia* lineage, presumably an independent evolutionary event), and a second in which the internal cartilages are relatively narrow and slightly curved (character 30). Also contributing to this polychotomy are two genera that appear
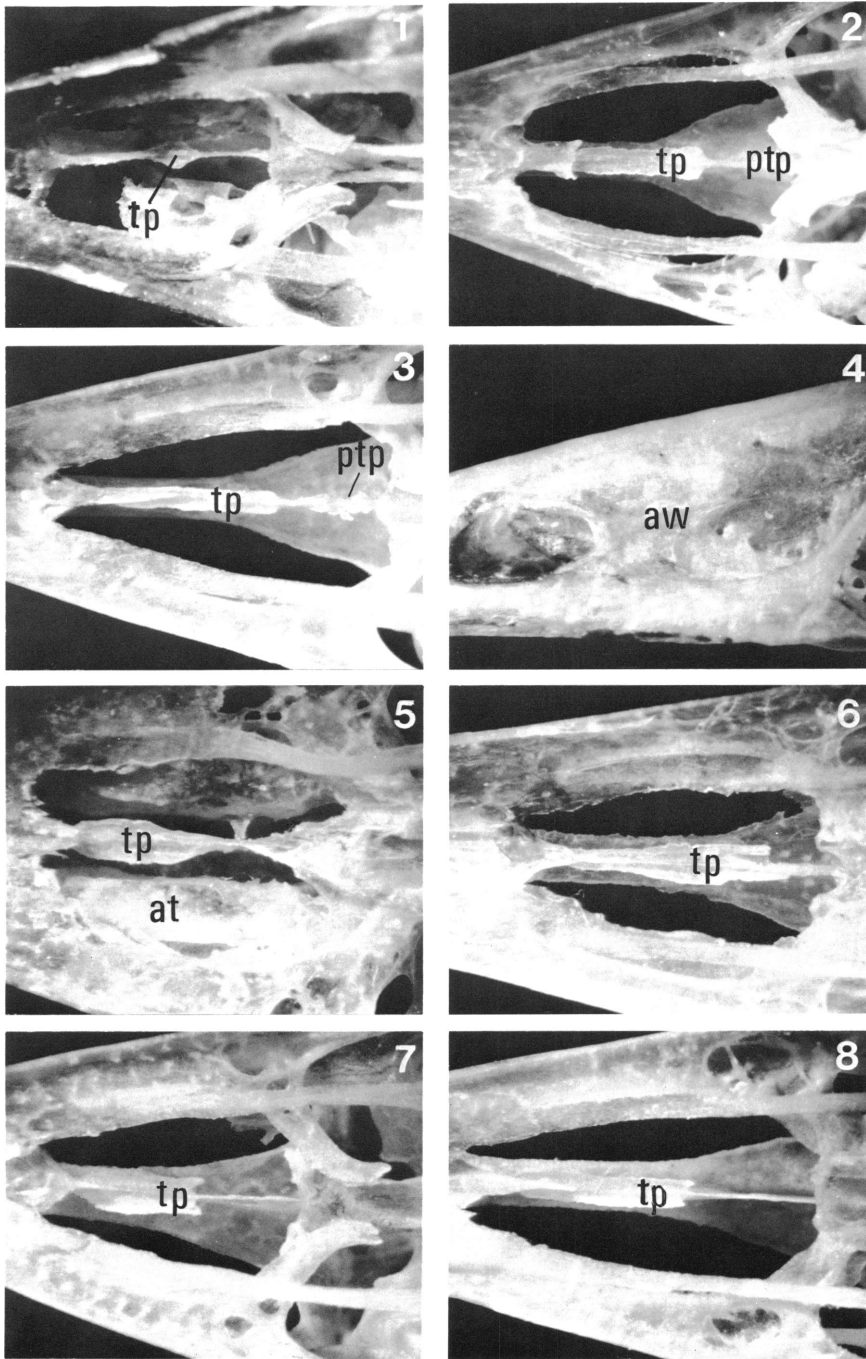
Fig. 23.   Cranial characters in seven genera in the *Elaenia* group (anterior end of skull to left; ventral views, except lateral in 4; magnification ×10). (1) *Ornithion inerme*, FMNH 315854; (2) *Camptostoma obsoletum*, AMNH 7188; (3) "*Mecocerculus*" *stictopterus*, LSU 97504; (4, 5) *Suiriri suiriri*, AMNH 14471; (6) *Pseudocolopteryx acutipennis*, LSU 101520; (7) *Polystictus pectoralis*, UMMZ 218535; (8) *Mecocerculus leucophrys*, AMNH 10704. at = alinasal turbinal; aw = alinasal wall; ptp = posterior trabecular plate; tp = trabecular plate.

to have no close relatives, *Pseudocolopteryx* and *Polystictus*.

Within the lineage having evolved the well-developed intrinsic syringeal musculature (character 2), *Ornithion, Camptostoma,* and a second division of "*Mecocerculus*" cluster together by virtue of their having internal cartilages that are straight and broad, and that have a ventral extension from the distal half of the cartilage (character 14; fig. 24: 1–3). In *Ornithion* (four specimens of two species; *brunneicapillum* lacking) and *Camptostoma* (five specimens of the two species), this ventral extension is poorly staining and amorphous (character 15), and the dorsal ends of the A1 elements are broad (character 16). In fact, there is little significant difference between the syringes of these two genera and, if it were not for differences in their nesting biology and in their nasal septa noted below, one might argue for their merger, as did Sclater (1888). Sclater also regarded *Ornithion* as closely allied to *Tyrannulus,* but at that time Sclater's *Tyrannulus* contained *semiflavus* and *brunneicapillus,* two species that Ridgway (1905) and Hellmayr (1927) transferred to *Microtriccus* and that Zimmer (1941) and Traylor (1977) later merged with *Ornithion.* Syringeal morphology supports the merger of *Microtriccus* with *Ornithion,* and argues against a sister-taxa relationship between *Ornithion* and *Tyrannulus.*

The nasal septum of *Ornithion* (four specimens of the three species) has a small, ovate trabecular plate located within the septum at the base of the internal supporting rod (character 17; fig. 23: 1). In one of the four specimens there is in addition a short, narrow plate located within the anterior portion of the septum. In *Camptostoma* (six specimens of the two species) there is a long, narrow trabecular plate within and for most of the length of the anterior section of the septum (character 18; fig. 23: 2). One of the six specimens has the plate divided into a small ovate section at the base of the internal supporting rod, similar to that of *Ornithion,* and another section within the anterior portion of the septum (but not nearly as prominent as in the other *Camptostoma* specimens).

The nest of *Ornithion brunneicapillum* is reported to be a shallow cup (Wetmore, 1972);

the eggs have not been described. On the other hand, the nests of both species of *Camptostoma* are highly derived, being enclosed and with side entrances, and generally located within a clump of vegetation such as mistletoe or *Tillandsia* (character 19), not suspended as in the tody-tyrant assemblage (AMNH coll.; Euler, 1900; Ihering, 1904; Snethlage, 1935; Bent, 1942; Anderson and Anderson, 1948; Haverschmidt, 1954, 1968; Marchant, 1960; Rowley, 1962, 1984; ffrench, 1976; Harrison, 1979; Belton, 1985). Enclosed nests, having side entrances, have evolved independently in one other lineage within the *Elaenia* assemblage (four genera within the *Phylloscartes* group).

I have already introduced my hypothesis that the genus *Mecocerculus* of Zimmer (MS) and Traylor (1979) is polyphyletic, in my assignment of the first of three divisions of this genus to the *Elaenia* branch of this group (cf. p. 39). The second division appears to be the sister taxon of *Ornithion* and *Camptostoma,* in that the syringes of "*Mecocerculus*" *stictopterus* (two specimens) and *poecilocercus* (one specimen) have internal cartilages that are straight, broad, and have a ventral extension from the distal half (character 14; fig. 24: 3). However, the ventral extension from the internal cartilages in these two species stains better and is well-formed, in the shape of a fully extended and nearly square flag (character 20; fig. 24: 3), unlike the poorly staining, amorphous extension in the sister taxa. In addition, the anterior portion of the nasal septum of *stictopterus* (three specimens) and *poecilocercus* (one specimen) is poorly ossified and may even be missing entirely, along with any evidence of a trabecular plate. When present, the anterior section of the septum has a long, narrow plate located within it; all specimens have a similar but shorter, less prominent plate located just posterior to the internal supporting rod (character 21; fig. 23: 3).

I have seen neither skull nor syrinx of "*Mecocerculus*" *hellmayri,* but, since that species is closest to *poecilocercus* in external morphology (Hellmayr, 1927), I provisionally retain this species within this division of "*Mecocerculus.*"

I refrain from proposing a new generic name
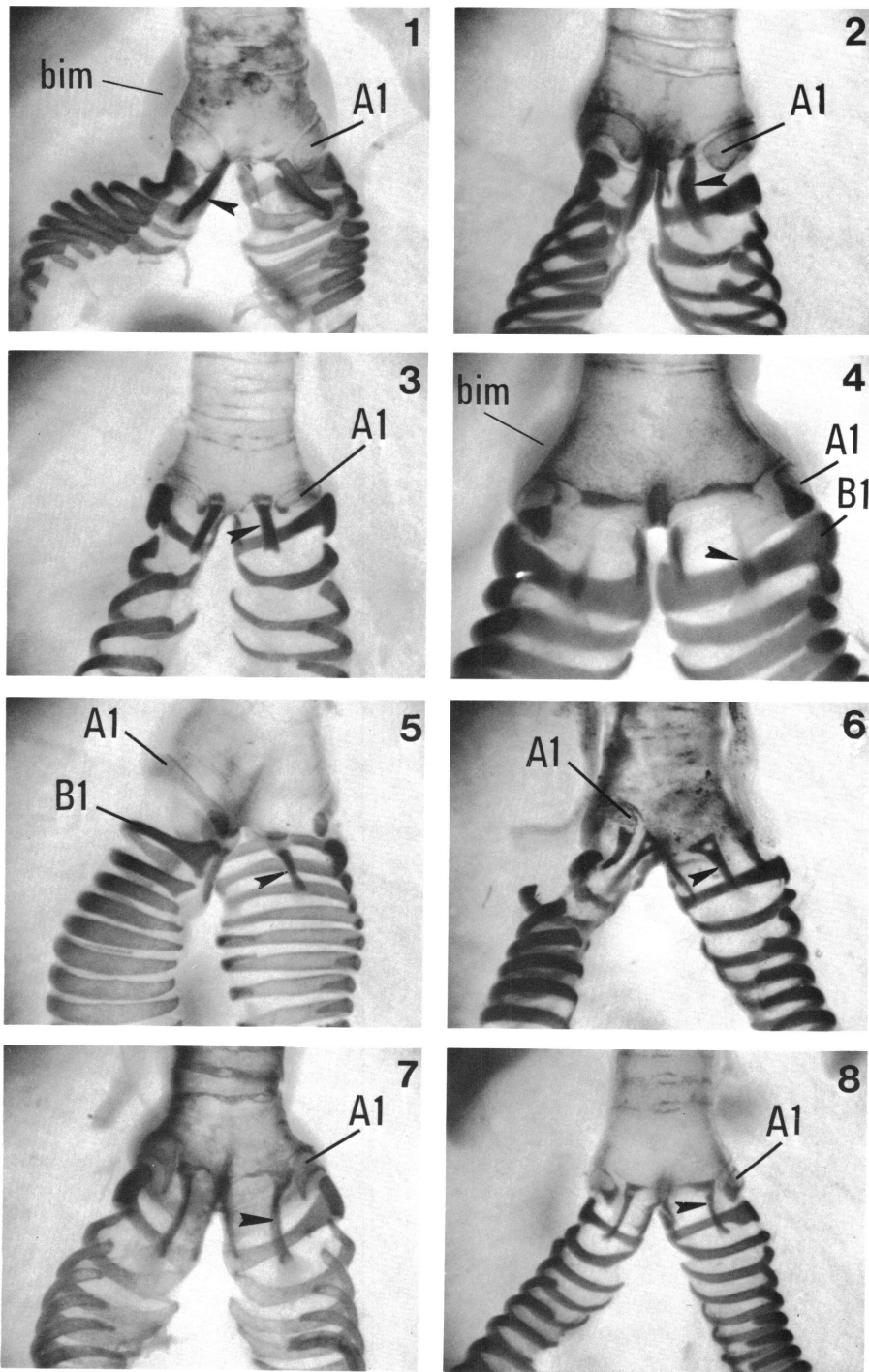
Fig. 24.   Syringes of eight genera in the *Elaenia* group (dorsal aspect; magnification ×14). (1) *Ornithion inerme,* LSU 133594; (2) *Camptostoma obsoletum,* AMNH 6756; (3) *"Mecocerculus" stictopterus,* LSU 107667; (4) *Suiriri suiriri,* PMNH 2787; (5) *Pseudocolopteryx acutipennis,* LSU 102642; (6) *Polystictus pectoralis,* FMNH 289135; (7) *Mecocerculus leucophrys,* AMNH 816789; (8) *Uromyias agraphia,* LSU 79602. Arrows indicate internal cartilages; bim = bulging intrinsic muscle; A and B elements as numbered.

for these three species of "*Mecocerculus*" un-
til we have more information about their
morphology and behavior. Their nests are
unreported.

The monotypic *Suiriri* traditionally has
been allied with *Elaenia* and its closest rel-
atives (Berlepsch, 1907; Hellmayr, 1927;
Zimmer, MS; Traylor, 1977). Syringeal mor-
phology (four specimens) suggests that the
genus, though clearly a member of the *Elae-
nia* group (character I), is closer to *Ornithion*
and allies than to *Elaenia,* since the A2 ele-
ments are included within the drum (char-
acter 13; fig. 24: 4). But *Suiriri* differs from
Ornithion, and indeed from all other genera
within the *Elaenia* assemblage, in two char-
acters: the internal cartilages stain very poor-
ly, except distally, to the point where it is
difficult to determine their exact configura-
tion (character 22); and the B1 elements are
very broad throughout their length (character
23; fig. 24: 4). The nasal capsule of *Suiriri*
(two specimens examined) is more fully os-
sified, including the alinasal walls and tur-
binals, than in *Ornithion* and its allies (char-
acter 7; fig. 23: 4, 5). The nest of *Suiriri* is a
simple cup and the eggs are white and un-
marked (AMNH coll.), shedding no light on
relationships.

Pseudocolopteryx traditionally has been
placed at the end of Hellmayr's (1927) Eu-
scarthminae with such genera as *Culicivora,
Polystictus,* and *Euscarthmus.* Traylor (1977)
speculated that *Pseudocolopteryx* and its al-
lies probably belong "somewhere between the
Tit-tyrants [*Anairetes* and allies] and the
Tody-tyrants [*Hemitriccus* and allies], al-
though not part of the lineage of either." The
syrinx (five specimens of *sclateri* and *acuti-
pennis* examined; *dinellianus* and *flaviventris*
lacking) has internal cartilages that are straight
and of uniform width. The dorsal ends of the
B1 elements are slightly forked (character 24),
and the A1 elements are comparatively nar-
row dorsally and terminate in small carti-
laginous knobs (character 25; fig. 24: 5). The
nasal septum (five specimens of three species
examined; *dinellianus* lacking) is fully ossi-
fied and there is a well-developed trabecular
plate within the septum that widens some-
what in the region beneath the internal sup-
porting rod and is deeply forked posteriorly
(character 26; fig. 23: 6), a unique configu-

ration within the entire assemblage. The
plumage of the underparts of the four species
of *Pseudocolopteryx* is an unstreaked, bright
yellow (character 27). Nests have been re-
ported for all four species, but are of the prim-
itive type, a deep, open cup, and the eggs are
cream colored and unmarked (Ihering, 1902;
Oates and Reid, 1903; Gibson, 1918; Dinelli,
1918, 1933; Hudson, 1920; Smyth, 1928;
Hellmayr, 1932; Herklots, 1961; Johnson,
1967; ffrench, 1976; Belton, 1985).

Hellmayr (1927) used the name *Habrura*
for the two species now in *Polystictus,* and
placed them at the end of his Euscarthminae,
along with *Pseudocolopteryx.* But he ac-
knowledged that "this genus is likewise of
doubtful affinities. While Ridgway . . . sug-
gests it might be referable to the Cotingidae,
Cherrie . . . is inclined to leave it with the
Flycatchers." Warter's (1965) report that
Polystictus has a type 6 nasal septum (like
that of the fluvicolines) understandably puz-
zled Traylor (1977), who maintained the ge-
nus within his Elaeniinae with the explana-
tion that the cranium must be aberrant. My
single skull of *Polystictus pectoralis* (*super-
ciliaris* lacking) has a nasal septum like that
of the rest of my *Elaenia* assemblage, i.e.,
with a trabecular plate that lies within the
septum and no anterior notch (character A).
The plate is quite broad and slightly deflected
ventrally along its lateral margins, and is just
barely forked posteriorly (character 28; fig.
23: 7). The only unique feature of the two
syringes of *Polystictus pectoralis* (*superciliaris*
lacking) is that the internal cartilages are
straight, wider basally than distally, and have
a peculiar nonstaining centrum in the basal
segment (character 29; fig. 24: 6). Traylor and
Fitzpatrick (1982) indicate that the nest is
known for one of the two species (presumably
pectoralis) and is an open cup. According to
Oates and Reid (1903) the eggs are pale cream
and unmarked. Lack of anatomical material
prevents me from commenting on the ap-
propriateness of maintaining *superciliaris* in
this genus, a question raised by Allen (1889)
and Hellmayr (1927).

The relationship of *Pseudocolopteryx* and
Polystictus to each other and to the rest of
this branch of the *Elaenia* group remains ob-
scure; cranial and syringeal morphology does
not resolve the polychotomy in figure 16. The

presumed closely related and monotypic *Culicivora* (Hellmayr, 1927; Zimmer, MS; Traylor, 1977) must remain incertae sedis for the present. There is no skull extant for this genus, the only genus of tyrant flycatcher unrepresented in skeletal collections. The single syrinx available for *Culicivora* has well-formed internal cartilages, which counters Ridgway's (1907) claim that this genus "is almost certainly not a member of the Tyrannidae," but does not have the derived characters found in *Pseudocolopteryx, Polystictus,* and the other members of the *Elaenia* group.

Turning now to the lineage in which the internal cartilages are relatively narrow and slightly curved (character 30), there are two genera that clearly belong here but whose relationships are unresolved by cranial and syringeal morphology, hence the trichotomy in figure 16. These are *Mecocerculus* (now monotypic, after removal of five species from that genus) and *Uromyias.*

The nasal septum of *Mecocerculus leucophrys* (four specimens) has a well-developed, long, and rather narrow trabecular plate within its anterior section, and no suggestion of a plate posterior to the internal supporting rod (fig. 23: 8); there are no derived characters that suggest unequivocal alliance with any other genus. The syrinx (six specimens) differs from that of other genera within this lineage in having the internal cartilages somewhat larger and more robust, and terminating in a poorly staining, amorphous segment (character 31; fig. 24: 7). The inclusion of the A2 elements within the drum, the shape of the internal cartilages, and the absence of a posterior trabecular plate in the nasal septum distinguish *leucophrys* from "*Mecocerculus*" *calopterus* and *minor* (assigned to the *Elaenia* branch of this group), while the shape of the internal cartilages and the absence of a posterior plate separate *leucophrys* from "*Mecocerculus*" *stictopterus* and its allies. The open, cup nest of *leucophrys* and the white, unmarked eggs (AMNH coll.; Hilty and Brown, 1986) provide no clue to its nearest relative.

Sclater's *agilis* formerly was assigned to *Anairetes* (Sclater, 1888; Chapman, 1917), but Chapman (1926) expressed some reservation: " . . . [it] is so distinct that it is possibly deserving of generic separation"; and again,

"A distinct species with no near relatives." In 1919 Chapman described a new species, *agraphia,* assigned it to *Anairetes,* and remarked: "Quite unlike any described species of the genus, but most nearly resembling *Anairetes agilis.*" Hellmayr (1927) proposed a new genus, *Uromyias,* for *agilis* and *agraphia,* on the basis of their external morphology, and Zimmer (MS) agreed; both workers maintained *Uromyias* next to *Anairetes.* Traylor (1977) followed the recommendation by Smith (1971) that *Uromyias* be reunited with *Anairetes.*

The syrinx of *Uromyias* (one of each species examined) confirms the affinity of this genus with *Anairetes* and its allies, in that it has the appropriate configuration of the tracheobronchial junction (character 13) and the internal cartilages are relatively narrow and slightly curved (character 30; fig. 24: 8). In fact, it would be difficult if not impossible to distinguish between the *Uromyias* syringes and those of *Anairetes* and *Serpophaga.* But the nasal septum of *Uromyias* (two specimens of *agraphia* examined; *agilis* lacking), though possessing the characters of the assemblage, lacks any of the derived characters that might suggest affinities within the *Serpophaga/Anairetes* lineage. The septum is fully ossified and there is a well-developed trabecular plate within its anterior section (fig. 25: 1). What impresses me most, however, is the absence of any suggestion of posterior forking of the plate, the character (33) that argues for monophyly of *Anairetes* and its closest allies.

The lack of posterior forking of the trabecular plate, combined with the differences in external morphology that have been noted by Hellmayr (1927) and others, is sufficient reason to maintain the separate generic status of *Uromyias* and to retain it just outside the *Serpophaga/Anairetes* lineage. The strongest of the derived external morphological characters is probably the relatively long and graduated tail (character 32). The nests of the two *Uromyias* species are unknown.

As implied above, the remaining genera within the *Elaenia* group cluster by virtue of their having the trabecular plate (within the septum) conspicuously forked posteriorly in the shape of a slender tuning fork, with the prongs of the fork close to the septum and hence to each other (character 33; fig. 25: 2,
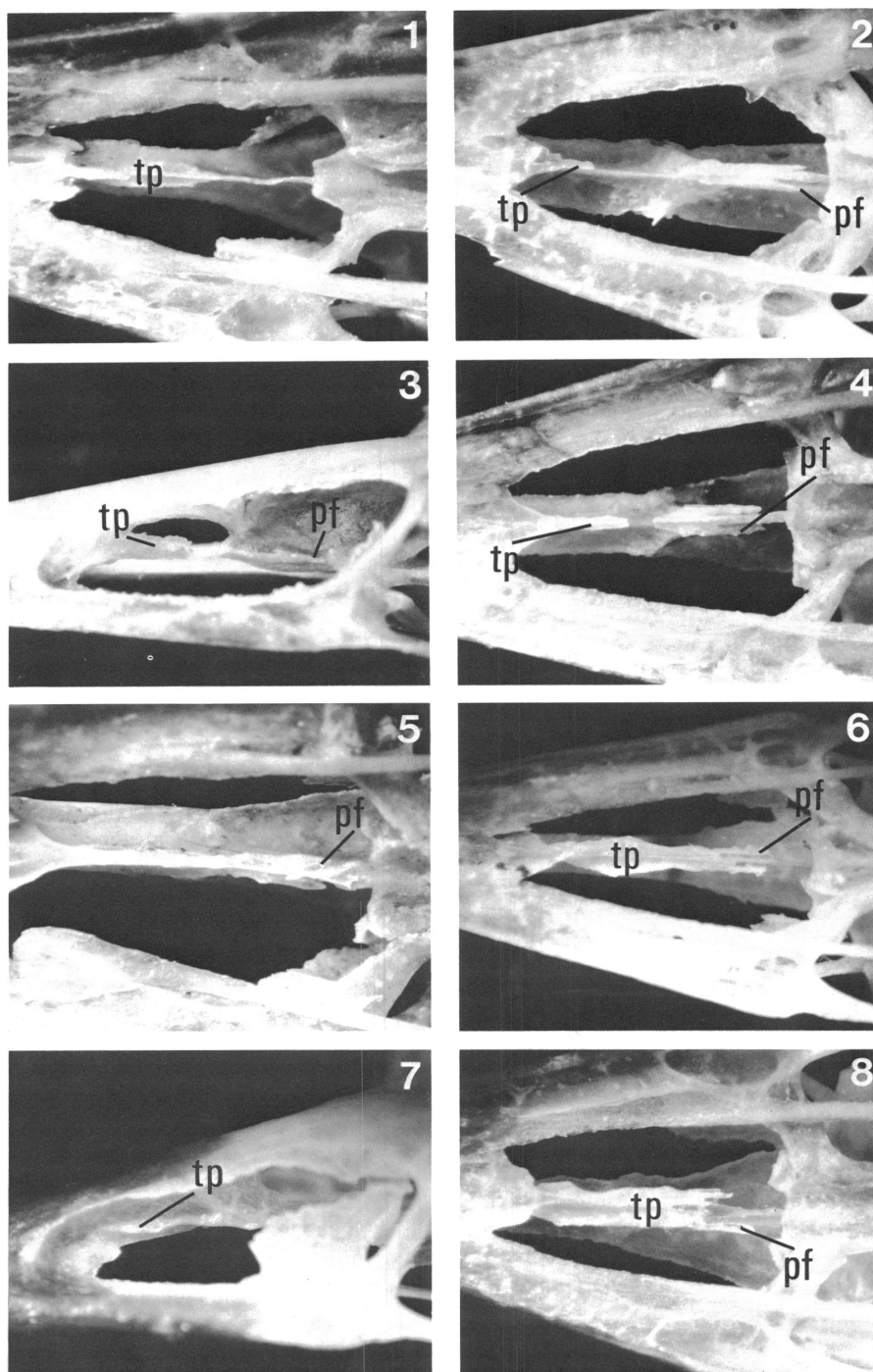
Fig. 25.   Cranial characters in six genera in the *Elaenia* group (anterior end of skull to left; ventral views, except lateral in 3, 7; magnification ×10). (**1**) *Uromyias agraphia,* LSU 90080; (**2**) *Capsiempis flaveola,* UMMZ 200869; (**3, 4**) *Phaeomyias murina,* AMNH 7306; (**5**) *Nesotriccus ridgwayi,* AMNH 9210; (**6**) *Anairetes flavirostris,* AMNH 7184; (**7, 8**) *Serpophaga cinerea,* LSU 50821. pf = posterior forking of trabecular plate; tp = trabecular plate.

4–6, 8). This configuration is unique among all tyrant flycatchers, hence clearly derived and strong argument for monophyly of this particular lineage (*Serpophaga/Anairetes*).

There is no historical basis for the clustering of *Capsiempis, Phaeomyias,* and *Nesotriccus* (treated here as monotypic genera); the failure of workers to appreciate this relationship represents an outstanding example of how misleading or uninformative external morphological characters can be in the reconstruction of tyrant phylogenies. Hellmayr (1927) had these genera in three different subfamilies: *Capsiempis* was placed near *Phylloscartes* in his Euscarthminae, *Phaeomyias* was placed between *Sublegatus* and *Camptostoma* in the Elaeniinae, and *Nesotriccus* was allied with *Myiarchus magnirostris* in the Myiarchinae. Not only were their affinities for one another unappreciated, in no instance was one of these genera allied with any of the taxa in my *Serpophaga/Anairetes* lineage. Zimmer (MS) made no changes in Hellmayr's positioning of these genera. Traylor (1977) followed Zimmer and Hellmayr with respect to the placement of *Capsiempis* and *Phaeomyias,* but went somewhat further in actually merging *Capsiempis flaveola* with his enlarged *Phylloscartes.* However, Traylor broke with tradition with respect to *Nesotriccus* by removing it from the myiarchine flycatchers and placing it near *Empidonax* in another subfamily. I (Lanyon, 1978, 1985) concurred with the view that *Nesotriccus* is not a myiarchine, but presented morphological evidence (Lanyon, 1984a, 1986) against its membership in my *Empidonax* assemblage.

The nasal septa of *Capsiempis flaveola* (one specimen), *Phaeomyias murina* (two specimens), and *Nesotriccus ridgwayi* (two specimens) are poorly ossified in the anterior region and sometimes missing all together; if present, there may be a very narrow, inconspicuous trabecular plate within that region of the septum (character 34; fig. 25: 2–4). All specimens have a remnant of this narrow trabecular plate (within the septum) at the ventral end of the internal supporting rod, and this remnant is deeply forked posteriorly as in all members of the *Serpophaga/Anairetes* lineage (character 33; fig. 25: 2–4). In addition, the syringes of these three monotypic

genera (10 specimens examined, representing all 3 species) have the internal cartilages attached to the dorsal ends of the A1 elements as well as to the drum (character 35; fig. 26: 1–3), which is unique within the assemblage. All three species build simple cup nests and lay white, unmarked eggs, presumably the primitive patterns for the assemblage (Carriker, 1910; Cherrie, 1916; Snethlage, 1935; Marchant, 1960; Skutch, 1960; Herklots, 1961; Haverschmidt, 1968, 1970; Sherry, 1986).

Within the *Serpophaga/Anairetes* lineage, *Capsiempis* and *Phaeomyias* are the only genera to have evolved well-developed intrinsic syringeal muscles, to the point where they form bulging masses of tissue laterally (character 2; fig. 26: 1, 2); as pointed out earlier, this development is presumed to have occurred independently in two other lineages within the assemblage (see fig. 16). Their syringes are more similar than either is to the syrinx of *Nesotriccus* (see below). I refrain from merging these two monotypic genera because of slight differences in syringeal morphology, expressed here as three characters for diagnosing the syrinx of *Capsiempis* (fig. 26: 1): there are long cartilaginous extensions from the dorsal ends of the A1s (character 36), the internal cartilages are attached closer together on the drum (character 37), and the ventral ends of the B1 elements are broader (character 38).

Capsiempis and *Phaeomyias* have not always been monotypic genera as conceived here. Cabanis (1873) and Sclater (1888) had assigned *orbitalis* to *Capsiempis,* but Hellmayr (1927) moved this species to *Pogonotriccus.* Traylor (1977) merged *Pogonotriccus* with his enlarged *Phylloscartes* and syringeal morphology supports this treatment (see my *Phylloscartes* group). Zimmer (1941) assigned Taczanowski's *leucospodia* to *Phaeomyias* but, for reasons expressed above (see my *Stigmatura* group), *leucospodia* is deserving of generic status in a separate lineage from *Phaeomyias.* Hellmayr (1927) had *tenuirostris* in *Phaeomyias,* but Zimmer (1955) removed it to *Inezia* and cranial morphology supports that move (see my *Phylloscartes* group).

The syrinx of *Nesotriccus* (two specimens) lacks the well-developed intrinsic muscula-
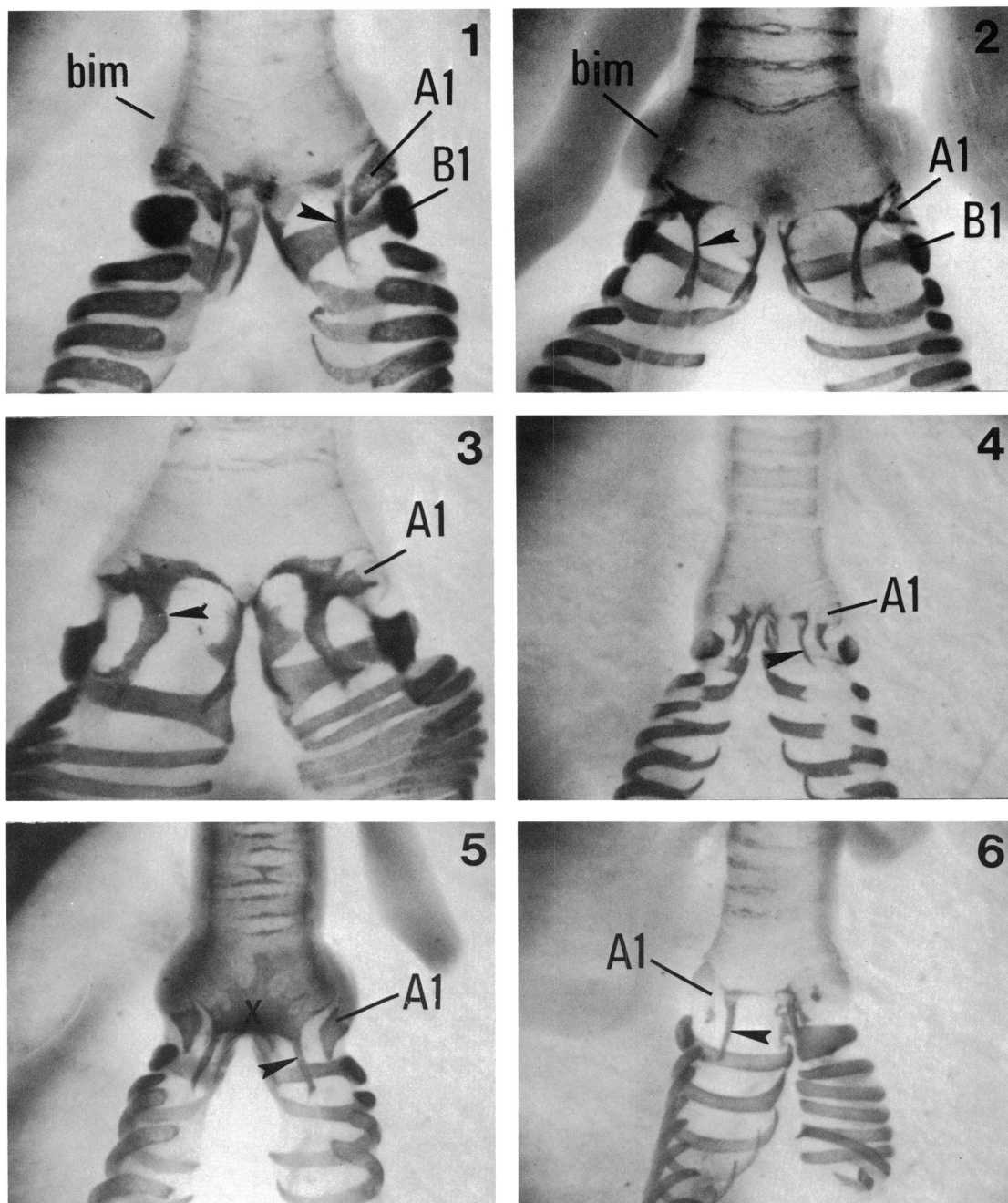
Fig. 26. Syringes of five genera in the *Elaenia* group (dorsal aspect; magnification ×18). (**1**) *Capsiempis flaveola*, AMNH 7709; (**2**) *Phaeomyias murina*, FMNH 291280; (**3**) *Nesotriccus ridgwayi*, AMNH 8067; (**4**) *Serpophaga subcristata*, AMNH 2466; (**5**) *Serpophaga cinerea*, PMNH 4693; (**6**) *Anairetes parulus*, LSU 102646. Arrows indicate internal cartilages; bim = bulging intrinsic muscle; x = possible early cartilaginous stage of formation of drum; A and B elements as numbered.

ture of *Capsiempis* and *Phaeomyias*, and in addition has internal cartilages that are much broader and more robust (character 39; fig. 26: 3) than in those genera. Sherry (1985) has

discussed the ecological and behavioral implications of the special adaptations by which this Cocos Island Flycatcher differs from its mainland near-relatives (*Capsiempis* and *Phaeomyias*), notably the much longer bill (character 40) so often evident in insular forms.

Serpophaga and *Anairetes* traditionally have been considered closely related genera; the only surprises in the phylogeny reconstructed here may be my exclusion of the alleged near-relatives: *Inezia, Stigmatura, Uromyias, Mecocerculus, Colorhamphus, Tachuris,* and *Xenopsaris* (Sclater, 1888; Berlepsch, 1907; Hellmayr, 1927; Zimmer, MS; Smith, 1971; Traylor, 1977) from the immediate *Serpophaga/Anairetes* cluster. *Uromyias* and *Mecocerculus* clearly are members of the *Serpophaga/Anairetes* lineage but, for reasons explained above, are more distant from those two genera than are *Capsiempis* and allies (fig. 16). *Inezia* has the characters shared by my *Phylloscartes* group and appears to be the sister taxon of *Sublegatus* in that group, while *Stigmatura* has a syrinx that is very different from either the *Phylloscartes* group or the *Elaenia* group and has been placed in a distinct group within the assemblage (fig. 2).

Colorhamphus parvirostris was maintained as a monotypic genus near *Serpophaga* by Ridgway (1907), Hellmayr (1927), and Zimmer (MS). Traylor (1977) merged *Colorhamphus* with *Ochthoeca,* following earlier suggestions by Berlepsch (1907) and Smith and Vuilleumier (1971). I (Lanyon, 1986) have already presented the cranial evidence for regarding *Colorhamphus* the sister taxon of *Ochthoeca* in my *Empidonax* assemblage.

Though traditionally allied with the *Serpophaga/Anairetes* lineage, the monotypic *Tachuris* is so different with respect to its external morphology, syrinx, behavior, and nesting biology that its affinities with those genera have not gone unquestioned (Zimmer, MS; Ames, 1971; Smith, 1971; Traylor, 1977). In the single skull available to me, there is only a shallow remnant of the nasal septum along the middorsal line, and no indication of a trabecular plate of any kind. The syrinx (three specimens examined) shows no similarity to that of *Serpophaga* and its allies: the tracheobronchial junction is unlike that of

my *Elaenia* group (there is no "drum"), and the very large, platelike internal cartilages are unique among all tyrants. *Tachuris* clearly is not a member of the *Serpophaga/Anairetes* lineage, but there is no compelling evidence at present as to where it does belong within the family.

The monotypic *Xenopsaris* has been moved back and forth between the Cotingidae and the Tyrannidae several times (Berlepsch, 1907; Hellmayr, 1927; Zimmer, MS; Snow, 1973); when assigned to the latter, it has usually been placed near *Serpophaga* (Hellmayr, 1927; Smith, 1971). Traylor (1977) believed this resemblance to be convergence and placed the genus at the end of the Tyrannidae incertae sedis. Cranial (one specimen) and syringeal morphology (two specimens) strongly argues against *Xenopsaris* being a relative of *Serpophaga* or of any member of the *Elaenia* group. Its true affinities are still unclear, however; I too retain it incertae sedis within the Tyrannidae, until we have additional (perhaps biochemical) data.

The nasal septum of *Serpophaga* (eight specimens, from five species; *araguayae* lacking) and of *Anairetes* (14 specimens, from 3 species; *alpinus* and *fernandezianus* lacking) is fully ossified, including the anterior segment in which there is a conspicuous, well-developed trabecular plate (character 41; fig. 25: 6–8), and this plate is conspicuously forked posteriorly (character 33; fig. 25: 6–8), as in *Capsiempis* and allies. In addition, *Serpophaga* and *Anairetes* cluster together by virtue of their having the plumage of the crown with streaks and/or a concealed patch of white or cream color (character 42). Concealed crown patches have evolved independently in one other lineage within this *Elaenia* group and in several of the other groups within the assemblage.

The syringes of *Serpophaga* (nine specimens, from five species; *araguayae* lacking) and *Anairetes* (seven specimens, from three species; *alpinus* and *fernandezianus* lacking) exhibit, on average, the least degree of fusion of the A elements, i.e., the poorest development of a drum (character 43; fig. 26: 4–6) of all the genera in the *Elaenia* group. However, there is still a demonstrable tendency toward fusion of the dorsal segments of the A2 through A5 elements to form the char-

acteristic shape of the pessulus (character 13) that is the diagnostic feature of this particular primary lineage within the *Elaenia* group (fig. 1: 9, 10). A specimen (PMNH 4693; fig 26: 5) of *Serpophaga cinerea* suggests an early ontogenetic stage of the formation of the syringeal drum, in that the fused dorsal ends of the A2 through A4 and the pessulus are still cartilaginous. There is enough overlap in the syringes of the two genera in my series that I cannot unequivocally distinguish between them on the basis of syringeal morphology. Hellmayr (1927) had *inornata* in *Serpophaga,* but Zimmer (1955) removed it to *Inezia* and syringeal morphology supports that move (see my *Phylloscartes* group).

The five species of *Anairetes* are separable from *Serpophaga* by the plumage of the crown, with its elongate black feathers; all but *alpinus* have the throat and chest heavily streaked with black (character 44). Carriker (1933) described a new species, *alpina,* which he considered to be somewhat intermediate between *Anairetes* and *Uromyias* and placed it in a new monotypic genus, *Yanacea*: "[it] has no very near relative, occupying a unique, solitary position." Zimmer (MS) merged *Yanacea* with *Anairetes,* and Traylor (1977) concurred. Since I have no anatomical specimens of *alpinus,* its inclusion in *Anairetes* must be considered provisional at this time.

The nests of *Serpophaga* and *Anairetes* are of the presumed primitive type, i.e., an open cup, and the eggs are white and unmarked (AMNH coll.; Barrows, 1883; Euler, 1900; Oates and Reid, 1903; Ihering, 1900, 1904; Dinelli, 1918; Gibson, 1918; Hudson, 1920; Smyth, 1928; Hellmayr, 1932; Skutch, 1960; Johnson, 1967; Smith, 1971; Wetmore, 1972; Belton, 1985).

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APPENDIX

List of anatomical specimens (249 skulls, 237 syringes) examined for developing a phylogeny of the *Elaenia* assemblage of flycatchers. Genera and species, including putative relatives and recent synonyms, are listed alphabetically. All known species within the assemblage are given, including those for which specimens are lacking. Not included here are the species in over 70 other genera of tyrant flycatchers whose skulls and syringes have been examined for outgroup comparison.

	Skulls	Syringes
Acrochordopus burmeisteri. See *Tyranniscus burmeisteri*		
Anairetes agilis. See *Uromyias agilis*		
A. agraphia. See *Uromyias agraphia*		
A. alpinus	Lacking	Lacking
A. fernandezianus	Lacking	Lacking
A. flavirostris	AMNH 7184, 7318	USNM 227582
A. parulus	DM 63775, 63776; FMNH 291886; LSU 79831, 79832; PMNH 7834, 11550; UK 78072, 78128; UMMZ 156755	LSU 102646, 102647; PMNH 2781, 2838
A. reguloides	LSU 79979, 113684	AMNH 6751, 6753
Caenotriccus ruficeps. See *Pseudotriccus ruficeps*		

APPENDIX—*(Continued)*

	Skulls	Syringes
C. simplex. See *Pseudotriccus simplex*		
Camptostoma imberbe	AMNH 11393	AMNH 2809; CM 919; UK 42017
C. obsoletum	AMNH 5832, 7188, 7189	AMNH 6756, 11596
Capsiempis flaveola	UMMZ 200869	AMNH 7709, 8242, 816786
Colorhamphus parvirostris	FMNH 316920	FMNH 316920; USNM 511875, 536383
Corythopis delalandi	AMNH 14476; UMMZ 159072, 202249	Lacking
C. torquata	AMNH 14164; FMNH 290301	AMNH 8963, 816755; LSU 101549, 102782
Culicivora caudacuta	Lacking	USNM 227339
Elaenia albiceps	AMNH 6684, 6709, 6715, 7186; 8553; FMNH 290284; USNM 343087	AMNH 2464, 2465; LSU 97550, 102660
E. chiriquensis	DM 57483, 63160; UMMZ 219584; USNM 428763	AMNH 6749; PMNH 4691, 6699
E. cristata	AMNH 11606, 11929; UK 32435, 71990; UMMZ 208536	AMNH 8089, 8091
E. dayi	Lacking	Lacking
E. fallax	PMNH 7432, 7434; UMMZ 152260; USNM 555840, 555841	PMNH 8889, 8890
E. flavogaster	AMNH 10320, 11931, 11932, 12069	AMNH 6742, 8090, 8092, 8095
E. frantzii	DM 62637, 62988; LSU 42906; MVZ 86092, 141806; UMMZ 219586; USNM 429599	CM 392; LSU 95077
E. gigas	FMNH 291858, 322868; ROM 114972	FMNH 291669
E. leucospodia. See *Pseudelaenia leucospodia*		
E. martinica	USNM 488003, 557744, 557787	AMNH 6738, 6739; CM 1065
E. mesoleuca	AMNH 13749; FMNH 105689	AMNH 9092, 9093
E. obscura	FMNH 105674; LSU 48851, 84041; UMMZ 222260; USNM 347156, 347157	PMNH 926, 928
E. pallatangae	AMNH 15224; FMNH 291859, 291860; LSU 48849, 75629; USNM 428746	AMNH 15224, 816791; FMNH 291670; LSU 103311
E. parvirostris	DM 68201; ROM 107545; UMMZ 202236	AMNH 2296; CM 1250; USNM 504593
E. pelzelni	LSU 111587	LSU 114510
E. ruficeps	AMNH 11451, 11921, 11922	AMNH 8093, 8094
E. spectabilis	LSU 28491; UMMZ 158834; USNM 491937, 491938	BM 1969.13.72; USNM 512631
E. strepera	Lacking	Lacking

APPENDIX—(Continued)

	Skulls	Syringes
Euscarthmus meloryphus	AMNH 7183; LSU 65323, 86418, 86574, 94084	AMNH 6782, 8866; CM 1878; LSU 113856; USNM 227325
E. rufomarginatus	Lacking	Lacking
Habrura pectoralis. See *Polystictus pectoralis*		
H. superciliaris. See *Polystictus superciliaris*		
Inezia inornata	LSU 95240	AMNH 6784; FMNH 330582
I. subflava	UMMZ 154740; USNM 491832	USNM 504599
I. tenuirostris	FMNH 313436	Lacking
Leptopogon amaurocephalus	FMNH 290290, 315944, 315946; PMNH 5528, 6020; UMMZ 158058	AMNH 2509, 8234, 8235, 8236, 8548, 8712; LSU 102685, 123046, 123215; UK 66662, 66850, 73358
L. nigrifrons. See *Phylloscartes nigrifrons*		
L. rufipectus	LSU 97509	LSU 97549
L. superciliaris	AMNH 14153; DM 68207, 68208; FMNH 291883, 291879, 323101; UMMZ 153270	FMNH 323097; LSU 91224, 95557, 108509, 118055; USNM 511999, 512059, 512061
L. taczanowski	LSU 79834, 107337, 107338	LSU 79606, 107670
Leptotriccus sylviolus. See *Phylloscartes sylviolus*		
"*Mecocerculus*" *calopterus*	LSU 94087	AMNH 8862, 8863
"*M.*" *hellmayri*	Lacking	Lacking
Mecocerculus leucophrys	AMNH 10704, 15221, 15222; DM 61815	AMNH 4636, 6743, 6744, 816789, 816790; FMNH 319352
"*Mecocerculus*" *minor*	Lacking	LSU 91532
"*M.*" *poecilocercus*	LSU 84039	LSU 107665
"*M.*" *stictopterus*	LSU 84040, 97504	LSU 102653, 107667
Mecocerculus superciliaris. See *Phylloscartes superciliaris*		
Microtriccus brunneicapillus. See *Ornithion brunneicapillum*		
M. semiflavus. See *Ornithion semiflavum*		
Mionectes macconnelli	AMNH 11940, 12048, 12049; FMNH 315934	AMNH 8085, 8086, 8087; LSU 102773
M. oleagineus	AMNH 15225, 15226; UK 67604, 69666; UMMZ 153274	AMNH 6701, 6702, 7712, 8263, 15225; LSU 102717
M. olivaceus	AMNH 7192; DM 57989, 58264; FMNH 315876, 315897	LSU 79609, 108515
M. rufiventris	UMMZ 200882	AMNH 6705; FMNH 107235
M. striaticollis	FMNH 291861, 291863, 322880; MVZ 141809;	AMNH 6801; LSU 102694, 102695, 102699

APPENDIX—(Continued)

	Skulls	Syringes
	LSU 79836, 84050; PMNH 11710, 11713	
Myiopagis caniceps	UMMZ 158836	PMNH 2719, 2720
M. cotta	ROM 113164	Lacking
M. flavivertex	Lacking	AMNH 8864
M. gaimardii	UK 32436, 32438; UMMZ 208538; USNM 344217	FMNH 330576; LSU 102672
M. leucospodia. See *Pseudelaenia leucospodia*		
M. subplacens	LSU 94091	LSU 91535, 113861
M. viridicata	AMNH 12984; UMMZ 153267	AMNH 8238; UK 40688
"*Myiophobus*" *lintoni*	Lacking	Lacking
"*M.*" *ochraceiventris*	AMNH 14155; LSU 74894, 113683	LSU 102581, 107658, 113743
"*M.*" *phoenicomitra*	LSU 86568	LSU 85982
"*M.*" *roraimae*	FMNH 319446; LSU 107313	AMNH 816778; LSU 118050; USNM 504572, 504574, 504577
Myiotriccus ornatus	AMNH 14158; FMNH 288172, 323249, 323253, 323255, 323257–323259, 323264, 323268; LSU 86414, 90046	LSU 85983, 85984, 117203
Nesotriccus ridgwayi	AMNH 9210; LSU 42902	AMNH 8067, 8068
Oreotriccus plumbeiceps. See *Tyranniscus plumbeiceps*		
Ornithion brunneicapillum	AMNH 14470	Lacking
O. inerme	FMNH 315854; LSU 115993	LSU 133593, 133594
O. semiflavum	UMMZ 156494	PMNH 2125, 6417
Phaeomyias leucospodia. See *Pseudelaenia leucospodia*		
P. murina	AMNH 7305, 7306	AMNH 6700; FMNH 291280, 291281, 291284; LSU 113868
P. tenuirostris. See *Inezia tenuirostris*		
Phylloscartes chapmani	AMNH 15219	AMNH 816785; USNM 504590
P. difficilis	Lacking	Lacking
P. eximius	PMNH 6431; UMMZ 158054	PMNH 2761, 2764
P. flaveolus. See *Capsiempis flaveola*		
P. flaviventris	Lacking	Lacking
P. flavovirens	UMMZ 219205	Lacking
P. nigrifrons	Lacking	USNM 504591
P. ophthalmicus	FMNH 291884; LSU 90074, 95432	FMNH 291691; LSU 91223
P. orbitalis	AMNH 9146; FMNH 323141	FMNH 323143; LSU 102639
P. oustaleti	Lacking	Lacking
P. paulistus	Lacking	Lacking

APPENDIX—(Continued)

	Skulls	Syringes
P. poecilotis	LSU 90075	LSU 97548
P. qualaquizae	Lacking	ANSP 176931, 176932
P. roquettei	Lacking	Lacking
P. superciliaris	Lacking	ANSP 176970; USNM 510881
P. sylviolus	Lacking	PMNH 2691
P. venezuelanus	Lacking	Lacking
P. ventralis	FMNH 323150; PMNH 5576, 5579; UMMZ 158815	LSU 117259; PMNH 2754, 2755
P. virescens	ROM 125892	Lacking
Pipromorpha macconnelli. See *Mionectes macconnelli*		
P. oleaginea. See *Mionectes oleagineus*		
P. rufiventris. See *Mionectes rufiventris*		
Pogonotriccus eximius. See *Phylloscartes eximius*		
P. flaviventris. See *Phylloscartes flaviventris*		
P. gualaquizae. See *Phylloscartes gualaquizae*		
P. ophthalmicus. See *Phylloscartes ophthalmicus*		
P. orbitalis. See *Phylloscartes orbitalis*		
P. poecilotis. See *Phylloscartes poecilotis*		
P. venezuelanus. See *Phylloscartes venezuelanus*		
Polystictus pectoralis	UMMZ 218535	FMNH 289135; UK 73313
P. superciliaris	Lacking	Lacking
Pseudelaenia leucospodia	LSU 86587, 114319	LSU 91536, 113863, 114008
Pseudocolopteryx acutipennis	LSU 101520	LSU 102642, 102644
P. dinellianus	Lacking	Lacking
P. flaviventris	LSU 95270; UMMZ 158820, 158822	Lacking
P. sclateri	UMMZ 158825	USNM 227580
Pseudotriccus pelzelni	LSU 86573	AMNH 8714; UK 69000, 69001
P. ruficeps	AMNH 6936, 6937, 6938	AMNH 3524; LSU 102626, 102627
P. simplex	FMNH 323152; LSU 99426	FMNH 323153; LSU 98046
Serpophaga araguayae	Lacking	Lacking
S. cinerea	LSU 50821; MVZ 141804	AMNH 6736; PMNH 4693, 7715
S. hypoleuca	LSU 111585	LSU 111089; USNM 512298
S. inornata. See *Inezia inornata*		
S. munda	LSU 125910	USNM 227736, 227738
S. nigricans	UMMZ 158832	LACM 93337
S. subcristata	AMNH 14472; USNM 227411	AMNH 2466

APPENDIX—(*Continued*)

	Skulls	Syringes
Spizatornis. See *Anairetes*		
Stigmatura budytoides	FMNH 317865; LSU 125906, 125907; PMNH 4537, 4538; UK 78023, 78035; UMMZ 209231; USNM 227781	PMNH 4537, 4538
S. napensis	LSU 111583, 118565	AMNH 2392, 2393
Sublegatus arenarum	USNM 431173	USNM 318148, 504597
S. modestus	USNM 346034	AMNH 6815; FMNH 322863; USNM 343907
Suiriri suiriri	AMNH 14471; USNM 227409	AMNH 6813; PMNH 2787, 2789; USNM 227631
Tachuris rubrigastra	UMMZ 157090	AMNH 6808, 6809; PMNH 2800
Tyranniscus bolivianus. See *Zimmerius bolivianus*		
T. burmeisteri	Lacking	FMNH 322860; LSU 117275
T. cinereicapillus. See *Zimmerius cinereicapillus*		
T. cinereiceps	LSU 97508	LSU 129647
T. gracilipes. See *Zimmerius gracilipes*		
T. nigrocapillus	LSU 107330	LSU 107668
T. plumbeiceps	Lacking	LSU 129650
T. sclateri	Lacking	Lacking
T. uropygialis	AMNH 14154	LSU 102676, 102677
T. vilissimus. See *Zimmerius vilissimus*		
T. virescens	UMMZ 158855	Lacking
T. viridiflavus. See *Zimmerius viridiflavus*		
Tyrannulus elatus	AMNH 11930; FMNH 315856	AMNH 7718, 8088
Uromyias agilis	Lacking	CM 1942
U. agraphia	LSU 90080, 90081	LSU 79602
Xanthomyias sclateri. See *Tyranniscus sclateri*		
X. virescens. See *Tyranniscus virescens*		
Xenopsaris albinucha	AMNH 15000	AMNH 3520, 8389
Yanacea alpina. See *Anairetes alpinus*		
Zimmerius bolivianus	FMNH 291857; LSU 99434; UMMZ 200610	FMNH 291668; LSU 70641
Z. cinereicapillus	FMNH 315849	FMNH 315848
Z. gracilipes	LSU 118515	AMNH 7703; LSU 102680, 115990
Z. vilissimus	AMNH 14553; UMMZ 133958	LSU 108939
Z. viridiflavus	USNM 344216, 428800; MVZ 141808	PMNH 1725, 1741