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A Phylogeny of the Thirty-Three Genera in the *Empidonax* Assemblage of Tyrant Flycatchers

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ABSTRACT

A phylogeny is developed for those genera of tyrant flycatchers that historically have been treated in two unrelated groups: Hellmayr's (1927) Fluvicolinae, dominated numerically by *Muscisaxicola* and *Knipolegus*, and a major portion of Hellmayr's Myiarchinae, dominated numerically by *Empidonax* and *Contopus*. Monophyly of the assemblage is established by a configuration of the nasal septum that is shared only by the constituent genera and considered thus to be derived. Putative relatives that do not share this derived condition are excluded from this assemblage: *Zimmerius*, *Polystictus*, *Mecocerculus*, *Onychorhynchus*, *Myiobius*, *Terenotriccus*, *Myiobius*, some species of "*Myiophobus*," *Nesotriccus*, *Colonia*, *Muscigralia*, and *Machetornis*.

Generic limits and relationships of the 33 genera admitted to the *Empidonax* assemblage are determined primarily by the morphology of the syrinx, and secondarily by nesting behavior and external morphology.

Three primary lineages in the assemblage are defined by basic differences in the degree to which the A elements of the syrinx provide support for each bronchus. One of these lineages, in which there is little support for the bronchi, is dominated by *Ochthoeca* (including *Tumbezia*), and in ad-

dition includes *Arundinicola*, *Fluvicola*, *Alectrurus*, *Silvicultrix* (a new genus for the three forest species of "*Ochthoeca*"), and *Colorhamphus*.

A second lineage, in which the A elements form complete and calcified rings around the bronchi, consists of *Myiophobus* and the two monotypic genera *Pyrrhomys* and *Hirundinea*.

The remaining 24 genera belong to a third lineage, characterized by the presence of a plug of cartilaginous tissue just caudal to the tracheobronchial junction, and consisting of several groups whose interrelationships are unresolved. The largest of these groups consists of *Muscisaxicola*, *Agriornis*, *Xolmis*, *Heteroxolmis* (a new genus for *dominicana*), *Myiotheretes*, *Cnemarchus*, *Polioxolmis* (a new genus for *rufipennis*), *Neoxolmis*, *Gubernetes*, and *Muscipipra*. Another monophyletic group in this large lineage is dominated by *Empidonax*, and in addition includes *Sayornis*, *Contopus*, *Mitrephanes*, *Xenotriccus*, *Cnemotriccus*, *Aphanotriccus*, and *Lathrotriccus*. *Knipolegus*, *Hymenops*, *Lessonia*, and *Pyrocephalus* cluster by virtue of pronounced sexual dimorphism in their plumage. In addition, this large lineage also includes the monotypic *Ochthornis* and *Satrapa*, which have no obvious close relatives.

RESUMEN

Se elabora una filogenia para aquellos géneros de tiránidos atrapamoscas que históricamente han sido considerados como dos grupos no relacionados: los Fluvicolinae de Hellmayr (1927), dominados por *Muscisaxicola* y *Knipolegus*, y la mayor parte de Myiarchinae de Hellmayr, dominados por *Empidonax* and *Contopus*. La monofilia de este conjunto está establecida por una configuración derivada de la septa nasal presente solamente en los géneros considerados. Los relacionados putativos que no comparten esta condición derivada están excluidas de este conjunto: *Zimmerius*, *Polystictus*, *Mecocerculus*, *Onychorhynchus*, *Myiobius*, *Terenotriccus*, *Myiobius*, algunas de las especies de "*Myiophobus*," *Nesotriccus*, *Colonia*, *Muscigralia*, y *Machetornis*.

Los límites genéricos y relaciones de los 33 géneros incluidos en el conjunto de *Empidonax* están determinados principalmente en base a la morfología de la siringe y, secundariamente, en el comportamiento de anidación y de morfología externa.

Tres lineajes primarios del conjunto están definidas por la diferencia básica del grado en que el elemento A de la siringe ofrece soporte para cada bronquio. En uno de estos lineajes con poco soporte para los bronquios, domina *Ochthoeca* (incluyendo *Tumbezia*) e incluye también *Arun-*

dinicola, *Fluvicola*, *Alectrurus*, *Silvicultrix* (un nuevo género para las tres especies selváticas de "*Ochthoeca*," y *Colorhamphus*.

Un segundo lineaje, en el cual el elemento A forma anillos completos y calcificados alrededor de los bronquios, consiste de *Myiophobus* y los géneros monotípicos *Pyrrhomys* y *Hirundinea*.

Los 24 géneros restantes pertenecen a un tercer lineaje, caracterizado por la presencia de un tapón de tejido cartilaginoso situado caudalmente inmediato a la unión traqueobronquial, y que consiste de varios grupos cuyas interrelaciones no están resueltas. El grupo más grande consiste de *Muscisaxicola*, *Agriornis*, *Xolmis*, *Heteroxolmis* (un nuevo género para *dominicana*), *Myiotheretes*, *Cnemarchus*, *Polioxolmis* (un nuevo género para *rufipennis*), *Neoxolmis*, *Gubernetes*, and *Muscipipra*. Un otro grupo monofilético en este gran lineaje está dominado por *Empidonax* que, además, incluye *Sayornis*, *Contopus*, *Mitrephanes*, *Xenotriccus*, *Cnemotriccus*, *Aphanotriccus*, y *Lathrotriccus*. *Knipolegus*, *Hymenops*, *Lessonia*, y *Pyrocephalus* se agrupan por virtud de pronunciado dimorfismo sexual de su plumaje. En adición, este gran lineaje incluye los géneros monotípicos *Ochthornis* y *Satrapa*, sin relacionados cercanos obvios.

INTRODUCTION

Among the tyrant flycatchers (Tyrannidae) there are assemblages of genera whose monophyly can be demonstrated by the sharing of different combinations of uniquely derived character states of the nasal septum. These cranial characters are more conservative than external morphology, syringeal morphology, nesting behavior, and foraging behavior, and transgress the limits of clusters of genera defined by those morphological and behavioral characters, as I have demonstrated in reconstructing phylogenies for the kingbirds and their allies (Lanyon, 1984b) and for the myiarchine flycatchers (Lanyon, 1985).

The third assemblage in my ongoing analysis of evolution of tyrant flycatchers consists of genera that historically have been placed in two unrelated groups. One of these is Hellmayr's (1927) Fluvicolinae, dominated numerically by the genera *Muscisaxicola* and *Knipolegus*. This group is the equivalent of the Taeniopterinae of Sclater (1888) and Berlepsch (1907). The second group, dominated numerically by *Empidonax* and *Contopus*, constitutes the major portion of the Myiarchinae of Hellmayr (1927) and Berlepsch (1907) and was included in Sclater's Tyranninae. Warter (1965) called attention to the similarities shown by the skulls of these two groups and argued for bringing them together within an enlarged Fluvicolinae. Traylor (1977) adopted Warter's suggestion in the most recent classification of the Tyrannidae, in Peters' Check-list (Traylor, 1979).

This is the group, modified somewhat by the exclusion of certain genera and given the working name of *Empidonax* assemblage for reasons given below, for which a phylogeny is developed in 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 sharing of derived states of the nasal capsule. As Warter (1965) reported, the nasal capsule 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 one. Figure 1 illustrates some of the diversity of character states of the nasal capsule among tyrant flycatchers. The skull of *Hemitriccus flammulatus* is representative of the presumed primitive condition in "flat-bills" and "tody-tyrants," in which the nasal septum is unossified or represented only by a heavily buttressed but shallow structure dorsally (fig. 1: 1, 2). In the kingbirds (*Tyrannus*) and their allies, the septum is fully ossified but without any modification or specialization, and its ventral edge is knifelike, without lateral projections of any kind (fig. 1: 3, 4). The myiarchine flycatchers have a fully ossified nasal capsule, including the alinasal walls and turbinals (fig. 1: 5, 6). When

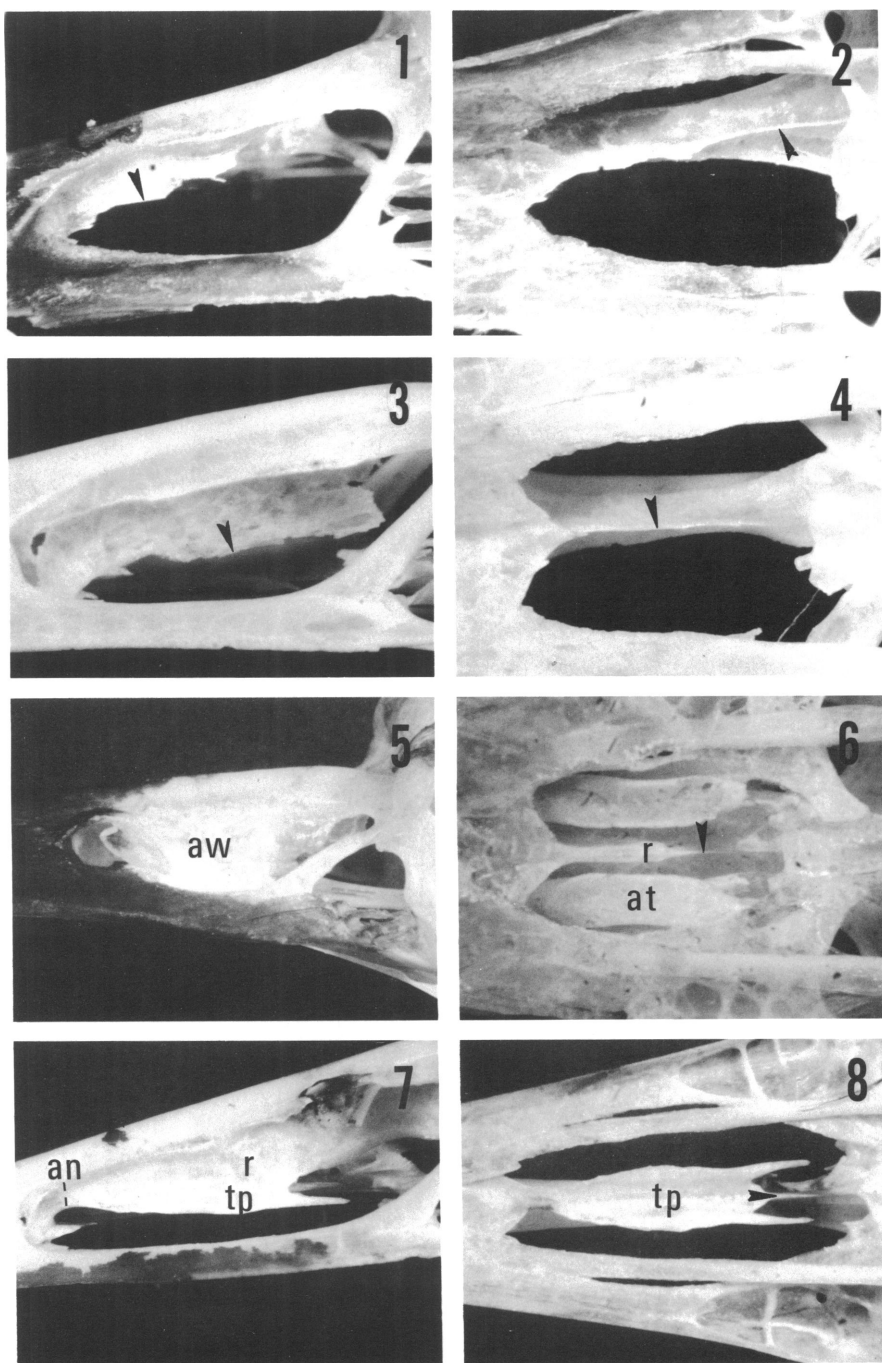


FIG. 1. The nasal capsule in various tyrant flycatchers and in a representative (7, 8) of the *Empidonax* assemblage (anterior end of skull to left; magnification = $6\times$ except $9\times$ in 1, 2 and $4\times$ in 7, 8): (1, 2) *Hemitriccus flammulatus*, LSU 94080, lateral and ventral views; (3, 4) *Tyrannus caudifasciatus*, USNM 553494, lateral and ventral views; (5, 6) *Myiarchus venezuelensis*, AMNH 9246, lateral and ventral views; (7, 8) *Agriornis montana*, AMNH 7152, lateral and ventral views. Arrows indicate ventral edge of nasal septum; an = anterior notch; at = alinasal turbinal; aw = alinasal wall; r = internal supporting rod; tp = trabecular plate.

viewed ventrally (fig. 1: 6), the myiarchine nasal septum has a conspicuous internal supporting rod, which gives a bulbous appearance to that segment; but again, there are no lateral projections from the ventral edge of the myiarchine septum. The very different appearing nasal septum of the *Empidonax* assemblage is illustrated in figure 1: 7, 8, and will be discussed in detail in my argument for monophyly of the 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).

For establishing relationships within clusters of genera whose monophyly has been established with syringeal characters, secondary considerations are given to what I interpret as derived characters in nesting behavior, external morphology, and foraging behavior. Derived patterns of nesting behavior in this assemblage include the construction of ball-shaped nests or of enclosed pensile nests, the use of crevices and cavities in trees or banks, and the inclusion of mud in the nest. Because of intra- and interspecific variability, whether the eggs are marked or unmarked is a character that must be used with caution and only as additional support for hypotheses of relationships based primarily on other, more conservative, characters. Within the large genus *Empidonax*, for example, there are species that normally lay only marked eggs and others that lay only unmarked eggs. In some *Empidonax* nests there are clutches with both marked and unmarked eggs (AMNH collection).

Though the sexes of tyrant flycatchers may differ slightly with respect to the size and color of a concealed crown patch or the intensity of pigmentation in restricted parts of the plumage, the family is not known for sexual dimorphism in plumage coloration and pattern sufficient enough to make identity of the sexes readily apparent in the field. This marked degree of plumage dimorphism between the sexes is found in *Tityra* and *Pachyramphus*, two genera of uncertain relationships within Tyrannidae, and in two species currently assigned to the genus *Poecilotriccus* (Traylor, 1977, 1979) in the "tody-tyrant group" (Traylor and Fitzpatrick, 1982). But it is within six of the genera in my *Empidonax* assemblage (the four genera in my *Knipolegus* group, and *Arundinicola* and *Alectrurus*) that sexual dimorphism in plumage coloration and pattern reaches its greatest development in the Tyrannidae. For this reason I assign considerable weight to the sharing of this character by genera having a similar syringeal morphology.

Character states are identified which separate a genus or cluster of genera; they are assigned numbers in the text that 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. Swainson's (1837, 1862) use of the name *Fluvicolinae* for a group of five terrestrial and riverine genera, including *Fluvicola*, was the basis for Hellmayr's (1927) subfamily *Fluvicolinae*. However, the three older names available for this assemblage, *Knipolegus*, *Xolmis*, and *Fluvicola*, are assigned to specialized genera that are unrepresentative of the group as a whole. In lieu of a suitable older name, I have selected the largest genus, *Empidonax*, as the basis for a working name for the assemblage.

I consider the tyrant flycatchers (Tyrannidae) to be a monophyletic group on the basis of their internal cartilages in the syrinx, structures uniquely derived within all subos-

cine 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, ms; McKittrick, 1985). For my outgroup comparisons I have examined the skulls of 139 and the syringes of 143 of the 149 genera of New World Tyrannoidea (Tyrannidae, Pipridae, Cotingidae, Oxyruncidae, and Phytotomidae). Within the Tyrannidae (sensu Traylor, 1979), I have examined over 700 skulls of 88 of the 90 genera, over 800 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 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 Paraense Emilio Goeldi (MG) in 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 Univer-

sity (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 (WVZ) in Los Angeles. Specimens cited in the text, figure captions, and in the Appendix are identified to collection by the abbreviations given above.

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MONOPHYLY AND THE LIMITS OF THE ASSEMBLAGE

Monophyly of the *Empidonax* assemblage rests on a derived configuration of the nasal septum that is shared only by the constituent genera and found nowhere else within the Tyrannidae (or within the Tyrannoidea, for that matter). In this assemblage the nasal septum is fully ossified, and there is a prominent transverse trabecular plate that is located along the entire ventral edge of the septum

anterior to the ventral end of the internal supporting rod. Viewed from the ventral aspect (fig. 1: 8) the plate is forked at its posterior end, with the base of the fork coinciding with the ventral end of the internal supporting rod. When viewed in cross section, the plate is slightly concave. In a lateral view (fig. 1: 7) the plate curves dorsally at its anterior end, much as a rocker on a rocking

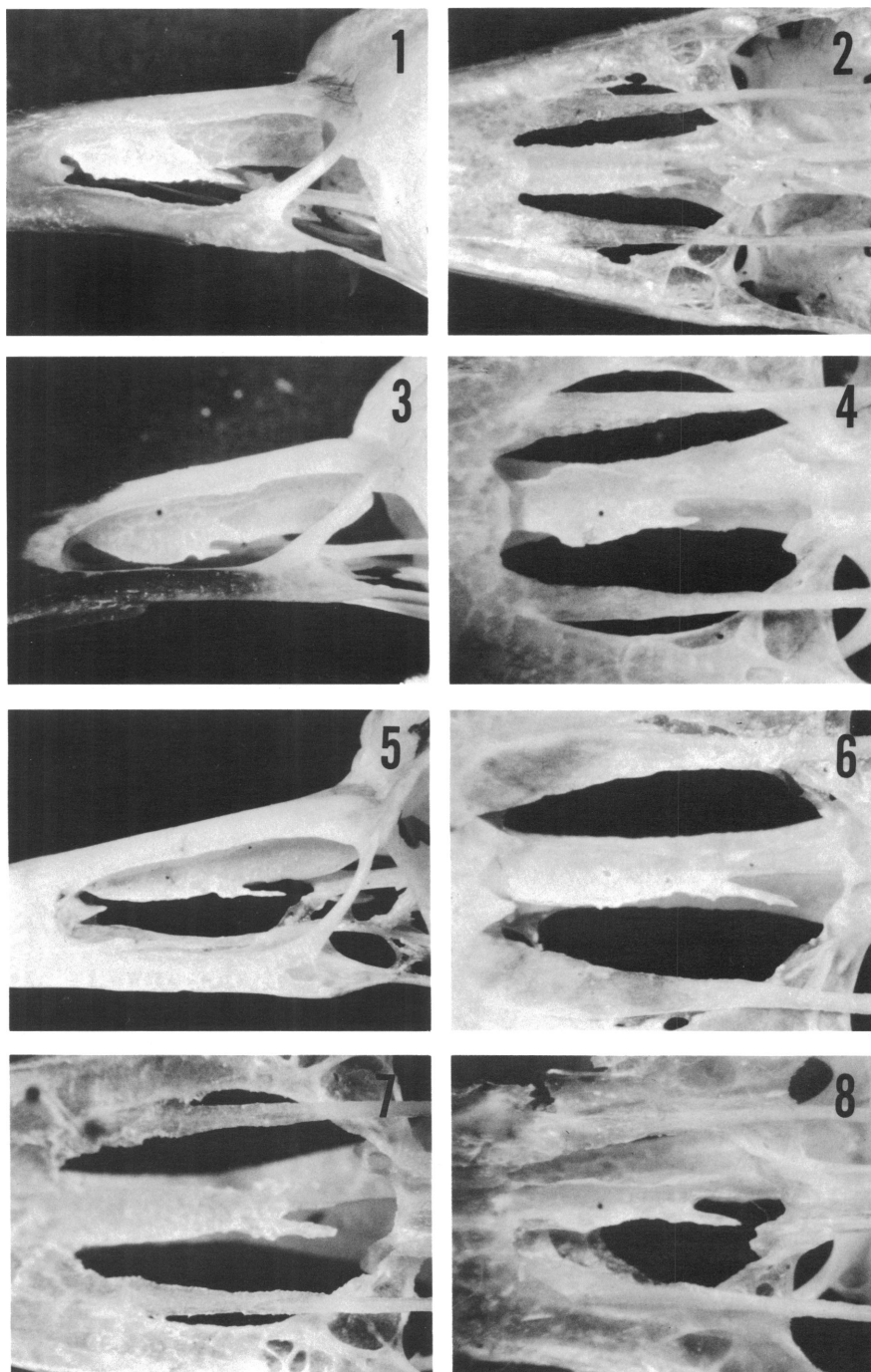


FIG. 2. Intraspecific variation in the nasal capsule within the genus *Empidonax* (anterior end of skull to left; magnification = $6\times$ in 1-4, $9\times$ in 5-8): (1, 2) *E. minimus*, AMNH 5562, lateral and ventral views; (3, 4) *E. virescens*, LSU 105277, lateral and ventral views; (5, 6) *E. albigularis*, UK 69672, lateral and ventral views; (7) *E. hammondi*, FMNH 288099, ventral view; (8) *E. fulvifrons*, LSU 31944, ventral view.

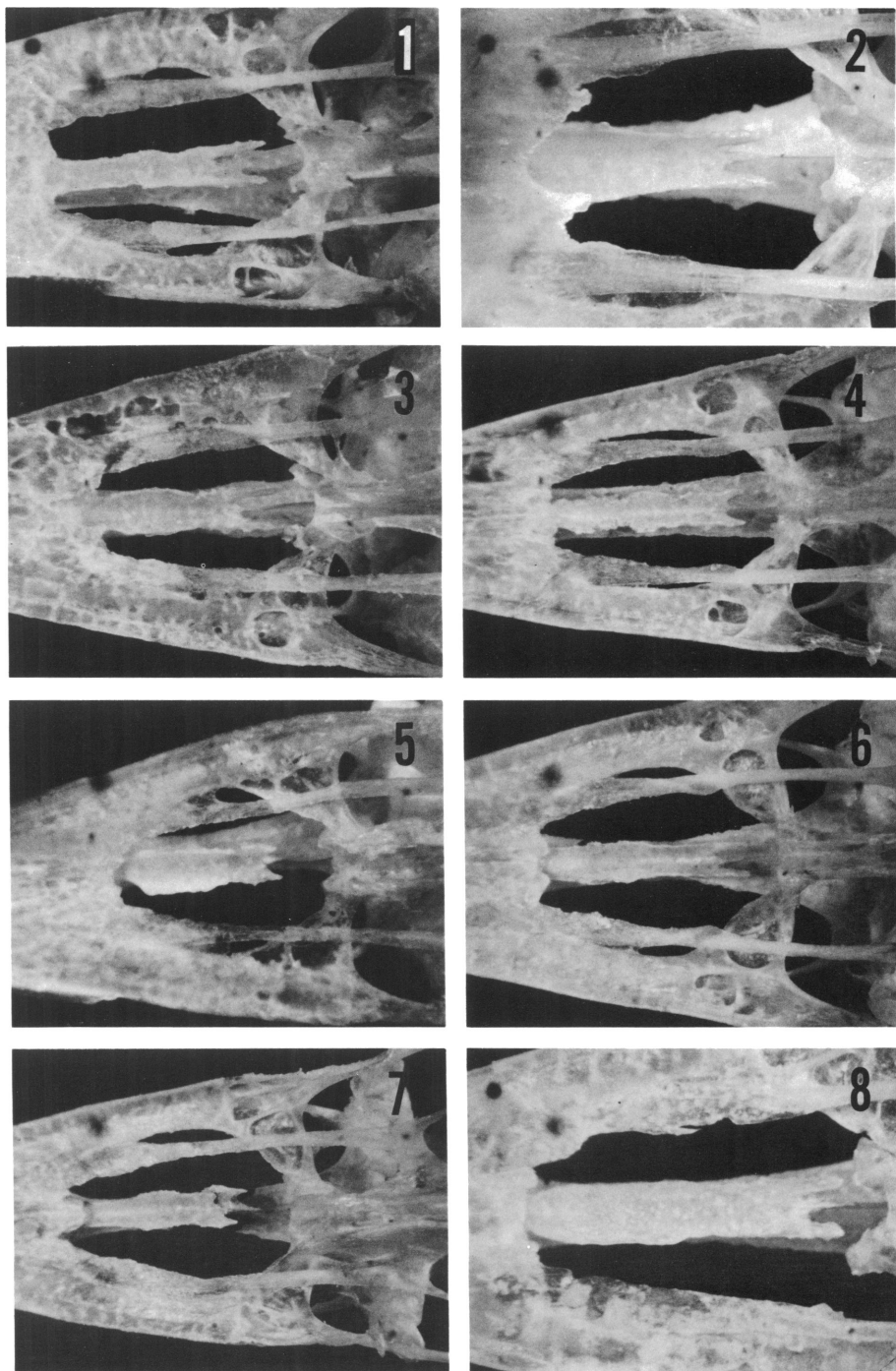


FIG. 3. Intrageneric variation in the nasal capsule within the genus *Empidonax* (anterior end of skull to left, ventral views; magnification = $6\times$, except $9\times$ in 8): (1) *E. difficilis*, UMMZ 208993; (2) *E. traillii*, AMNH 10245; (3) *E. wrightii*, UMMZ 159155; (4) *E. oberholseri*, UMMZ 155406; (5) *E. flaviventris*, AMNH 5776; (6) *E. flavescens*, UMMZ 156488; (7) *E. atriceps*, UMMZ 153239; (8) *E. affinis*, UMMZ 159156.

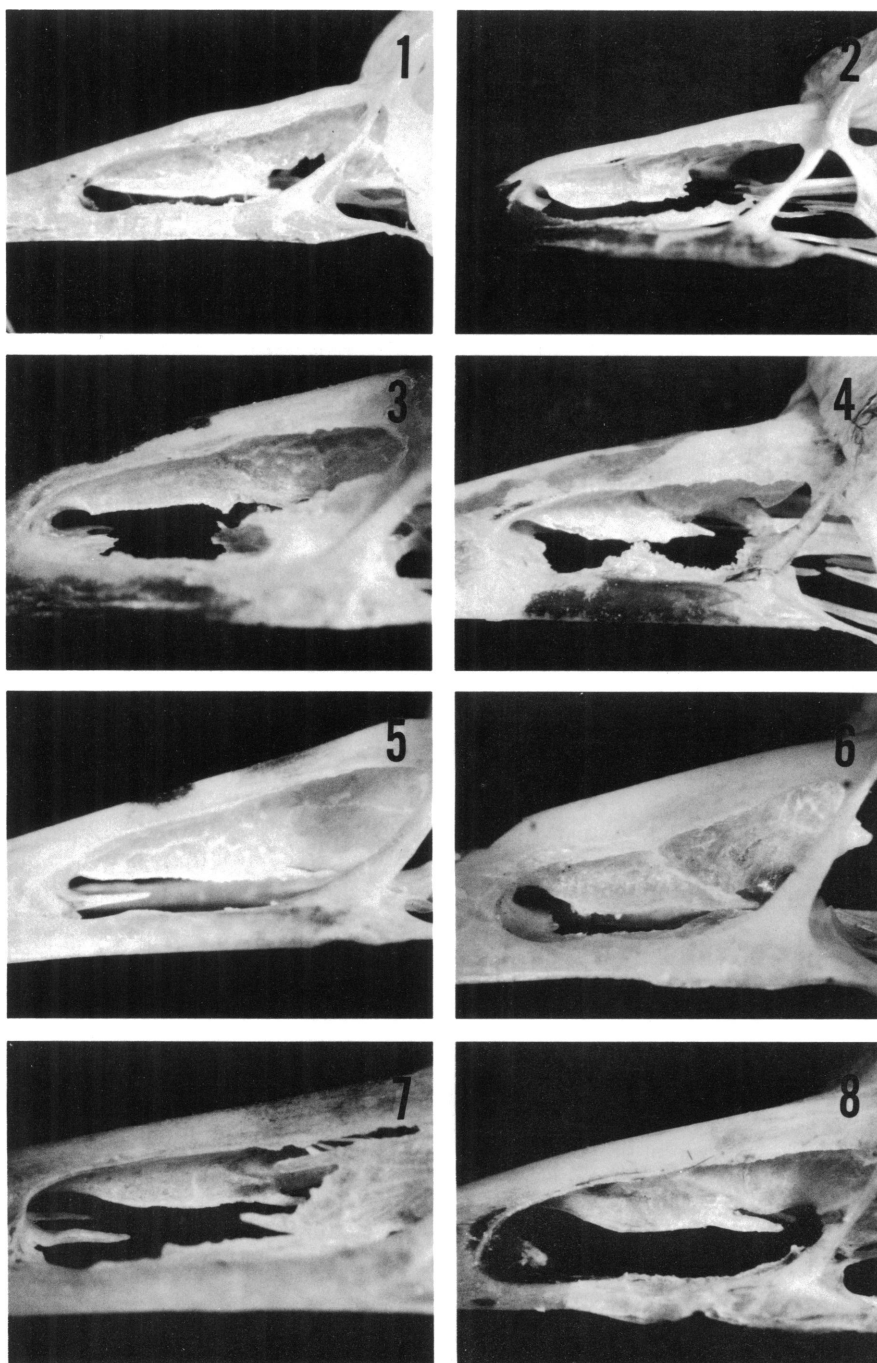


FIG. 4. Intergeneric variation in the size and shape of the anterior notch within the *Empidonax* assemblage (anterior end of skull to left, lateral views; magnification = $6\times$ in 1, 2, 4, 6, and $9\times$ in 3, 5, 7, 8): (1) *Knipolegus striaticeps*, USNM 227410; (2) *Pyrrhomys cinnamomea*, LSU 79825; (3) *Myiophobus flavicans*, AMNH 14156; (4) *Cnemotriccus fuscatus*, AMNH 6685; (5) *Myiophobus fasciatus*, LSU 81265; (6) *Contopus borealis*, AMNH 5904; (7) *Fluvicola nengeta*, AMNH 14625; (8) *Lessonia rufa*, AMNH 14468.

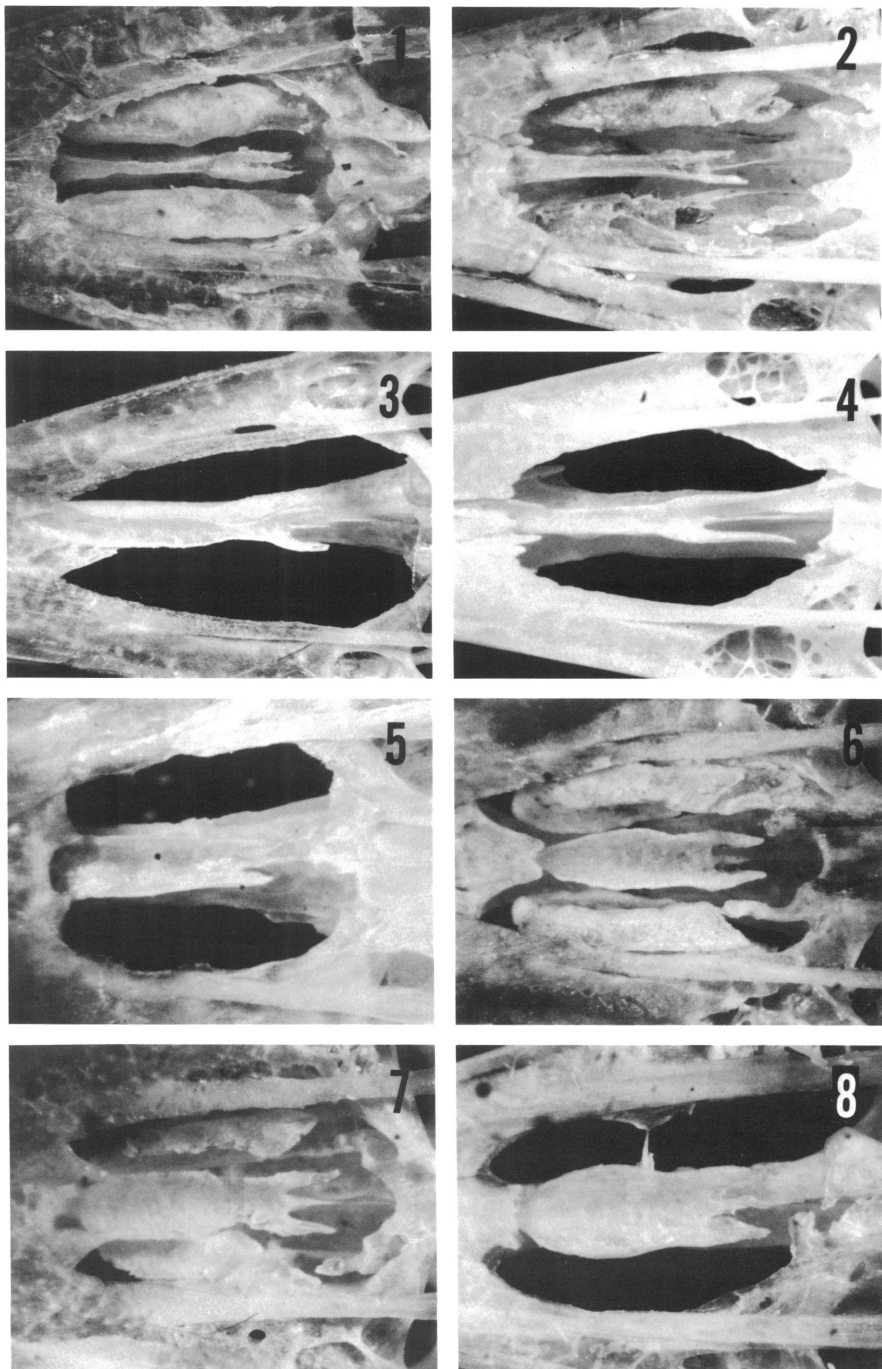


FIG. 5. Intergeneric variation in the width and shape of the trabecular plate within the *Empidonax* assemblage (anterior end of skull to left; ventral views; magnification = $6\times$ in 1, 2, 4, 8, and $9\times$ in 3, 5–7): (1) *Alectrurus risora*, AMNH 14473; (2) *Heteroxolmis dominicana*, AMNH 6652; (3) *Silvicultrix frontalis*, UK 80547; (4) *Knipolegus lophotes*, USNM 321628; (5) *Ochthornis littoralis*, LSU 64864; (6) *Fluvicola pica*, AMNH 12068; (7) *Lathrotriccus euleri*, AMNH 6934; (8) *Xolmis coronata*, UMMZ 158765.

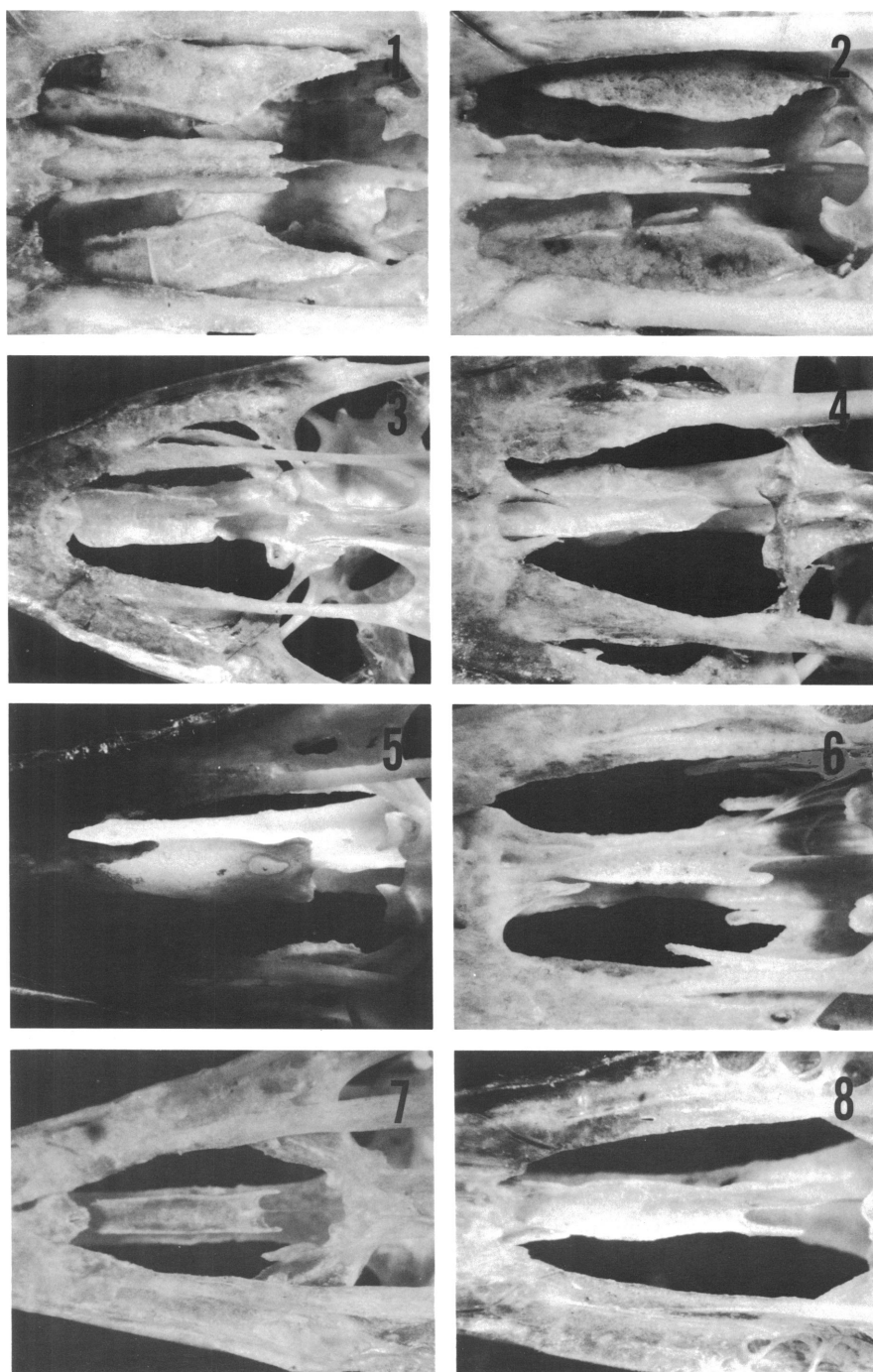


FIG. 6. Intergeneric variation in the width and shape of the trabecular plate within the *Empidonax* assemblage (anterior end of skull to left; magnification = $6\times$, except $9\times$ in 6, 8): (1) *Gubernetes yetapa*, AMNH 14469; (2) *G. yetapa*, UMMZ 200837; (3) *Pyrrhomyias cinnamomea*, LSU 79825; (4) *Hirundinea ferruginea*, LSU 118266; (5) *Cnemarchus erythropygius*, LSU 113675; (6) *Fluvicola nengeta*, AMNH 14625; (7) *Hymenops perspicillata*, UMMZ 157080; (8) *Ochthoeca fumicolor*, LSU 79820.

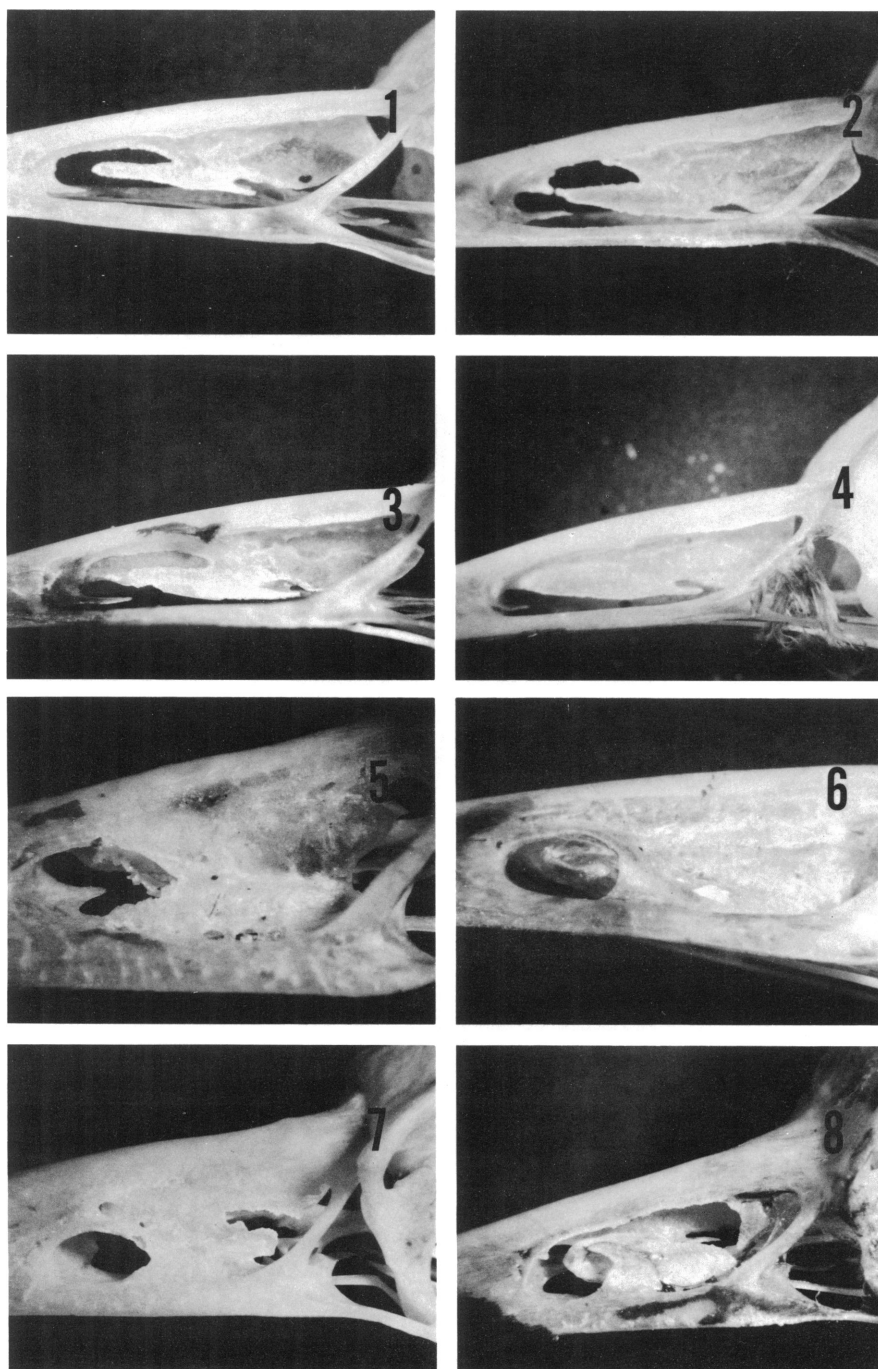


FIG. 7. Intergeneric variation in the lateral aspect of the nasal capsule within the *Empidonax* assemblage (anterior end of skull to left; magnification = 6 \times , except 4 \times in 4 and 9 \times in 5): (1) *Muscisaxicola rufivertex*, AMNH 7157; (2) *M. macloviana*, UMMZ 136211; (3) *M. alpina*, AMNH 6929; (4) *M. frontalis*, LSU 101480; (5) *Lathrotriccus euleri*, AMNH 6934; (6) *Heteroxolmis dominicana*, AMNH 6652; (7) *Arundinicola leucocephala*, AMNH 6703; (8) *Fluvicola pica*, AMNH 12068.

chair. The septum beneath this anterior portion of the plate remains unossified, creating an illusion that the septum bears an anterior notch. This configuration of the septum is equivalent to Warter's (1965) "type 6," in which he notes that the trabecular plate "bases the septum."

There is much variation in the size and shape of the anterior notch, in the width and shape of the trabecular plate, and in the length and conspicuousness of the posterior forking. Figures 2 and 3 illustrate the extent of intra-generic variation in these characters in the skulls of 13 of the 15 species of *Empidonax*, the largest genus in the assemblage. Inter-generic variation in these characters is illustrated in figures 4–6.

Warter (1965, pp. 69–70) states that there is a further subdivision of his type 6 septum, with those genera in Hellmayr's *Fluvicolinae* having a "long, broad fork," while the genera in Hellmayr's *Myiarchinae*, sensu lato, have a "short, narrow fork." I can find no such correlation in my sample of skulls. Within the large genus *Empidonax* I found both short- and long-forked plates (in fig. 2, compare 4 with 6–8), and *Fluvicola nengeta* (fig. 6: 6) may have a shorter fork than *Empidonax albigularis* (fig. 2: 6). The short- and long-forked conditions occur among individuals of the same species, for example in *Gubernetes yetapa* (fig. 6: 1, 2).

The series of photographs in figure 7: 1–4 suggests a transformation series in ossification of the anterior region of the nasal septum, as illustrated in four different species of *Muscisaxicola*. Unfortunately there are no comparable data on the transformation from the normal forked condition to the rare unforked condition, though the latter is presumed to have arisen in three monotypic genera in the assemblage (fig. 6: 3–5). By back-lighting the skull of *Cnemarchus* (fig. 6: 5), one can see a thinly ossified area near the posterior end of the plate, suggesting that this character state (lack of posterior forking) has been derived from the normal forked condition through progressive ossification and

closure of the fork. I have found this kind of a trabecular plate (i.e., like that characterizing the *Empidonax* assemblage but lacking the posterior forking) in only two species of flycatchers outside of this assemblage (*Elaenia albiceps* and *Elaenia fallax*), where it is presumably convergent.

Some of these variants in the morphology of the nasal capsule have value either for clustering genera or for determining generic limits, because of their limited distribution within the assemblage and congruence with divergences in other character complexes. An extremely narrow or laterally constricted trabecular plate (fig. 5: 1–3) is one example. In a few genera the capsule has become fully ossified quite independently, to the extent that the ossified alinasal walls obscure a lateral view of the septum (fig. 7: 5–8). In these genera in which the capsule is fully ossified, the ossified alinasal turbinals are conspicuous when viewed from a ventral aspect (fig. 5: 1, 2, 6, 7; fig. 6: 1, 2).

Other tyrant genera, notably some of those that Taylor (1977) assigned to his *Elaeniinae*, also possess a prominent transverse trabecular plate, which is elevated somewhat above the ventral edge of the nasal septum, creating the appearance of a sagittal ridge when viewed from below (fig. 8: 1, 2). 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." There is no suggestion of a sagittal ridge on the trabecular plate of the genera in my *Empidonax* assemblage.

Though in general I concur with Warter (1965) with regard to the genera that he characterized as having a type 6 nasal septum, I disagree with his findings on certain genera (these will be discussed fully in the section on putative relatives) and I am able to add several genera that were unavailable to him. There were no surprises, in the sense that I found no genus with a nasal septum like that of my *Empidonax* assemblage that had not already been regarded as a member of this complex.

THE PUTATIVE RELATIVES

In this section I present my arguments for excluding from my *Empidonax* assemblage

some of the genera that historically have been regarded as members either of Hellmayr's

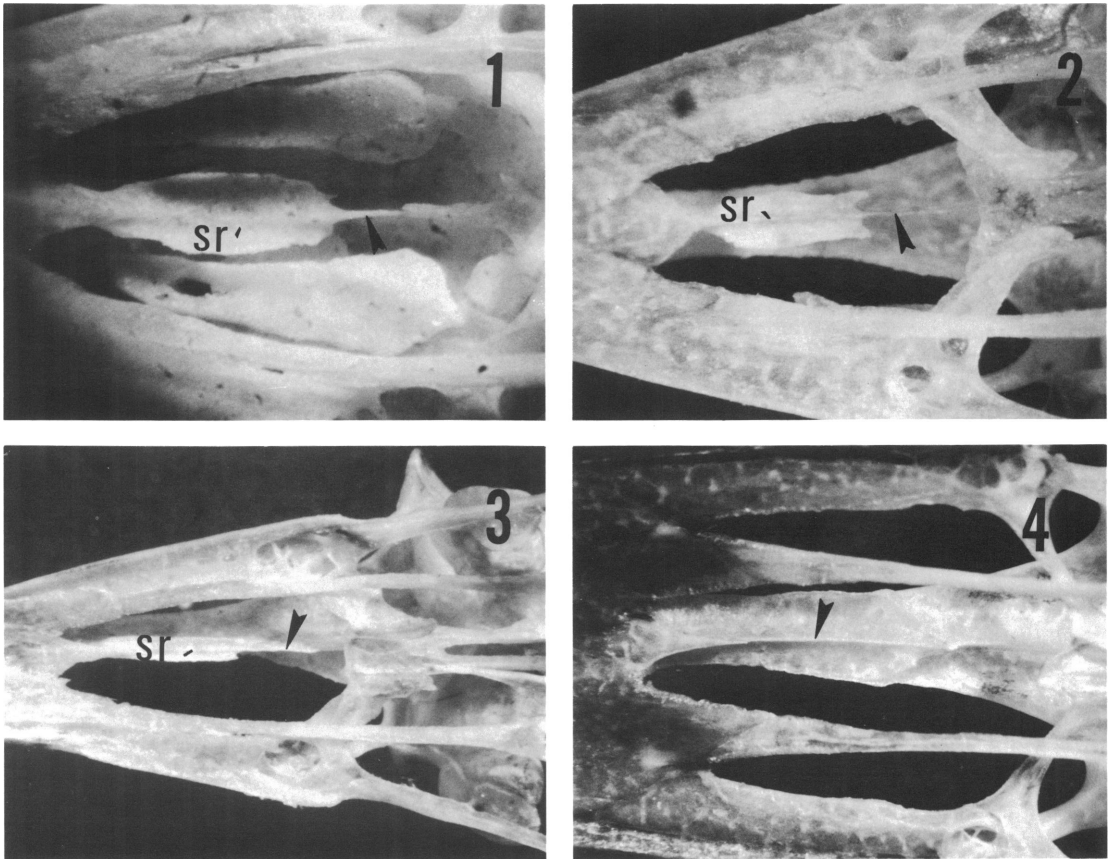


FIG. 8. Ventral views of the nasal capsules of putative relatives of the *Empidonax* assemblage (anterior end of skull to left; magnification = $8\times$, except $15\times$ in 1 and $11\times$ in 2): (1) *Zimmerius viridiflavus*, USNM 344216; (2) *Polystictus pectoralis*, UMMZ 218535; (3) *Mecocerculus leucophrys*, AMNH 10704; (4) *Onychorhynchus coronatus*, AMNH 14163. Arrows indicate ventral edge of nasal septum; sr = sagittal ridge on trabecular plate.

(1927) Fluvicolinae or of the *Empidonax* portion of his Myiarchinae and, in addition, two genera outside of these subfamilies that Warter (1965) reported as having a type 6 nasal septum. The sequence in which I discuss these genera is that used by Traylor (1979) in the most recent classification of the family. They remain incertae sedis until studies are completed on the remaining assemblages within the family.

Zimmerius and *Polystictus*

The only genera outside Hellmayr's Fluvicolinae and Myiarchinae that Warter (1965) found to have a type 6 nasal septum were *Tyranniscus* (= *Zimmerius*) and *Habrura* (= *Polystictus*). Traylor (1977) was aware of

Warter's findings, but preferred to regard these aberrant occurrences of a type 6 septum as due to convergence, and he assigned both of these genera to his subfamily Elaeniinae. I can find no basis for Warter's claim. My four specimens of *Zimmerius* and one specimen of *Polystictus* all have nasal septa that I would classify as Warter's type 5, which is indeed characteristic of many of the genera in Traylor's Elaeniinae. There is no suggestion of an anterior notch, and the trabecular plate has a prominent sagittal ridge (i.e., the plate is "within the septum") (fig. 8: 1, 2).

Mecocerculus

In reference to *Mecocerculus*, Sclater (1888) remarked that "this little group is closely al-

lied to *Ochthoeca*, but distinguished by its more compressed bill and longer tail." He placed it next to *Ochthoeca* in his Taeniop-
terinae. Berlepsch (1907) had *Mecocerculus*
incertae sedis in his Serpophaginae; Hellmayr
(1927) had no reservations in listing it within
his Serpophaginae. Warter (1965) found it to
have a nasal septum like that of other genera
in Hellmayr's Serpophaginae. Traylor (1977)
placed *Mecocerculus* next to *Serpophaga* in
his enlarged subfamily Elaeniinae.

I have examined the nasal septa of four of
the six species of *Mecocerculus* (fig. 8: 3). They
lack an anterior notch and possess a trabec-
ular plate that is long, narrow, not forked
posteriorly, and elevated somewhat above the
ventral edge of the septum (type 5). I con-
cluded that the genus does not belong in my
Empidonax assemblage.

Onychorhynchus

Traylor (1977) began his Fluvicolinae with
Onychorhynchus, a monotypic genus that
Hellmayr (1927) and Berlepsch (1907) placed
at the end of their subfamily Myiarchinae.
Berlepsch revealed his uncertainty, however,
by suggesting that it may well be related to
his Platyrhynchinae. Warter (1965) found that
Onychorhynchus does not possess a type 6
nasal septum and proposed to transfer it to
the subfamily Platyrinchinae.

There is little ossification of the nasal cap-
sule in *Onychorhynchus*. All that remains of
the nasal septum is a shallow ridge along the
midline of the roof of the nasal region (fig. 8:
4); consequently there is no suggestion of
either a transverse trabecular plate or a prom-
inent notch anteriorly that characterizes the
genera in my *Empidonax* assemblage. In the
morphology of the nasal capsule, *Onycho-
rhynchus* most resembles *Platyrinchus* and
Tolmomyias. This similarity may reflect a
primitive character state, however, and the
affinities of *Onychorhynchus* must await
studies of other assemblages within the fam-
ily.

Myiotriccus, *Terenotriccus*, and *Myiobius*

Sclater (1888) and Berlepsch (1907) in-
cluded this cluster within the genus *Myiobius*.
Following Ridgway's (1905) proposal to rec-
ognize the monotypic genera *Myiotriccus* and
Terenotriccus, Hellmayr (1927) placed all

three genera in the nonmyiarchine portion of
his Myiarchinae. Warter (1965) did not have
access to a skull of *Myiotriccus*, but consid-
ered his specimens of *Terenotriccus* (provi-
sionally?) and *Myiobius* to be sufficiently flu-
vicoline as to include them within his enlarged
concept of the Fluvicolinae. Traylor (1977)
followed Warter's recommendation and po-
sitioned this cluster of three genera after *On-
ychorhynchus* in his Fluvicolinae.

The nasal septa in these three genera pos-
sess well-developed trabecular plates that are
tapered gradually at the caudal ends (i.e., not
forked in the manner of my *Empidonax* as-
semblage). In *Myiotriccus* (fig. 9: 1, 2) and
some specimens of *Myiobius* (fig. 9: 8) there
is no suggestion of an anterior notch and the
trabecular plate is elevated somewhat above
the ventral edge of the septum. Had Warter
had access to a skull of *Myiotriccus*, he prob-
ably would have classified its nasal septum
as type 5. Clearly it is not part of the *Em-
pidonax* lineage. *Terenotriccus* and some
specimens of *Myiobius*, on the other hand,
have the trabecular plate located along the
ventral edge of the septum and there is a
suggestion of an anterior notch (fig. 9: 3–7),
as in the *Empidonax* assemblage. Lack of
posterior forking of the plate argues against
the inclusion of these taxa within this lineage,
as defined here, though they may well have
evolved from or be related to a form ancestral
to this assemblage.

"*Myiophobus*" (*phoenicomitra*, *roraimae*,
and *ochraceiventris*)

The relationships of *Myiophobus* have been
obscure and equivocal due to the lack of an-
atomical material. Warter (1965) had access
only to specimens of *fasciatus*, which he con-
sidered fluvicoline, while Ames (1971) looked
at a single specimen of *fasciatus* but did not
include the genus in any of his syringeal
groups. Sclater (1888) and Berlepsch (1907)
had placed most of the species (including
phoenicomitra and *roraimae*) in *Myiobius*, but
assigned *ochraceiventris* to *Mitrephanes*.
Hellmayr (1927) considered them all within
Myiophobus but quite clearly had some res-
ervations. Of *ochraceiventris* he wrote: "...
certainly out of place in *Mitrephanes* and
seems to be more nearly related to *M. (yio-
phobus) pulcher*, though differing from the

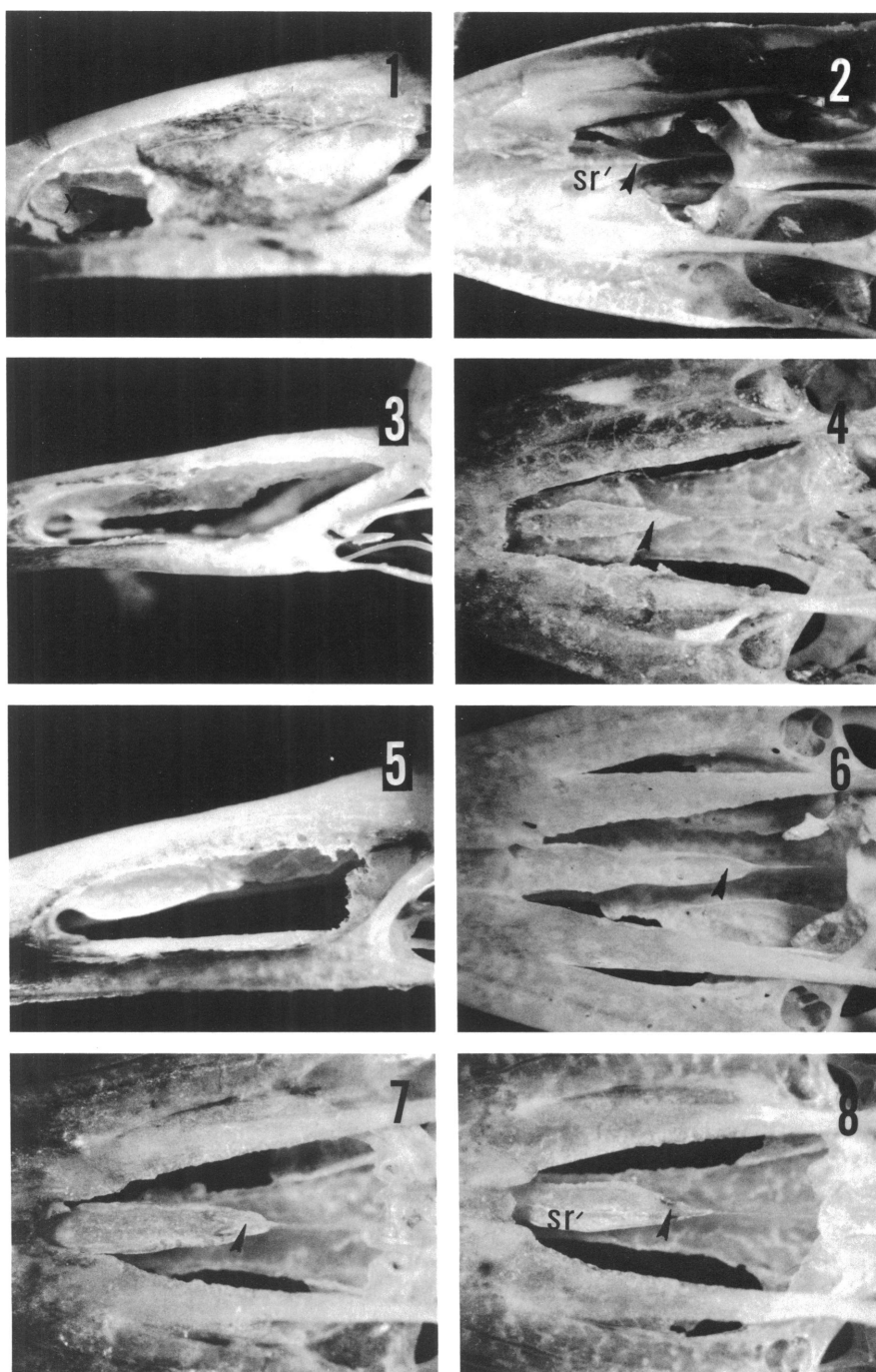


FIG. 9. Nasal capsules of putative relatives of the *Empidonax* assemblage (anterior end of skull to left; magnification = 9 \times , except 6 \times in 2): (1, 2) *Myiotriccus ornatus*, LSU 90046, lateral and ventral views; (3) *Terenotriccus erythrurus*, USNM 347158, lateral view; (4) *T. erythrurus*, UMMZ 214047, ventral view; (5) *Myiobius barbatus*, LSU 111557, lateral view; (6) *M. barbatus*, UK 71554, ventral view; (7) *M. villosus*, LSU 99590, lateral view; (8) *M. atricaudus*, LSU 108929, ventral view. Arrows indicate tapered caudal end of trabecular plate; sr = sagittal ridge on trabecular plate; x = absence of anterior notch.

members of the genus *Myiophobus* by its much longer tail, besides other structural details," and later he added: "*Myiophobus roraimae* is a very peculiar species and stands quite by itself." Zimmer (MS) also had a problem with *ochraceiventris* as revealed in this unpublished note dated February 25, 1938: "This bird looks somewhat out of place in *Myiophobus* but there is no other genus where it fits as well, and careful comparison shows no real generic characters for it."

Traylor (1977) wrote: "*Myiophobus* is a genus that is superficially like *Myiobius*, but probably not closely related It is risky to generalize about *Myiophobus*, because the only species for which the syrinx and cranium were available, and whose nest and habits have been recorded, is *fasciatus*, the least typical ecologically." He recognized nine species in *Myiophobus*, including *phoenicomitra*, *roraimae*, and *ochraceiventris*.

I have examined 16 skulls of the 9 species (*lintoni* and *cryptoxanthus* lacking) of *Myiophobus* and find that the genus as now constituted (Traylor, 1979) is polyphyletic. I agree with Warter (1965) that *fasciatus* has a fluvicoline skull, and can add that so do *flavicans* and *inornatus*. These taxa will be discussed in the section on relationships within the assemblage. Since *fasciatus* has been designated the type of *Myiophobus* Reichenbach, that generic name is retained for those species having nasal septa characteristic of the *Empidonax* assemblage.

The nasal septa of *phoenicomitra*, *roraimae*, and *ochraceiventris* do not share the derived character states 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. The septum can be seen beneath the anterior portion of the plate in figure 10: 1, 5, and as a sagittal ridge on the ventral surface of the plate in figure 10: 2–4, 6. The trabecular plate is tapered posteriorly, not forked, in all but one of my skulls of these three species. The exception is a *roraimae* skull (FMNH 319446) in which the nasal septum lacks an anterior notch (fig. 10: 5) and the trabecular plate has a conspicuous sagittal ridge (fig. 10: 6) as in my other specimens of these species, but the plate is forked caudally (10: 6). This is the only occurrence that I have found of a well-

developed posterior forking of the trabecular plate in a species outside my *Empidonax* assemblage.

The syrinxes of *phoenicomitra* and *roraimae* are similar to one another, while the syrinx of *ochraceiventris* is different, suggesting that they may ultimately be assigned to two new genera. If Parker et al. (1985) and Remsen (1984) are correct in their belief that *lintoni* and *ochraceiventris* form a superspecies, then *lintoni* should be removed from *Myiophobus* as well and placed next to *ochraceiventris*.

Nesotriccus

Traylor (1977) removed the monotypic *Nesotriccus* from its traditional position among the myiarchine flycatchers and placed it in his subfamily Fluvicolinae, between *Empidonax* and *Cnemotriccus*, on the basis of external morphology. I have demonstrated elsewhere (Lanyon, 1984a) that *Nesotriccus* is not a member of the *Empidonax* assemblage, for it does not share the uniquely derived character states of the nasal septum that characterize that group. The morphology of the skull and the syrinx suggest that *Nesotriccus* is related to *Phaeomyias* and *Cap-siempis* in another tyrant assemblage.

Colonia

Historically this monotypic genus has been regarded as part of the Fluvicolinae (=Tainiopterinae of Sclater, 1888, and Berlepsch, 1907; Hellmayr, 1927; Traylor, 1977). Warter (1965) classified the nasal septum of *Colonia* as type 6 and recommended that it and the other long-tailed nonterrestrial tyrants (*Gubernetes*, *Yetapa*, and *Alectrurus*?) constitute a distinct tribe within his Fluvicolinae. Traylor (1977) wrote: "While I accept the near relationship of *Colonia*, *Gubernetes* and *Alectrurus* as shown by the cranial characters, I do not consider them more distinct than the other groups of Fluvicoline genera."

Contrary to Warter's findings, the nasal capsule of *Colonia* (fig. 10: 7, 8) is not at all like that of the fluvicolines. The nasal septum lacks any suggestion of an anterior notch. There is a uniquely shaped trabecular plate that occupies less than half of the length of the ventral edge of the septum anterior to the internal supporting rod, and that is very broad

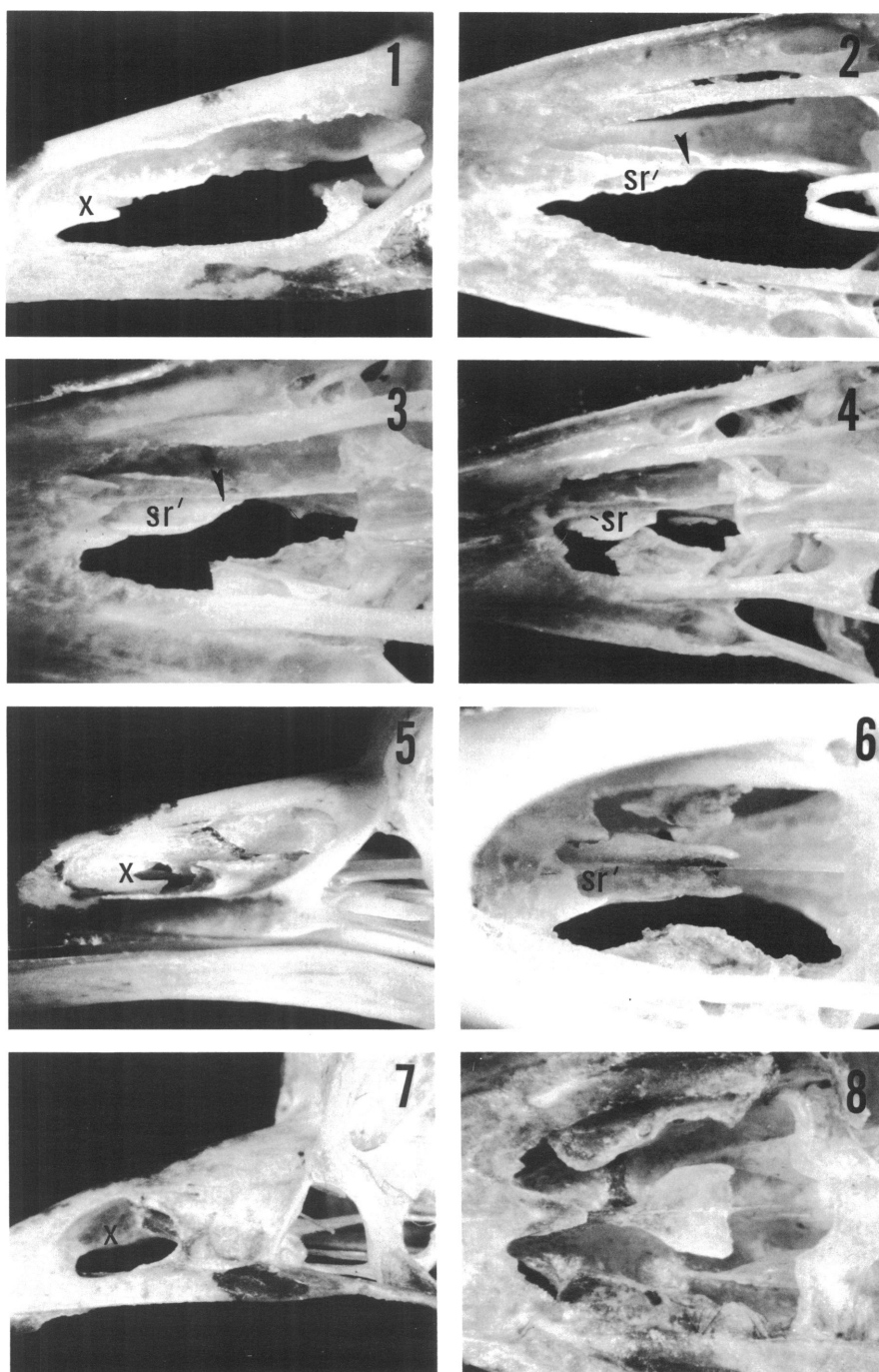


FIG. 10. Nasal capsules of putative relatives of the *Empidonax* assemblage (anterior end of skull to left; magnification = $9\times$, except $6\times$ in 4, 5, 7): (1, 2) "*Myiophobus*" *ochraceiventris*, LSU 74895, lateral and ventral views; (3) "*Myiophobus*" *phoenicomitra*, LSU 86568, ventral view; (4) "*Myiophobus*" *roraimeae*, LSU 107313, ventral view; (5, 6) "*Myiophobus*" *roraimeae*, FMNH 319446, lateral and ventral views; (7) *Colonia colonus*, AMNH 11612, lateral view; (8) *C. colonus*, AMNH 11613, ventral view. Arrows indicate tapered caudal end of trabecular plate; sr = sagittal ridge on trabecular plate; x = absence of anterior notch.

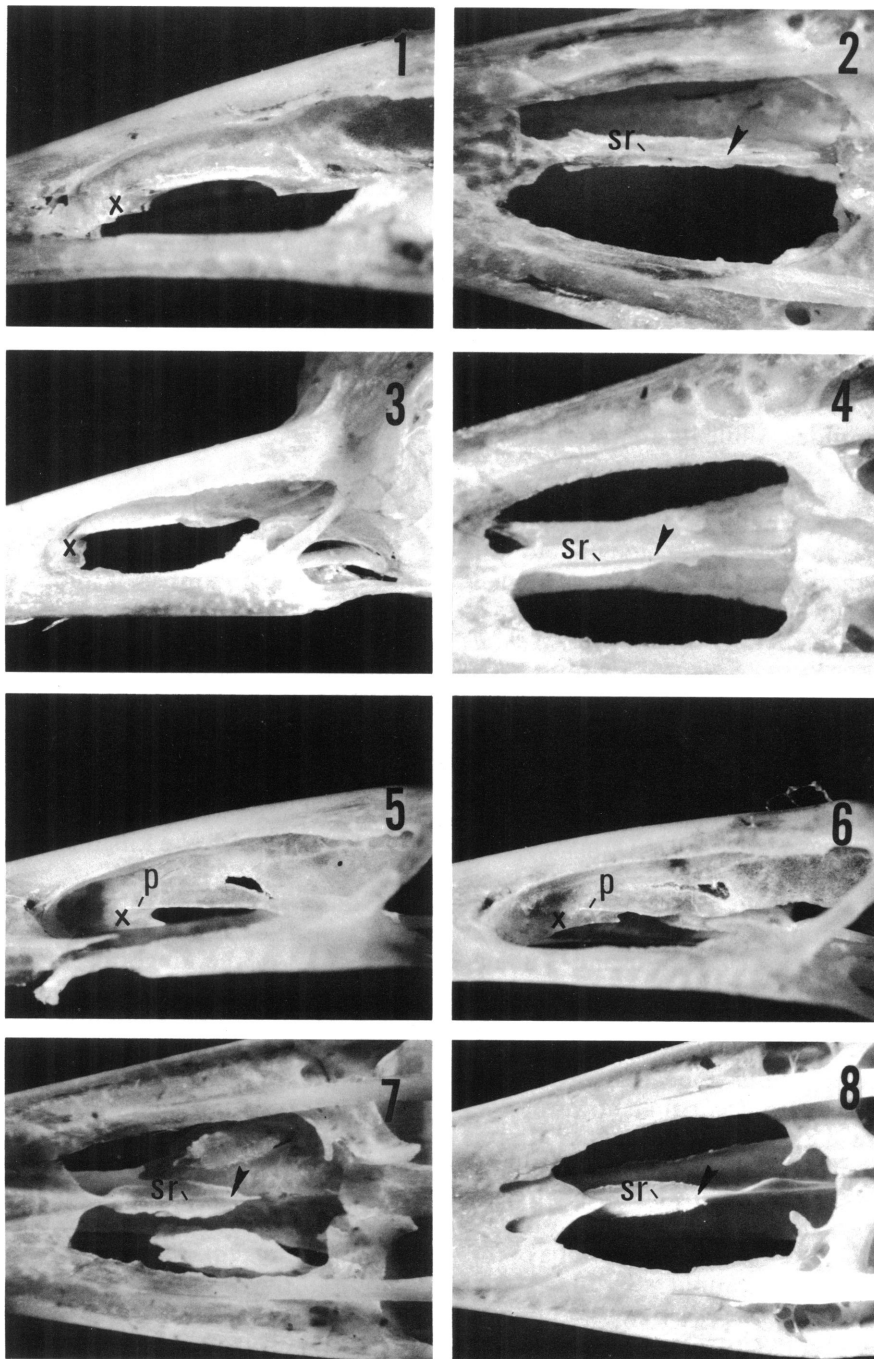


FIG. 11. Nasal capsules of putative relatives of the *Empidonax* assemblage (anterior end of skull to left; magnification = $9\times$ in 1–4, $6\times$ in 5–8): (1, 2) *Muscigralla brevicauda*, UMMZ 156848, lateral and ventral views; (3, 4) *M. brevicauda*, LSU 48837, lateral and ventral views; (5) *Machetornis rixosus*, AMNH 6657, lateral view; (6) *M. rixosus*, UMMZ 157087, lateral view; (7) *M. rixosus*, USNM 499048, ventral view; (8) *M. rixosus*, LACM 93329, ventral view. Arrows indicate tapered caudal end of trabecular plate; p = elevation of trabecular plate above ventral edge of nasal septum; sr = sagittal ridge on trabecular plate; x = absence of anterior notch.

for its length. This plate is truncated posteriorly, not forked. The nasal septa of *Gubernetes* and *Alectrurus* are very different and have been discussed in the previous section dealing with monophyly of the assemblage.

Muscigralla

The monotypic *Muscigralla* has been an enigma to avian systematists; most workers have placed it among a number of "aberrant genera" at the end of the Fluvicolinae. Ridgway (1907) wrote: "*Muscigralla* is a very peculiar looking form, the appearance of which does not in the least suggest any relationship to the Tyrannidae, while its holaspidean tarsi certainly exclude it from that family. It probably belongs to the Formicariidae." Hellmayr (1927) remarked that it is "a genus of doubtful affinity, possibly not belonging to this family [Tyrannidae]." Zimmer (MS) thought the tarsi might show relationship to one of several tyrant genera (*Euscarthmus*, *Xenomyias*), none of which is a member of my *Empidonax* assemblage. Warter (1965) acknowledged that *Muscigralla* does not have a nasal septum characteristic of the fluvicolines, but made no recommendation as to where it belongs. Ames (1971) argued for retaining it within the Tyrannidae on the basis of syringeal characters and tentatively included it within his *Empidonax/Contopus* group. Vuilleumier (*in* Smith and Vuilleumier, 1971) argued for merging *Muscigralla* with *Muscisaxicola* (the latter a bona fide member of my *Empidonax* assemblage; see below): "*Muscigralla* appears more closely related to *Muscisaxicola* than to any other taxon." But the similarities in external morphology and behavior between *Muscigralla* and *Muscisaxicola* might well be due to convergence in taxa that are highly terrestrial in habit, and Traylor (1977) was dubious of this alleged affinity: "I cannot see that *Muscigralla* has any close relatives; morphologically and anatomically it is not typical of the Fluvicolines. On the other hand, it is equally out of place in any other group . . . probably an early offshoot of the Fluvicoline stock, and I shall keep it at the end of that group with other aberrant genera." Fitzpatrick (*in* Traylor and Fitzpatrick, 1982) agreed with Vuil-

leumier that *Muscigralla* is "simply an extremely derived *Muscisaxicola* offshoot."

The nasal septum of *Muscigralla* (fig. 11: 1-4) has no suggestion of an anterior notch. There is a rather long and narrow trabecular plate that is elevated just above the ventral edge of the septum and is tapered gradually at its posterior end (not forked). There is nothing in the septum that would relate *Muscigralla* to my *Empidonax* assemblage. The syrinx (Lanyon, MS), though tyrannid with respect to the internal cartilages, is unlike the syringes of any of the genera in this assemblage. Thus, the position of *Muscigralla* remains enigmatic.

Machetornis

The monotypic *Machetornis* traditionally has been placed near the end of the fluvicolines, among a number of monotypic genera with no obvious close relatives. Warter (1965) reported the nasal septum to be type 6 like that of the fluvicolines. Fitzpatrick (1978) has argued that the striking plumage and behavioral similarities between *Machetornis* and *Tyrannus* (kingbirds) are not due to convergence, "but rather, they reflect phylogenetic affinities between the genera." He would place *Machetornis* with the kingbirds and their allies.

I have presented anatomical evidence (Lanyon, 1984b) that *Machetornis* cannot be a member of the kingbird assemblage. The nasal septum has a well-developed trabecular plate, lacking in all kingbirds and relatives, and this plate is tapered caudally (fig. 11: 7, 8). In previous remarks on the nasal septum of *Machetornis* (Lanyon, 1984b, p. 11) I erred in stating that the trabecular plate is "located along the ventral edge of the septum." In all 10 skulls examined, the plate is slightly elevated above the ventral edge, equivalent to the condition in Warter's type 5. This elevation of the plate is particularly evident at its anterior end, when the skull is viewed from the lateral aspect (fig. 11: 5, 6), but is also suggested by the presence of a sagittal ridge on the plate when the skull is viewed from the ventral aspect (fig. 11: 7, 8). This error was responsible for my premature identification of an anterior notch in the septum of *Machetornis*, when clearly there can be no

"notch" since the septum at that point is fully ossified and the trabecular plate is actually elevated above the ventral edge of the sep-

tum. The taxonomic position of *Machetornis* is still unclear, awaiting studies on other assemblages within the Tyrannidae.

PHYLOGENETIC RELATIONSHIPS WITHIN THE ASSEMBLAGE

An overview of syringeal morphology among the 33 genera admitted to my *Empidonax* assemblage reveals three basic types of syringes that differ in the degree to which the A elements provide support for each bronchus (fig. 12). These variants in morphology are more conservative than other aspects of syringeal evolution (e.g., size, form, and position of internal cartilages and of A and B elements) and therefore are useful in defining primary lineages within assemblages of tyrant flycatchers.

In the most simplified of these three types of syrinx, found only in six genera within the *Empidonax* assemblage, none of the A elements forms a complete ring around either of the bronchi. The paired A1 elements are incomplete medially, as they are in all flycatchers; the A2s connect directly to the tracheobronchial junction, or to the junction by way of the internal cartilages; consequently the internal tympaniform membranes extend all the way to this junction (character B in tables 1, 2, and figs. 12–14).

In all of the remaining genera in the assemblage, the A2 elements (and sometimes the A3s as well) are complete and form bronchial rings that are conspicuously independent of the tracheobronchial junction; the internal tympaniform membranes extend only as far as the medial segments of these bronchial rings, rather than to the junction (character C in fig. 13). With the evolution of the complete A2 elements, free from the tracheobronchial junction, the stage appears to have been set for the independent development of the other two basic types of syrinx. In one of these lineages, involving the majority of the genera in the assemblage, the A2 elements remain cartilaginous medially and there is a plug of tissue just caudal to the tracheobronchial junction (between the medial cartilaginous segments of the A2s) that stains weakly for cartilage (character D in fig. 12: 3, 4 and fig. 13). Ames (1971) reported the presence of a "cartilaginous plug" in a number of ty-

rant genera, most of which I have admitted to my *Empidonax* assemblage. It is questionable, however, that Ames and I are referring to the same structure in all cases, for I have not found this plug of tissue in any tyrant genus outside my *Empidonax* assemblage, nor in a number of the same specimens that Ames reported as having a plug. The lack of a stain for cartilage may have misled Ames in such instances. I regard the presence of this plug of tissue as an extremely useful derived character for establishing monophyly of 24 of the genera in this assemblage.

In the remaining three genera there is no plug of cartilaginous tissue between the medial segments of the A2s, and one or two A elements (usually A2 and A3, either fused or independently) form complete and calcified rings around the bronchi (character E in fig. 12: 5, 6 and fig. 13). I would argue that it is more likely that this third type of syrinx evolved from an ancestral form prior to the evolution of the plug of cartilaginous tissue that characterizes the second type of syrinx. To argue otherwise would require the subsequent loss of such a structure, a less parsimonious solution.

The phylogenetic diagram in figure 13 illustrates the application of this concept of the evolution of syringeal morphology to the reconstruction of the evolution of the entire *Empidonax* assemblage, and should be referred to as I discuss relationships among genera and clusters of genera.

The *Ochthoeca* Group (fig. 14 and table 2)

My *Ochthoeca* group is dominated numerically by *Ochthoeca* (including *Tumbesia*), and in addition includes *Arundinicola*, *Fluvicola*, *Alectrurus*, *Silvicultrix* (a new genus described below), and *Colorhamphus*. I have examined the skulls and syringes of all six genera. Of the 16 species, I lack skulls of *Alectrurus tricolor* and *Ochthoeca piurae*, and the syrinx of *Alectrurus tricolor*.

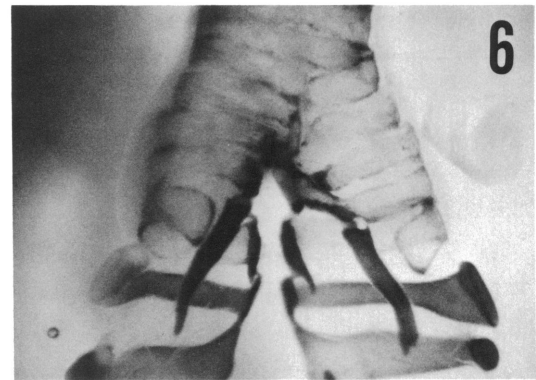
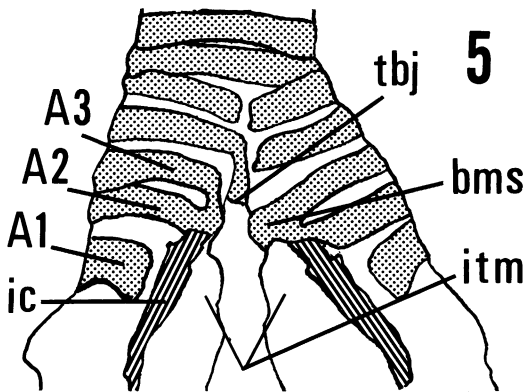
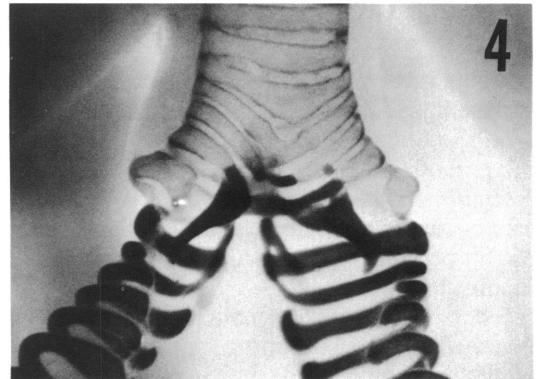
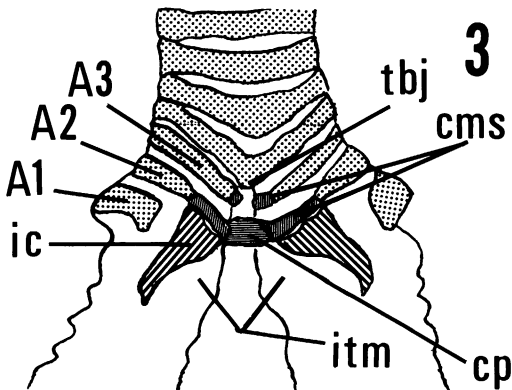
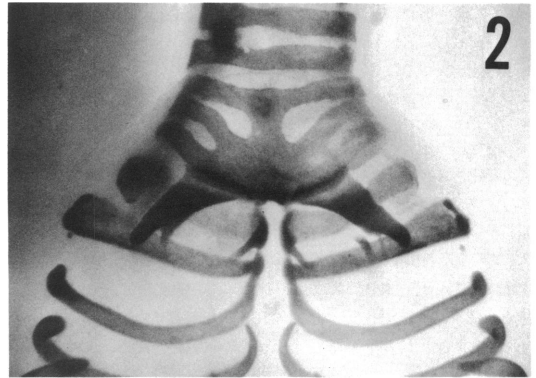
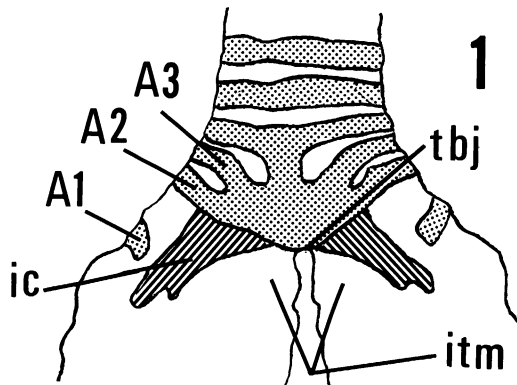


FIG. 12. Drawings and photographs of the three basic types of syringes in the *Empidonax* assemblage (dorsal aspect; magnification = 19×): (1, 2) Character B—no complete A ring around either bronchus (*Ochthoeca fumicolor*, AMNH 7890); (3, 4) Character D—plug of cartilaginous tissue just caudal to the tracheobronchial junction and between the cartilaginous medial segments of the A2 elements (*Knipolegus aterrimus*, AMNH 2455); (5, 6) Character E—one or two A elements form complete and calcified rings around the bronchi (*Myiophobus fasciatus*, LSU 102584). 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; cms = cartilaginous medial segment of complete bronchial A ring; cp = plug of cartilaginous tissue between the cartilaginous medial segments of the A2 elements; bms = calcified medial segment of complete bronchial A ring.

TABLE 1
 Characters Used for Phylogeny of the *Empidonax* Assemblage

	Character, description	Distribution by taxa
A	Nasal septum with anterior notch and based with trabecular plate that is forked posteriorly	All taxa in <i>Empidonax</i> assemblage
B	No complete A ring around either bronchus	<i>Ochthoeca</i> group
C	A2 element continues medially around each bronchus (with or without contribution from A3 element), independent of tracheobronchial junction	All taxa in assemblage other than <i>Ochthoeca</i> group
D	Plug of tissue (stains weakly for cartilage) just caudal to tracheobronchial junction and between cartilaginous medial segments of A2 elements	All taxa in assemblage other than <i>Ochthoeca</i> and <i>Myiophobus</i> groups
E	One or two A elements (usually A2 and A3, either fused or independently) form complete and calcified rings around each bronchus	<i>Myiophobus</i> group

Historically *Ochthoeca* and its closest relatives consistently have been considered members of the "bush tyrant" group (along with *Xolmis* and *Myiotheretes*) as a result of emphasis on shared external morphological characters, as well as ecological and behavioral traits (Sclater, 1888; Berlepsch, 1907; Zimmer, MS; Meyer de Schauensee, 1966; Smith and Vuilleumier, 1971; Traylor, 1977; Traylor and Fitzpatrick, 1982). However, Ames (1971) found enough differences in syringeal morphology to warrant the omission of *Ochthoeca* from his group containing *Xolmis* and relatives. My interpretation of the syrinx of *Ochthoeca* is that it indeed has evolved in significantly different ways from that of *Xolmis*, and my phylogeny reflects these differences.

Ames (1971) included *Fluvicola* in a group with the bush and ground tyrants (*Xolmis*, *Muscisaxicola*, etc.) on the mistaken belief that the syrinx of *Fluvicola* possesses a "cartilaginous plug." The single example that Ames examined was a poorly preserved and unstained Kaempfer specimen (AMNH 6781). When the three better preserved specimens at my disposal were stained for cartilage, I found no evidence of the plug of tissue that characterizes the syrinx of that large cluster of genera to which I assign *Xolmis*, *Muscisaxicola*, and their close relatives. As noted below, there are other important distinctions between the syrinx of *Fluvicola* and those of the bush and ground tyrants.

Fluvicola and *Arundinicola* generally have been placed near *Knipolegus* and its allies (Hellmayr, 1927; Zimmer, MS; Meyer de Schauensee, 1966; Traylor, 1977; Traylor and Fitzpatrick, 1982), with sexual dimorphism being the usual reason given. *Alectrurus* traditionally has been regarded as a close relative of *Colonia* and *Gubernetes*, on the basis of greatly modified tails (Hellmayr, 1927; Zimmer, MS; Meyer de Schauensee, 1966; Traylor, 1977) and Warter (1965) placed these three genera in a separate tribe on cranial characters.

A sister-group relationship between *Arundinicola*, *Fluvicola*, and *Alectrurus* on the one hand, and *Ochthoeca* and its closest allies on the other, has not been suggested in the literature. My basis for this unique clustering is the fact that these genera, and only these genera, share the first of the three basic types of syrinx described above, in which there are no complete A elements caudal to the tracheobronchial junction (character B in figs. 12–14; syringes illustrated in figs. 15 and 16). It seems improbable that this type of syrinx would have evolved independently among the 33 genera that share the nasal septum of the *Empidonax* assemblage.

Within my *Ochthoeca* group, the monotypic *Arundinicola*, the two species of *Fluvicola*, and the two species of *Alectrurus* appear to be a natural cluster on the basis of the nearly complete ossification of the nasal capsule, including the alinasal walls and tur-

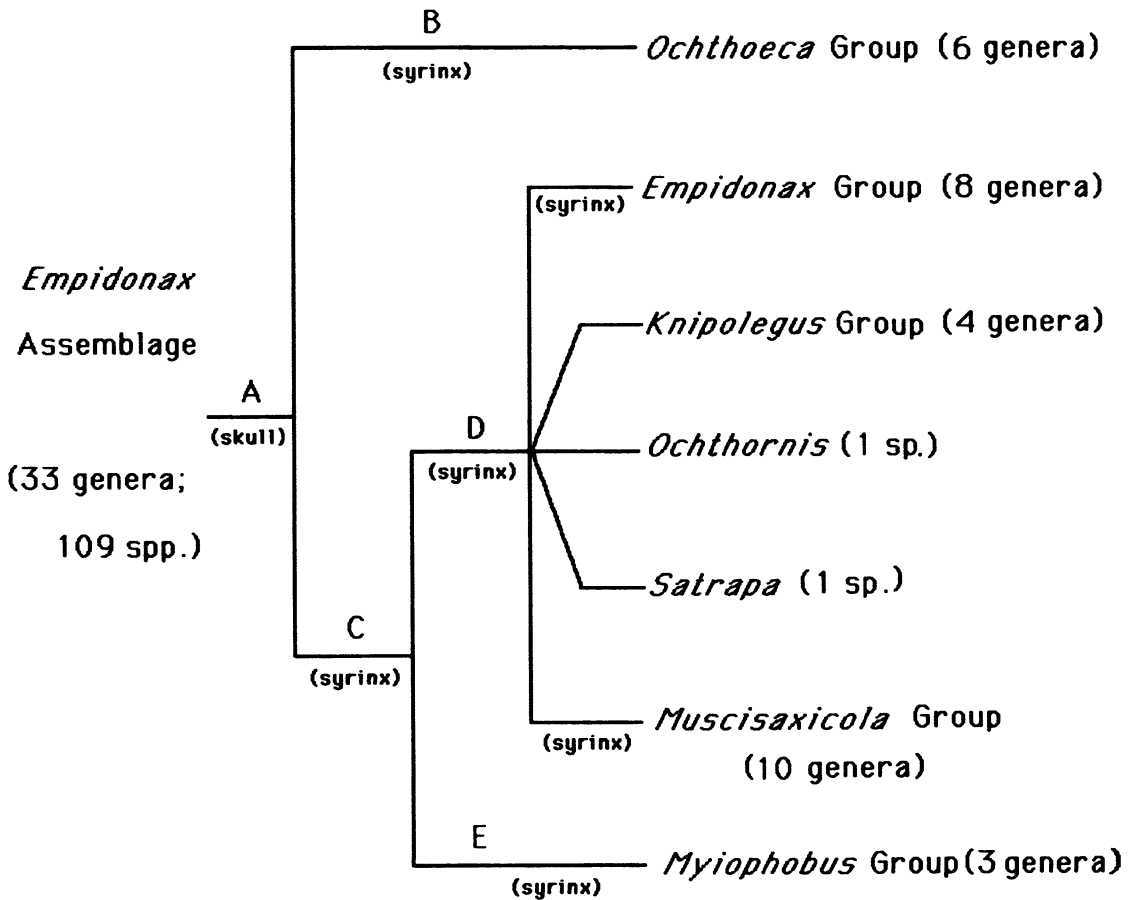


FIG. 13. Phylogenetic relationships within the *Empidonax* assemblage (33 genera; 109 species). Letters identify diagnostic character states described in text and in table 1. Monophyly determined by the sharing of derived states of the skull and the syrinx where indicated.

binals (character 2; fig. 5: 1, 6; fig. 7: 7, 8; fig. 15: 4). This is a derived character state that has evolved independently in only three other genera within the assemblage (*Lathrotricus*, *Heteroxolmis*, and *Gubernetes*). There is additional support for this grouping in the black and white or brown and white plumage (character 3) and the fact that all five species inhabit open marsh or grassland (character 4).

While the nest of *Alectrurus* is a neat cup built on the ground, like that of many other genera within the *Empidonax* assemblage (Gibson, 1885; Hudson, 1920), the nest of *Arundinicola* and *Fluvicola* is unique within the entire assemblage—an enclosed, untidy,

ball-shaped nest over or near water (character 5; AMNH collection; Cherrie, 1916; Hudson, 1920; Young, 1925; Naumburg, 1930; Delacour, 1935; Mitchell, 1957; Herklots, 1961; Haverschmidt, 1968; Wetmore, 1972; French, 1976). Traylor (1977) argued that the two genera be merged under the oldest name, *Fluvicola*, but Fitzpatrick (1978) favored the retention of *Arundinicola* “as a morphologically and behaviorally distinct, monotypic genus.” I believe a strong argument *can* be made for maintaining the two as separate genera, based on differences in syringeal morphology (fig. 15), degree of sexual dimorphism in plumage coloration, and on differences in pigmentation of the eggs. The internal

TABLE 2
 Characters Used for Phylogeny of the *Ochthoeca* Group

Character, description	Distribution by taxa
B No complete A ring around either bronchus	All taxa in <i>Ochthoeca</i> group
2 Alinasal walls and turbinals ossified	<i>Arundinicola</i> , <i>Fluvicola</i> , and <i>Alectrurus</i>
3 Black and white/brown and white plumage	As above
4 Inhabit marsh or grassland	As above
5 Enclosed, untidy, ball-shaped nest over or near water	<i>Arundinicola</i> and <i>Fluvicola</i>
6 Internal cartilages oriented nearly parallel with each other	<i>Arundinicola</i>
7 Greater degree of sexual dimorphism in plumage coloration and pattern	<i>Arundinicola</i>
8 Eggs unmarked	<i>Arundinicola</i>
9 Internal cartilages flared out laterally, forming an angle greater than 90°	<i>Fluvicola</i>
10 Ossification of the tracheobronchial junction, as well as parts of internal cartilages and B elements	<i>Fluvicola</i>
11 B2 elements rounded ventrally and not attached to B1s	<i>Fluvicola</i>
12 Trabecular plate very narrow	<i>Alectrurus</i>
13 Large membranous area between A1 and B1 elements	<i>Alectrurus</i>
14 Highly modified rectrices	<i>Alectrurus</i>
15 White, yellow, or cinnamon frontal and/or superciliary regions (lost in <i>Colorhamphus</i>)	<i>Silvicultrix</i> and <i>Ochthoeca</i>
16 Triangle of cartilage between and around A elements on dorsomedial surface of the syrinx	<i>Silvicultrix</i>
17 Internal cartilages linear and narrowly attached to cartilage along dorsomedial extension of the A2s	<i>Silvicultrix</i>
18 Transverse trabecular plate constricted and narrow medially	<i>Silvicultrix</i>
19 Enclosed, pensile nest and unmarked eggs (all species?)	<i>Silvicultrix</i>
20 A elements calcified and more or less fused into a drum	<i>Ochthoeca</i> and <i>Colorhamphus</i>
21 Internal cartilages triangular and broadly attached to dorsomedial edge of drum	As above
22 Dorsal ends of A1s very broad	<i>Colorhamphus</i>
23 B2s attached to B3s as well as to B1s	<i>Colorhamphus</i>
24 Loss of superciliary line	<i>Colorhamphus</i>

cartilages of *Arundinicola* are virtually parallel (character 6), while those in *Fluvicola* are flared out laterally, forming an angle between them greater than 90° (character 9). In *Fluvicola* there is extensive ossification of the supporting elements of the syrinx (character 10), including the entire tracheobronchial junction and substantial portions of the internal cartilages and of the B elements. Furthermore, the B2 elements in *Fluvicola* are rounded ventrally and not attached to the ventral ends of the B1s (character 11) as they are in *Arundinicola* and most genera within the assemblage. These differences in syringeal morphology far exceed intragenetic variation among tyrant flycatchers.

There is a greater degree of sexual dimorphism in the plumage of *Arundinicola*, with

the female lacking the intense deposits of melanin throughout the plumage except for the tail but introducing melanin on the crown and nape where the male has pure white feathering (character 7). Though both *Arundinicola* and *Fluvicola* evolved an enclosed type of nest, *Arundinicola* has lost the markings on the eggs (character 8) while the eggs of both species of *Fluvicola* are speckled or spotted with brown as is typical of most species in this assemblage (AMNH and WFVZ collections; Oates and Reid, 1903; Hudson, 1920; Young, 1925; Naumburg, 1930; Delacour, 1935; Herklots, 1961; Haverschmidt, 1968; French, 1976).

Ames (1971) reported a *second* pair of internal cartilages in *Arundinicola*, but these are merely small cartilaginous projections from

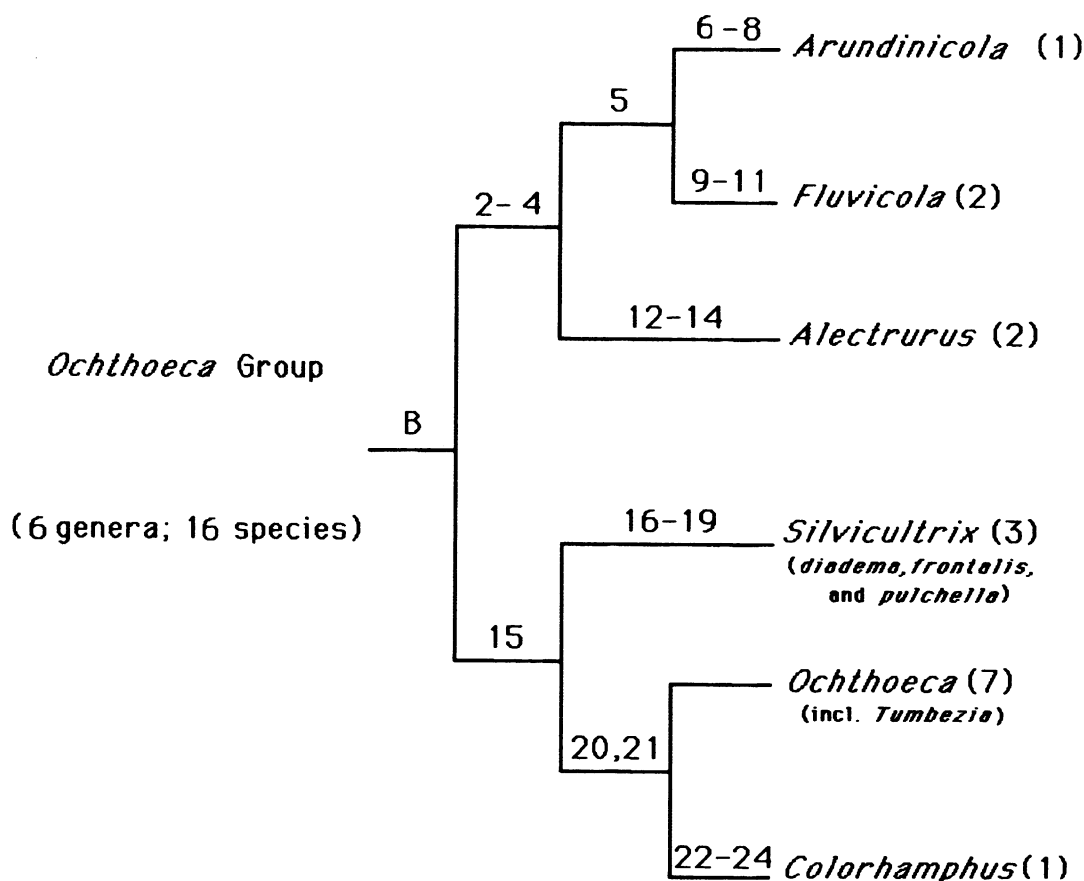


FIG. 14. Phylogenetic relationships within the *Ochthoeca* group (6 genera; 16 species). Numbers identify diagnostic character states described in text and in table 2. Numbers in parentheses indicate number of species per genus.

the ventral ends of the A1 elements, present in most tyrant syringes and not comparable to the second pair of cartilages that occurs, for example, in the myiarchine flycatchers (Lanyon, 1985).

I accept the suggestion by Short (1975) and Traylor (1977) that the monotypic *Yetapa* and *Alectrurus* be merged, even though I have yet to see anatomical specimens of *A. tricolor*. Warter's (1965) suggestion that *Alectrurus* (*Yetapa*) *risora* is closely related to *Colonia* and *Gubernetes* is not supported by my sample of skulls, which includes the LSU material that he worked with. The trabecular plate of *risora* is extremely narrow (character 12; fig. 5: 1), unlike that of any other species in the assemblage (see the skull of *Gubernetes* in fig. 6: 1, 2). But the nasal capsule of *Alectrurus*

risora meets all the criteria in my diagnosis of the *Empidonax* assemblage, whereas I have already argued that *Colonia* does not belong in this assemblage (see the skull of *Colonia* in fig. 10: 8). *Alectrurus risora* further differs from the other species in my *Ochthoeca* group in that the membranous area between the A1 and B1 elements in the syrinx is very large (character 13; fig. 15: 3). I see no evidence of a cartilaginous plug in the syrinx of *risora*, as reported by Ames (1971), though we examined the same specimen (the only one extant, apparently). The cartilaginous plug is restricted in my sample of syringes to those members of the assemblage that share another basic type of syrinx (my character D in figs. 12 and 13). I would argue that the highly modified rectrices of *Alectrurus* (character 14) are a good

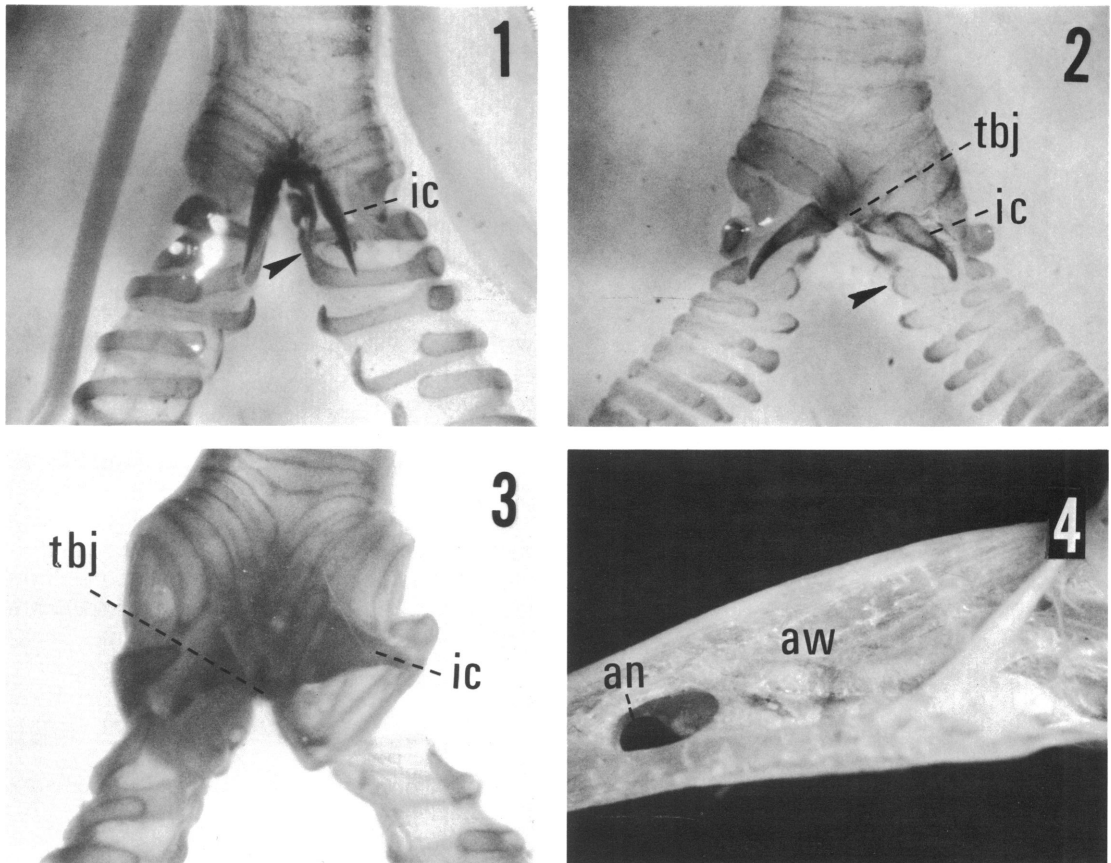


FIG. 15. Syringes of (1) *Arundinicola leucocephala*, CM 1344, (2) *Fluvicola pica*, AMNH 11603, and (3) *Alectrurus risora*, USNM 227318 (dorsal aspect; magnification = $15\times$); skull of (4) *Alectrurus risora*, UMMZ 158768 (lateral aspect; magnification = $7.5\times$). Arrows indicate configuration of ventral end of B2 element; internal cartilages (ic) narrow in *Arundinicola* and *Fluvicola* and broadly triangular in *Alectrurus*; tbj = tracheobronchial junction; aw = alinasal wall.

generic character but have evolved independent of other fancy-tailed tyrants.

Nine of the remaining 11 species in my *Ochthoeca* group were assigned to the genus *Ochthoeca* by Hellmayr (1927) and Traylor (1979). There has been little agreement as to the affinities of *Tumbezia salvini* and *Colo-rhamphus parvirostris*, and they will be given special attention below. Except for *parvirostris*, in which the character has presumably been lost, all of these remaining species have white, yellow, or cinnamon frontal and/or superciliary regions (character 15).

Three of the nine species traditionally assigned to *Ochthoeca* are largely forest dwellers and have been treated as members of a species group (Smith and Vuilleumier, 1971;

Fitzpatrick, 1973; Traylor, 1985): *diadema*, *frontalis*, and *pulchella*. Though the syrinx in these three species has the same general configuration as that in the other genera in this group (i.e., character B), it does not show the derived character states found exclusively in other *Ochthoeca*, as discussed below, and there are derived character states (the form of the nest and of the nasal septum) that set these species apart from other *Ochthoeca*. These differences are the basis for assigning these three species to a new genus.

Silvicultrix, new genus

TYPE SPECIES: *Myiobius diadema* Hartlaub (1843, p. 289)—New Grenada; restricted to

"Bogotá" by Hellmayr (1927, p. 53); Paris Museum.

INCLUDED SPECIES: The type species, plus *Tyrannula frontalis* Lafresnaye (1847, p. 70) and *Ochthoeca pulchella* Sclater and Salvin (1876, p. 355).

DISTRIBUTION: Subtropical and temperate zones of northern and western South America, from the coastal range of Venezuela to western Bolivia; see more detailed range for the three species in Traylor (1979).

ETYMOLOGY: From the Latin (feminine gender), meaning one who inhabits woods, in acknowledgment of the widely reported preference of these three species for a woodland habitat, in contrast to most *Ochthoeca*.

DIAGNOSIS: Separable from *Ochthoeca* and *Colorhamphus* by plumage characteristics, syringeal morphology, nesting behavior (all three species?), and morphology of the nasal septum.

All populations of *Silvicultrix* have a yellow frontal region, except for those of the Eastern Andes of Colombia, in which this region of the plumage is white as in most *Ochthoeca* (*Tumbezia salvini*, included within *Ochthoeca* here, has a yellow frontal region but has lemon-yellow underparts and white wing bars and outer webs of the outer rectrices).

The syringes of the three species of *Silvicultrix* differ from those of *Ochthoeca* with respect to two characters (fig. 16): (1) there is much cartilage between and around the A elements in a triangular area located on the dorsomedial surface of the syrinx (character 16), which is unique within the assemblage, and (2) the internal cartilages are linear, rather than triangular as in *Ochthoeca*, and are rather narrowly attached to cartilage along the dorsomedial extension of the A2s (character 17).

When I examined the nasal septa of *diadema*, *frontalis*, and *pulchella*, I found the trabecular plates to be constricted and narrow in the region just anterior to the posterior forking (character 18), a character not associated with the skulls of *Ochthoeca* (compare fig. 5: 3 with fig. 6: 8).

Morris D. Williams (personal commun.) has translated Stolzmann's description of the nest of *diadema* (as published by Taczanowski, 1879, 1884): "The nest has the shape of an elongated pear; the entrance is on the

underside, slightly to one side . . . constructed entirely of moss . . . lined with feathers." References to the nests of *Ochthoeca* species (Todd and Carriker, 1922; Smith and Vuilleumier, 1971; Vuilleumier and Ewert, 1978; Williams, personal commun.) suggest that the nest form for the two or three species for which there are published records is an open cup, sometimes placed in niches. Taczanowski's description (fide Williams) of the immaculate egg of *diadema* is in agreement with the description of an unmarked *diadema* egg in Oates and Reid (1903), and in contrast to reports and photographs of the marked eggs of *Ochthoeca* and *Colorhamphus* (WFWZ collection; Oates and Reid, 1903; Zotta, 1939; A. W. Johnson, 1967; Williams, personal commun.). I know of no published references to the nesting biology of *frontalis* and *pulchella*. Clearly the enclosed, pensile nest and unmarked eggs (character 19) of *diadema* are derived nesting characters that should be examined carefully for the other two species in this genus, and borne in mind as information becomes known on other species of *Ochthoeca*.

The remaining two genera in this group, *Ochthoeca* and the monotypic *Colorhamphus*, cluster together by having the A elements completely calcified and more or less fused into a drum (character 20; fig. 16: 3–8), and by having internal cartilages triangular in shape and broadly attached to the dorsomedial edge of that drum (character 21; fig. 16: 3–8). As noted above, the species in these two genera, so far as known, lay eggs that are speckled or blotched with reddish brown, unlike the unmarked eggs of *Silvicultrix*.

My referral of *Tumbezia salvini* to *Ochthoeca* requires further comment. *Salvini* was originally described in *Ochthoeca* (Taczanowski, 1877). It was Chapman (1925) who established the new genus *Tumbezia*: "It has no near relationship to *Ochthoeca* . . . nor, indeed, to any described genus." As Williams (personal commun.) has observed, it is not clear what characters Chapman considered to be of value in separating his new genus from *Ochthoeca*: "In view of the fact that the characters given by Chapman do not consistently separate *salvini* from other *Ochthoeca*, *Tumbezia* should either be redefined, or Taczanowski's generic allocation should stand."

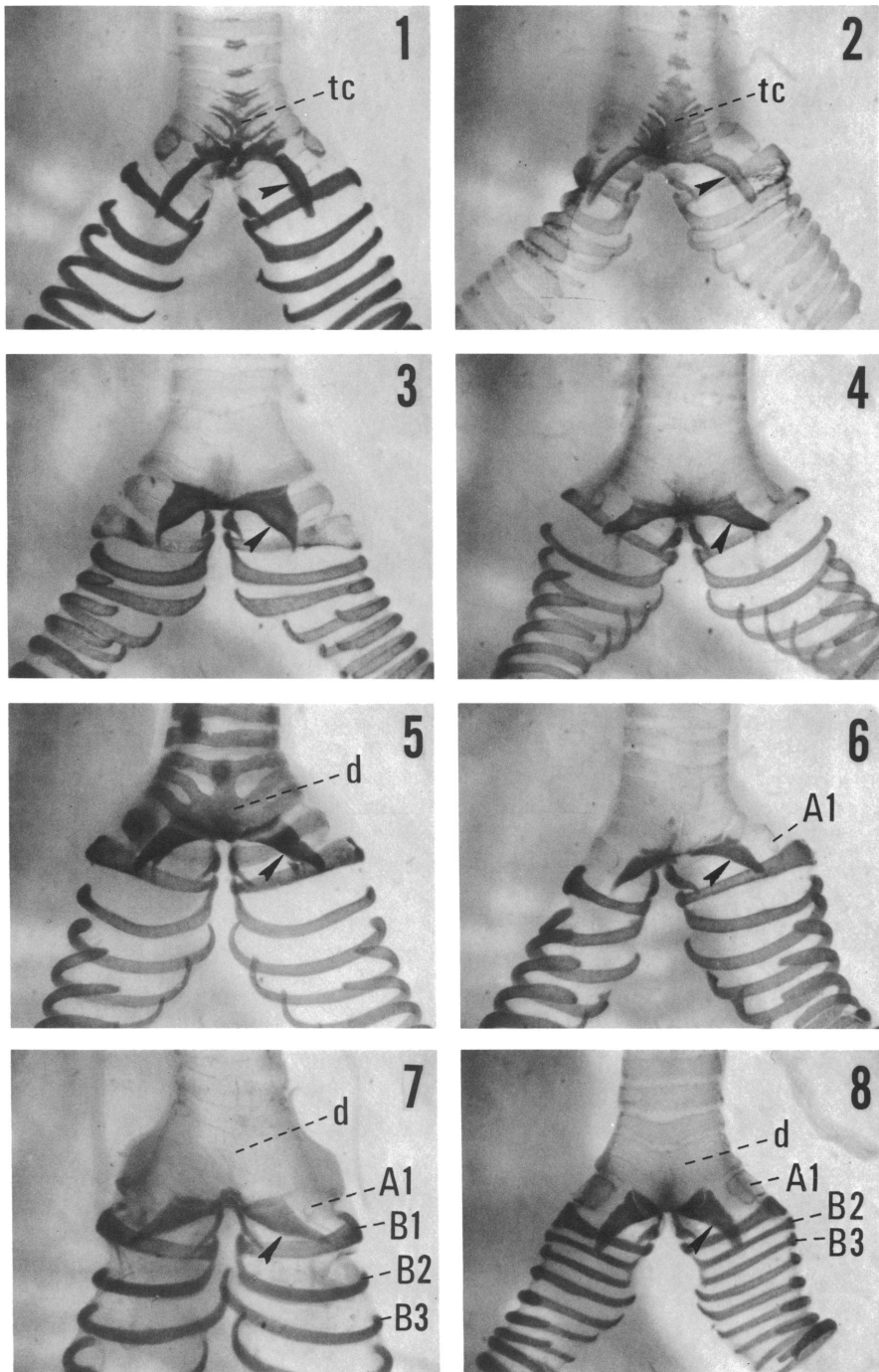


FIG. 16. The syringes of three genera within the *Ochthoeca* group (dorsal aspect; magnification = 12 \times): (1) *Silvicultrix diadema*, LSU 112842; (2) *S. frontalis*, LSU 102529; (3) *Ochthoeca cinnamo-meiventris*, LSU 104351; (4) *O. rufipectoralis*, LSU 102491; (5) *O. fumicolor*, AMNH 7890; (6) *O. piurae*, LSU 97546; (7) *O. salvini*, LSU 91523; (8) *Colorhamphus parvirostris*, USNM 511875. Arrows indicate internal cartilages (linear in *Silvicultrix*, 1–2; triangular in *Ochthoeca*, 3–8); A and B elements as indicated; d = drum resulting from fusion of calcified A elements; tc = triangle of dark-staining cartilage between and around the A elements that characterizes *Silvicultrix*.

Vuilleumier (in Smith and Vuilleumier, 1971) believed *Tumbezia* to be "closely related to, or even possibly congeneric with *Ochthoea*." Traylor (1977) regarded *Tumbezia* as monotypic and placed it more or less incertae sedis, along with other enigmatic genera such as *Satrappa* and *Muscigralla*.

The syrinx of *salvini* (fig. 16: 7) is not separable in any way from the highly derived and unique syrinx of the six traditional species of *Ochthoea* (fig. 16: 3–6). Once *diadema*, with its unusual pensile nest and unmarked eggs, is removed from the data set available for the known nests of *Ochthoea*, we are left with the concept of an *Ochthoea* nest as being an open cup, usually placed in bushes or trees but sometimes in grass in or near the ground (Todd and Carriker, 1922; Smith in Smith and Vuilleumier, 1971; Williams, personal commun.). Williams (personal commun.) reports that the typical cup nests of *salvini* are saddled on a branch about 5 m aboveground and composed of fine grasses and lined with feathers. The eggs are cream colored and marked with large blotches (more numerous at the larger end) of various shades of lavender, reddish-brown, and brown, not unlike the other known eggs of *Ochthoea* spp. There is nothing in Williams' thorough report on *salvini* that is incompatible with the concept of a merger of *salvini* with *Ochthoea*. I recommend returning *salvini* to its original genus.

There was uncertainty among earlier systematists as to the affinities of *Colorhamphus parvirostris*. Sclater (1888) had assigned it to *Serpophaga*, in a different subfamily from his Taeniopterinae (=Fluvicolinae). Hellmayr (1927) commented: "I fully agree with Ridgway . . . in considering this genus as perfectly distinct from *Serpophaga*. In coloration, the genotype (and only known species) shows some analogy to the members of the genus *Ochthoea* to which it was actually referred by the late Count Berlepsch." Zimmer (MS) and Meyer de Schauensee (1966) maintained it near *Serpophaga* and *Elaenia*. Vuilleumier (in Smith and Vuilleumier, 1971) believed *parvirostris* to be "closely related to, or even possibly congeneric with, *Ochthoea*." Traylor (1977) merged *Colorhamphus* with *Ochthoea*: "*Colorhamphus parvirostris* has been kept in the Serpophaginae (now Elaeni-

inae), but it also appears to be a dulled *Ochthoea*."

As Traylor (1977) remarked, examination of the skull (heretofore unavailable in collections) would settle unequivocally the question of the affinity of *Colorhamphus* with *Ochthoea* or with the Elaeniinae. Thanks to the cooperation of John W. Fitzpatrick of the Field Museum of Natural History, I was able to have a FMNH alcoholic specimen converted to a skeleton (after removal of the syrinx). The nasal septum of *Colorhamphus* has an anterior notch and is based by a trabecular plate that is forked posteriorly, and thus is indistinguishable from that of *Ochthoea* and most other genera within the *Empidonax* assemblage.

The sharing of derived syringeal morphology (characters 20 and 21, discussed above) is compelling support for the close relationship of *Colorhamphus* and *Ochthoea*. However, the syrinx of *Colorhamphus* (fig. 16: 8) differs from that of *Ochthoea* in two significant features that exceed intrageneric variation in syringeal morphology among tyrant flycatchers: the dorsal ends of the A1 elements are very broad (character 22), and the B2s are attached ventrally to the B3s as well as to the B1s (character 23). In addition, as noted above, *Colorhamphus* presumably has lost the superciliary line (character 24) that characterizes *Ochthoea* and *Silvicultrix*. I think it prudent to retain *Colorhamphus* and *Ochthoea* as separate genera.

The *Empidonax* Group (fig. 17 and table 3)

My *Empidonax* group is dominated numerically by two large genera, *Empidonax* and *Contopus*, and in addition includes *Cnemotriccus*, *Aphanotriccus* (including *Praedo*), *Lathrotricus* (a new genus to which "*Empidonax*" *euleri* has been assigned; see Lanyon and Lanyon, 1986), *Xenotriccus* (including *Aechmolophus*), *Sayornis*, and *Mitrephanes*. I have examined the skulls and syringes of all eight genera. Of the 37 species, I lack skulls of four (*Aphanotriccus capitalis*, *Contopus albobularis*, *C. ochraceus*, and *Empidonax griseipectus*) and syringes of four (*Contopus albobularis*, *C. ochraceus*, *C. nigrescens*, and *Empidonax griseipectus*).

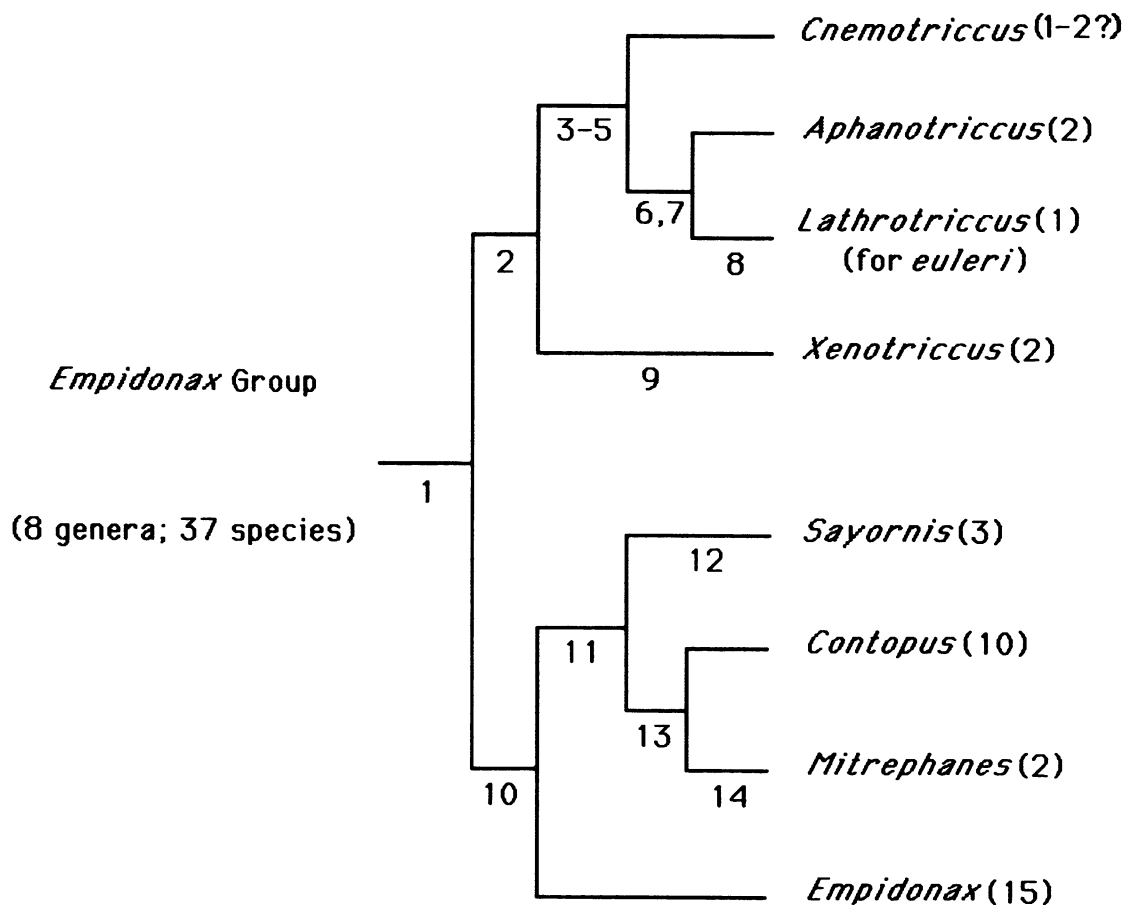


FIG. 17. Phylogenetic relationships within the *Empidonax* group (8 genera; 37 species). Numbers identify diagnostic character states described in text and in table 3. Numbers in parentheses indicate number of species per genus.

The clustering of these eight genera will not surprise ornithologists who are familiar with these birds. An earlier practice of maintaining *Sayornis* apart from the other genera and placing it nearer to *Ochthoeca* (Hellmayr, 1927; Zimmer, MS; Meyer de Schauensee, 1966) was remedied to some extent with the merger of Hellmayr's Fluvicolinae with part of his Myiarchinae (Warter, 1965; Traylor, 1977). Yet, Vuilleumier (*in* Smith and Vuilleumier, 1971) continued to support a close relationship between *Sayornis* and *Ochthoeca*, and Traylor and Fitzpatrick (1982) listed *Sayornis* as "transitional" between their "*Empidonax*" group and their "ground-tyrant" group (headed by *Ochthoeca*), reflecting this notion that *Sayornis* is somewhat differ-

ent from *Empidonax* and its allies. Ames (1971) included *Contopus*, *Sayornis*, *Empidonax*, *Aechmolophus*, and *Aphanotriccus* in his "*Nuttallornis*" group, on the basis of syringeal morphology, and reported that *Mitrephanes* "is like *Nuttallornis*." Webster (1968) and Traylor (1977) argued that *Pyrrhomyias* belongs here as well, but I present evidence below indicating that *Pyrrhomyias* is a close relative of *Hirundinea* and a member of my *Myiophobus* group.

The syringeal evidence for the close relationship of these eight genera is in the modifications of the cartilaginous segments of the A2 elements that are unique among tyrant flycatchers and provide for attachment of the internal cartilages. The first stage of this evo-

TABLE 3
 Characters Used for Phylogeny of the *Empidonax* Group

Character, description	Distribution by taxa
1 Cartilaginous segments of A2s modified for attachment of internal cartilages	All taxa in <i>Empidonax</i> group
2 Cartilaginous segments of A2s enlarged caudally but continuous (and in straight line) with calcified A2s	<i>Cnemotriccus</i> , <i>Aphanotriccus</i> , <i>Lathrotriccus</i> , and <i>Xenotriccus</i>
3 Adult plumage with rufous wing bars	<i>Cnemotriccus</i> , <i>Aphanotriccus</i> , and <i>Lathrotriccus</i>
4 Nests located in crevices and cavities in trees	<i>Cnemotriccus</i> , <i>Aphanotriccus</i> (?), and <i>Lathrotriccus</i>
5 Derived states of six protein coding loci	<i>Cnemotriccus</i> , <i>Aphanotriccus</i> , and <i>Lathrotriccus</i>
6 Presence of calcified nodule on lateral surface of each A1 and A2, with cartilaginous connection between them	<i>Aphanotriccus</i> and <i>Lathrotriccus</i>
7 Two synapomorphic allozymes	<i>Aphanotriccus</i> and <i>Lathrotriccus</i>
8 Nasal capsule ossified (incl. alinasal walls and turbinals)	<i>Lathrotriccus</i>
9 Pointed, prominent crest	<i>Xenotriccus</i>
10 Cartilaginous segments of A2s modified into broad, transverse cartilages at oblique angle to, and barely if at all connected with, dorsal ends of calcified A2s	<i>Sayornis</i> , <i>Contopus</i> , <i>Mitrephanes</i> , and <i>Empidonax</i>
11 Nests typically "saddled" on limb, ledge, beam, or similar substrate	<i>Sayornis</i> , <i>Contopus</i> , and <i>Mitrephanes</i>
12 Use of mud in nest foundation (being lost in <i>saya</i> ?)	<i>Sayornis</i>
13 Principal mode of foraging is aerial hawking and returning to same perch	<i>Contopus</i> and <i>Mitrephanes</i>
14 Pointed, prominent crest (derived independently from 9)	<i>Mitrephanes</i>

lution, in what I presume to be a transformation series, is the syringeal configuration that I designated as character C (fig. 13) in my overview of the basic types of syrinx in the assemblage: the A elements are complete and form bronchial rings that are conspicuously independent of the tracheobronchial junction. In the lineage leading to the majority of the remaining genera in the assemblage, these complete A2 elements have medial segments that remain cartilaginous and the syrinx acquires a plug of tissue (between the medial cartilaginous segments of the A2s) that stains weakly for cartilage (character D in figs. 12 and 13). In my *Empidonax* group the cartilaginous segments of the A2s are modified, presumably for the attachment of the internal cartilages (character 1; fig. 17). This modification may take the form of a bulbous enlargement on the caudal surface of the cartilaginous segment of the A2 element, which remains firmly connected to and in a straight line with the calcified A2 (character 2; fig. 17). This greatly altered configuration of the cartilaginous A2 is found in the sy-

ringes of *Cnemotriccus*, *Aphanotriccus*, *Lathrotriccus*, and *Xenotriccus* (fig. 18). In the remaining genera of the *Empidonax* group (*Sayornis*, *Contopus*, *Mitrephanes*, and *Empidonax*) the enlarged cartilaginous segment of the A2 element is modified into a broad, transverse cartilage that is displaced caudally to a point where it lies at an oblique angle to the dorsal end of the calcified A2 and is barely if at all connected to that element (character 10, fig. 17; syringes illustrated in figs. 19 and 20).

Relationships among the four genera that share the syringeal character 2 (fig. 17) have been discussed in detail elsewhere (Lanyon and Lanyon, 1986). In that study additional evidence for the clustering of *Cnemotriccus*, *Aphanotriccus*, and *Lathrotriccus* was drawn from the presence of rufous wing bars in the adult plumage (character 3), the placement of nests in crevices and cavities of trees (character 4), and the sharing of uniquely derived character states of six protein coding loci (character 5). An earlier recommendation from an electrophoretic study by Zink and

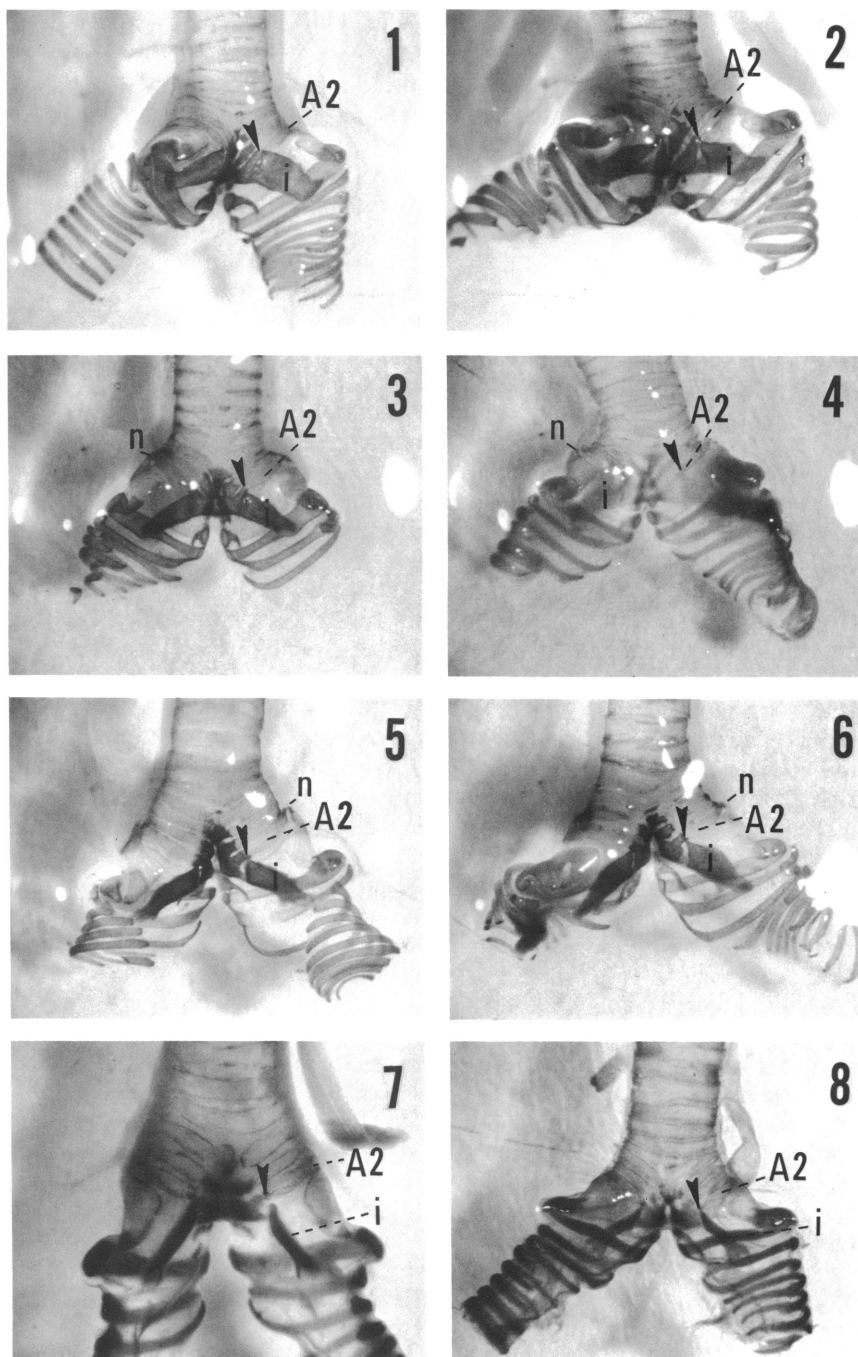


FIG. 18. The syringes of four genera that cluster within the *Empidonax* group (dorsal aspect; magnification = 9×): (1) *Cnemotriccus fuscatus*, LSU 114499; (2) *C. fuscatus*, USNM 505993; (3) *Aphanotriccus audax*, LSU 108499; (4) *A. capitalis*, AMNH 8244; (5) *Lathrotriccus euleri*, LSU 102573; (6) *L. euleri*, LSU 102571; (7) *Xenotriccus mexicanus*, ROM 109631; (8) *X. mexicanus*, AMNH 8789. Calcified A2 elements as labeled; i = internal cartilage; n = nodule on lateral surface of A1; arrows indicate straight connection between enlarged cartilaginous segment (medial) and calcified segment of A2.

Johnson (1984) that *euleri* be removed from its traditional place in *Empidonax* was supported by syringeal and additional biochemical evidence, leading to the proposal of a new genus, *Lathrotriccus*, for that widespread South American tyrant. Lanyon and Lanyon (1986) further argued for a sister-group relationship between *Lathrotriccus* and *Aphanotriccus* as a result of the sharing of a uniquely derived syringeal structure (character 6; fig. 18) and two synapomorphic allozymes (character 7), and on the comparatively low genetic distance between them. In *Lathrotriccus* the nasal capsule is virtually completely ossified, including the alinasal walls and turbinates (character 8; fig. 5: 7 and fig. 7: 5), while the nasal capsule of *Aphanotriccus* lacks this degree of ossification and appears like that of *Cnemotriccus*, illustrated in figure 4: 4, that of *Contopus* in figure 4: 6, and that of all of the capsules of *Empidonax* illustrated in figures 2 and 3. *Lathrotriccus euleri* is the only species in my *Empidonax* group that has this fully ossified condition.

Hellmayr (1927) reluctantly included *poecilurus* in *Cnemotriccus*, and added in a footnote that it differs from *C. fuscatus* "by more rounded wing, relatively shorter tail, and peculiar color pattern." Zimmer (1937) referred *poecilurus* to *Knipolegus* on the basis of external morphology, and Traylor (1979) concurred. Syringeal morphology is consistent with the referral of *poecilurus* to *Knipolegus*; it will be discussed in greater detail under my *Knipolegus* group.

Xenotriccus (including *Aechmolophus*) appears to represent a separate lineage among the four genera that share character 2. Its wing bars are white, as they are in the adults of most of the species in the *Empidonax* assemblage, its nesting behavior is of the more generalized type, and it differs from the other three genera in possessing a very prominent, pointed crest (character 9).

As noted above, the remaining four genera (*Sayornis*, *Contopus*, *Mitrephanes*, and *Empidonax*) possess a structure that I have labeled the transverse cartilage, unique among all tyrant flycatchers (character 10; syringes illustrated in figs. 19 and 20). In a few specimens the calcified A2 remains barely attached but at an oblique angle to the transverse cartilage. The medial, cartilaginous

segment of the A3 usually connects with the transverse cartilage, also at an oblique angle, but in a few specimens may continue around the medial wall of the bronchus, completing the A3 bronchial ring and without connection with the transverse cartilage. In most specimens, representing all four genera, the transverse cartilage is displaced caudally to such a degree that there is no connection between the dorsal end of the calcified A2 and the transverse cartilage. In this typical condition the internal cartilages are connected by thin cartilage to both the dorsal end of the calcified A2 and to the dorsocaudal corner of the transverse cartilage.

So similar are the syringes of *Sayornis*, *Contopus*, *Mitrephanes*, and *Empidonax* that identification to genus on the basis of syringeal morphology is not possible. This is reminiscent of the lack of evolution in syringeal morphology within the myiarchine assemblage (Lanyon, 1985): *Myiarchus*, *Sirystes*, *Casiornis*, and *Rhytipterna* can not be identified by syringeal characters alone. Likewise among the kingbirds and their allies (Lanyon, 1984b), syringeal characters fail to distinguish between *Tyrannus* and *Empidonomus*, and between *Myiodynastes* and *Conopias*.

Derived patterns of nesting and foraging behavior, though not completely satisfactory, represent the best characters available for determining relationships among these four genera. The nests of *Sayornis*, *Contopus*, and *Mitrephanes* typically are "saddled" on a limb, forking branch, ledge, or construction beam (character 11; AMNH collection; Bent, 1942; Skutch, 1960, 1967; Herklots, 1961; Rowley, 1962, 1966; Bond, 1971; Harrison, 1975, 1979; French, 1976). The nesting habits of *Empidonax* are more generalized, for most species normally build nests that are suspended "hammock-like" or supported in upright forks or crotches (AMNH collection; Bent, 1942; Dickerman, 1958; Stein, 1958; Rowley, 1962, 1963; N. K. Johnson, 1963; Alvarez del Toro, 1965; Harrison, 1975, 1979). This genus is large and successful, however, and has undergone considerable evolution that partially obscures any basic dichotomy in nest placement: *E. difficilis* and *E. flavescens* place their nests in a niche on a tree trunk, on a mossy ledge, or even on a beam of a building (Carriker, 1910; Dickey

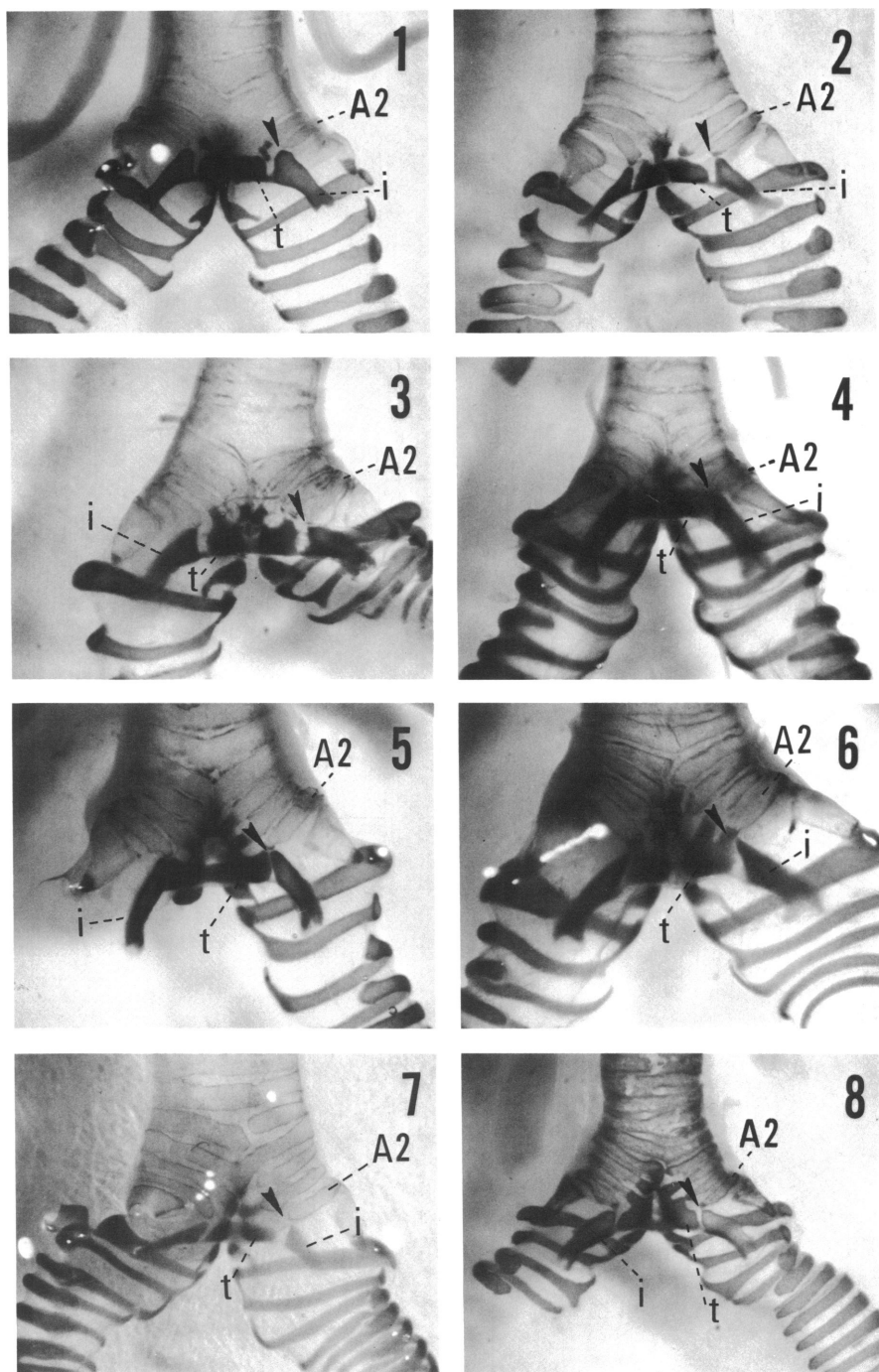


FIG. 19. The syringes of three genera that cluster within the *Empidonax* group (dorsal aspect; magnification = 12 \times): (1) *Sayornis nigricans*, PMNH 4695; (2) *S. phoebe*, AMNH 8199; (3) *Contopus cinereus*, LSU 102566; (4) *C. latirostris*, ROM 111691; (5) *C. virens*, UK 45187; (6) *C. fumigatus*, AMNH 8585; (7) *C. borealis*, LSU 103450; (8) *Mitrephanes olivaceus*, LSU 108479. Calcified A2 elements as labeled; i = internal cartilage; t = transverse cartilage; arrows indicate oblique angle between transverse cartilage and calcified A2 element.

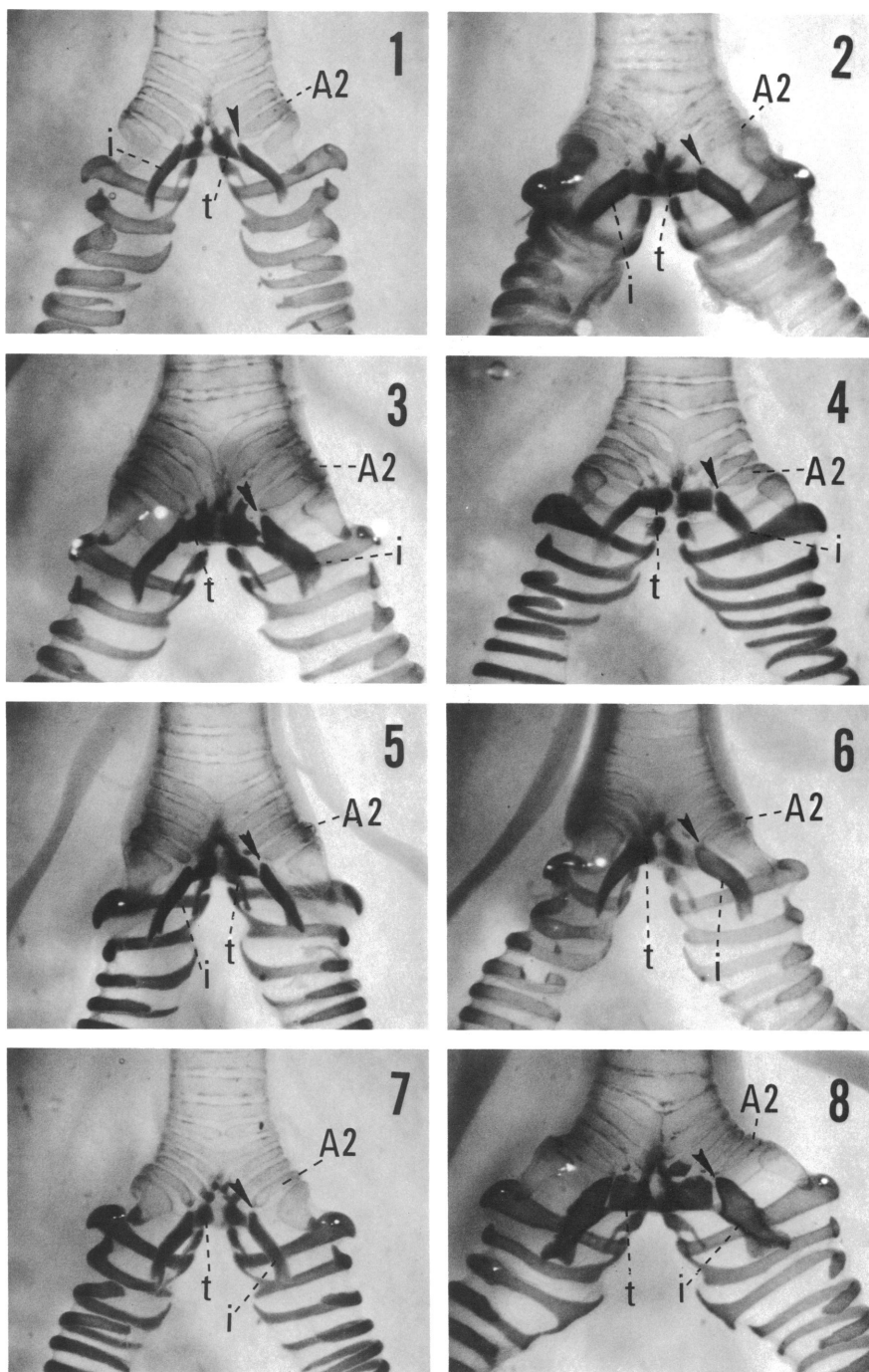


FIG. 20. Intrageneric variation in the syringes of eight species of *Empidonax* (dorsal aspect; magnification = 12×): (1) *E. minimus*, AMNH 8217; (2) *E. alnorum*, AMNH 12873; (3) *E. wrightii*, UK 51239; (4) *E. flaviventris*, AMNH 6770; (5) *E. oberholseri*, UK 51240; (6) *E. affinis*, USNM 506408; (7) *E. hammondi*, MVZ 4139; (8) *E. difficilis*, UK 66993. Labels as in figure 19.

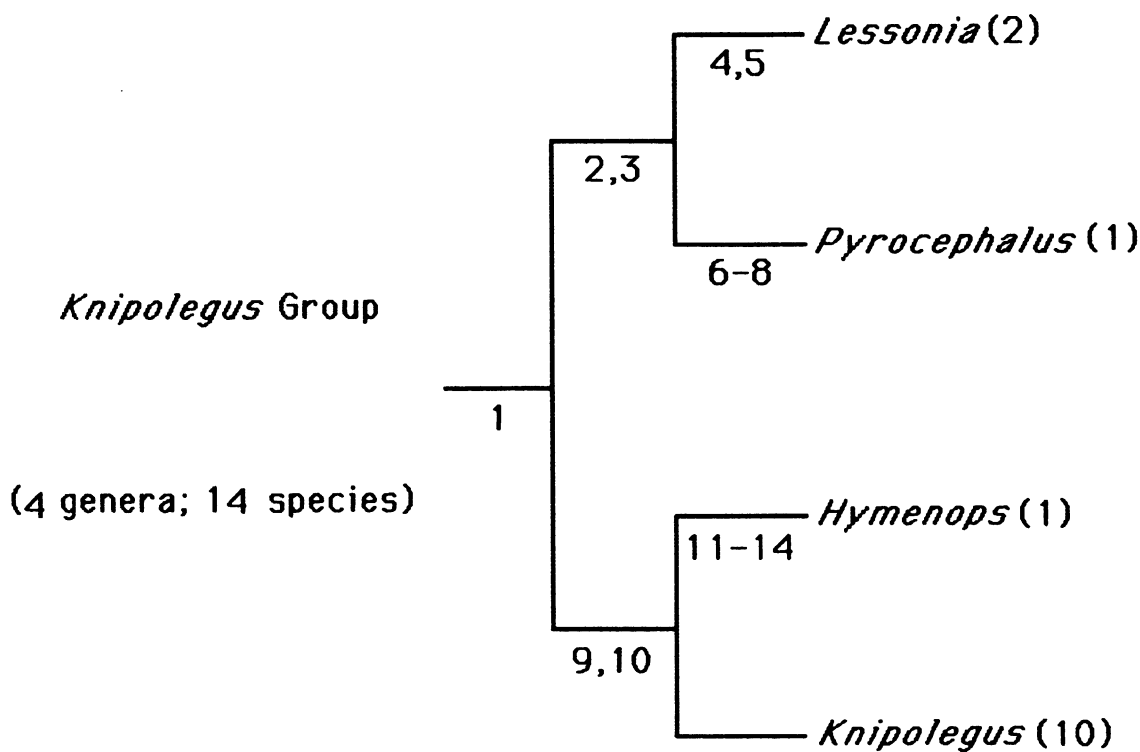


FIG. 21. Phylogenetic relationships within the *Knipolegus* group (4 genera; 13 species). Numbers identify diagnostic character states described in text and in table 4. Numbers in parentheses indicate number of species per genus.

and Van Rossem, 1938; Bent, 1942; Blake, 1956; Rowley, 1962, 1966; Skutch, 1967; Thurber, 1978; Harrison, 1979); *E. flaviventris* typically nests on the ground or in the roots of an upturned tree (Bent, 1942; Harrison, 1975); and *E. fulvifrons* and *E. hammondii* build nests that are "saddled" on limbs (AMNH collection; Bent, 1942; Harrison, 1979).

The use of mud in the foundation of the nest (character 12) appears to be a derived character that sets *Sayornis* apart from *Contopus* and *Mitrephanes*. I know of no reports of the use of mud pellets in the nests of any of the other genera in this assemblage. The behavior is not strong in *Sayornis saya*, however (AMNH collection; Bent, 1942; Harrison, 1979).

Contopus and *Mitrephanes* share a similar principal mode of foraging, i.e., aerial hawking and returning to the same perch (char-

acter 13; Skutch, 1960; Webster, 1968; Fitzpatrick, 1978). The prominent, pointed crest (character 14) is the strongest argument for maintaining *Mitrephanes* generically distinct from *Contopus* (Webster, 1968).

The *Knipolegus* Group (fig. 21 and table 4)

My *Knipolegus* group is dominated numerically by the large genus *Knipolegus* (10 species) and in addition includes the two species of *Lessonia* and the monotypic *Hymenops* and *Pyrocephalus*. Of these 14 species, I was able to examine the skulls of all but four species of *Knipolegus* (*hudsoni*, *poecilocercus*, *signatus*, and *nigerrimus*) and the syringes of all but two species of *Knipolegus* (*poecilocercus* and *signatus*).

Hellmayr (1927) placed *Lessonia* next to the ground tyrants (*Muscisaxicola* and allies)

TABLE 4
 Characters Used for Phylogeny of the *Knipolegus* Group

Character, description	Distribution by taxa
1 Plumage sexually dimorphic	All taxa in <i>Knipolegus</i> group
2 Internal cartilages more or less rectangular in shape	<i>Lessonia</i> and <i>Pyrocephalus</i>
3 A3 elements contribute to pessulus	As above
4 Dorsal ends of B1s partly calcified	<i>Lessonia</i>
5 Plumage of back cinnamon-rufous	<i>Lessonia</i>
6 B1 and B2 not connected ventrally	<i>Pyrocephalus</i>
7 Male with vermilion head and underparts	<i>Pyrocephalus</i>
8 Nests located in trees; eggs more heavily marked	<i>Pyrocephalus</i>
9 Internal cartilages triangular in shape, with base much broader than rest of cartilage	<i>Hymenops</i> and <i>Knipolegus</i>
10 A3 element forms a complete ring around each bronchus	As above
11 A1s twice the width of A2s, dorsally	<i>Hymenops</i>
12 Possession of unique cartilage at medial junction of M. obliquus ventralis	<i>Hymenops</i>
13 Unique restriction of ventral end of B1	<i>Hymenops</i>
14 Yellow wattle around eye	<i>Hymenops</i>

and maintained *Knipolegus* and *Lichenops* (= *Hymenops*) together in another part of his Fluvicolinae; Zimmer (MS) and Meyer de Schauensee (1966) continued this practice. Vuilleumier (in Smith and Vuilleumier, 1971) noted that *Lessonia*, "although strikingly dimorphic, bears some resemblance to *Muscisaxicola* in mannerisms, bill shape, and female plumage, but this could be convergence" due to their use of similar habitats. Traylor (1977) observed that "*Lessonia* appears to be a link, phenotypically at least, between the terrestrial *Muscisaxicola* and the more arboreal *Knipolegus*"; he listed *Lessonia*, *Knipolegus*, and *Hymenops* directly following *Muscisaxicola*. Hellmayr (1927) included *Pyrocephalus* in his Fluvicolinae, but with no obvious indication of relationship within that subfamily, and Meyer de Schauensee (1966) adopted Hellmayr's generic sequence. Vuilleumier (in Smith and Vuilleumier, 1971) was inclined to consider *Pyrocephalus* more closely related to the bush and ground tyrants (my *Muscisaxicola* group) than were Hellmayr and Meyer de Schauensee. Traylor (1977) considered *Pyrocephalus* to be part of his Central and North American radiation and hence a close relative of *Sayornis*, *Empidonax*, and *Contopus*. Ames (1971) was unable to place *Pyrocephalus* in any of his structural groups on the basis of syringeal morphology. I can find no suggestion in the

literature that *Pyrocephalus* should be clustered with *Knipolegus* and its allies.

The four genera in the *Knipolegus* group share a similar morphology of the syrinx. They all possess character D (figs. 12, 13; table 1), along with the majority of the genera in the assemblage; the upper bronchus is supported medially by one or two cartilaginous segments of the A2 and A3 elements and these segments are unmodified for the attachment of the internal cartilages (in contrast to the *Empidonax* group); and the internal cartilages are not broad and robust as in my *Muscisaxicola* group. But I can find no uniquely derived syringeal characters to suggest a sister-group relationship with any of the remaining genera, hence the *Knipolegus* group contributes to the polychotomy in figure 13.

The strongest argument for monophyly of the *Knipolegus* group is a marked degree of sexual dimorphism in plumage coloration and pattern (character 1). These are the only genera among those possessing character D that have evolved this degree of dimorphism. That this dimorphism in plumage coloration can be lost readily is illustrated by a local color phase of *Pyrocephalus* in Peru, in which both sexes are a rather uniform sooty brown. Within the genus *Knipolegus* sexual dimorphism is greatly reduced or lost entirely in 4 of the 10 species (*lophotes*, *poecilurus*, *nigerimus*, and *orenocensis*). As Zimmer (1937)

pointed out, however, even in *poecilurus* there is a tendency for the wing bars to be more prominent in the female as they are in most members of the group.

If one accepts monophyly of the *Knipolegus* group, then significant differences in syringeal morphology offer the best means of determining relationships within the group. In *Lessonia* and *Pyrocephalus* the internal cartilages are more or less rectangular in shape (character 2; fig. 22: 1, 2), and the A3 elements contribute to the formation of the pes-sulus (character 3). In *Hymenops* and *Knipolegus* the internal cartilages are triangular in shape, i.e., the base is much broader than the rest of the cartilage (character 9; fig. 22: 3–8), and the A3 element forms a complete ring around each bronchus (character 10).

Lessonia is defined generically by the partly calcified dorsal ends of the B1 elements (character 4) and by a cinnamon-rufous colored back plumage in both sexes (character 5). Both species of *Lessonia* nest on the ground and lay white eggs marked with large blotches of browns and grays (WFVZ collection; Taczanowski, 1884; Hellmayr, 1932; A. W. Johnson, 1967; Humphrey et al., 1970), which may be primitive for the *Knipolegus* group. *Pyrocephalus* differs from all of its near relatives by the lack of a connection between the ventral ends of the B1 and B2 elements (character 6) and, of course, by the evolution of the male's striking vermilion plumage of the head and underparts (character 7). Unlike other members of this group, *Pyrocephalus* builds a shallow cup nest in a fork or crotch of a tree, often at heights of 3 m or more, and its eggs are more heavily blotched (character 8; AMNH and WFVZ collections; Barrows, 1883; Oates and Reid, 1903; Cherrie, 1916; Hudson, 1920; Bent, 1942; Marchant, 1960; A. W. Johnson, 1967; Harrison, 1979; Belton, 1985).

The syrinx of the monotypic *Hymenops* is unique within the entire *Empidonax* assemblage with respect to three derived characters. When viewed dorsally, the A1 elements are at least twice the width of the A2s (character 11; fig. 22: 3), presumably providing a greater surface area for attachment of the exceptionally robust M. obliquus ventralis. At the medioventral junction of the paired Mm. obliqui ventrales there is a fairly long, narrow

cartilage (character 12; fig. 23: 1) and there is a unique restriction in the ventral end of each of the B1 elements (character 13; fig. 23: 1). In addition, the palustrine *Hymenops* is unique in that the male has yellow wattles or caruncles surrounding the eye (character 14). *Hymenops* builds a cup nest in reeds or bushes close to the ground (Barrows, 1883; Hudson, 1920; Hellmayr, 1932; A. W. Johnson, 1967).

Knipolegus, as presently constituted (Traylor, 1977, 1979), includes species formerly placed in separate genera on the basis of narrow, outer primaries and wing shape: *striaticeps* (*Entotriccus*), *hudsoni* and *poecilotriccus* (*Phaeotriccus*), and *poecilurus* (*Eumyiobius*). Several authors have questioned these generic separations (Hellmayr, 1927; Zimmer, 1937; Short, 1975) and the morphology of the syrinx is supportive of their recommended merger with *Knipolegus*. My syringes of *striaticeps*, *hudsoni*, and *poecilurus* are well within the range of variation found in my sample of other *Knipolegus* (fig. 22: 6).

Nests reported for 4 of the 10 species of *Knipolegus* (*aterrimus*, *lophotes*, *signatus*, and *striaticeps*) have been located on or near the ground, on ledges, or in crevices in banks or stone walls (AMNH collection; Dinelli, 1918; Reed, 1919; Belton, 1985).

Ochthornis (figs. 13, 23)

Though he formerly included *littoralis* Pelzeln (1868) within *Ochthoeca*, Sclater (1888) later proposed a new monotypic genus, *Ochthornis*, for this riverine species of Amazonia. Berlepsch (1907) was uncertain as to which subfamily *Ochthornis* should be assigned, and Hellmayr (1927) placed it with other genera of dubious affinities near the end of his Fluvicolinae. Traylor (1977) followed Vuilleumier's (in Smith and Vuilleumier, 1971) tentative recommendation that *Ochthornis* be reunited with *Ochthoeca*.

There can be no question that *Ochthornis* belongs in the *Empidonax* assemblage; its nasal septum has all of the diagnostic derived features (fig. 5: 5).

The syrinx of *Ochthornis* (fig. 23: 3) possesses characters C and D (figs. 12, 13; table 1) and hence this taxon can not be merged

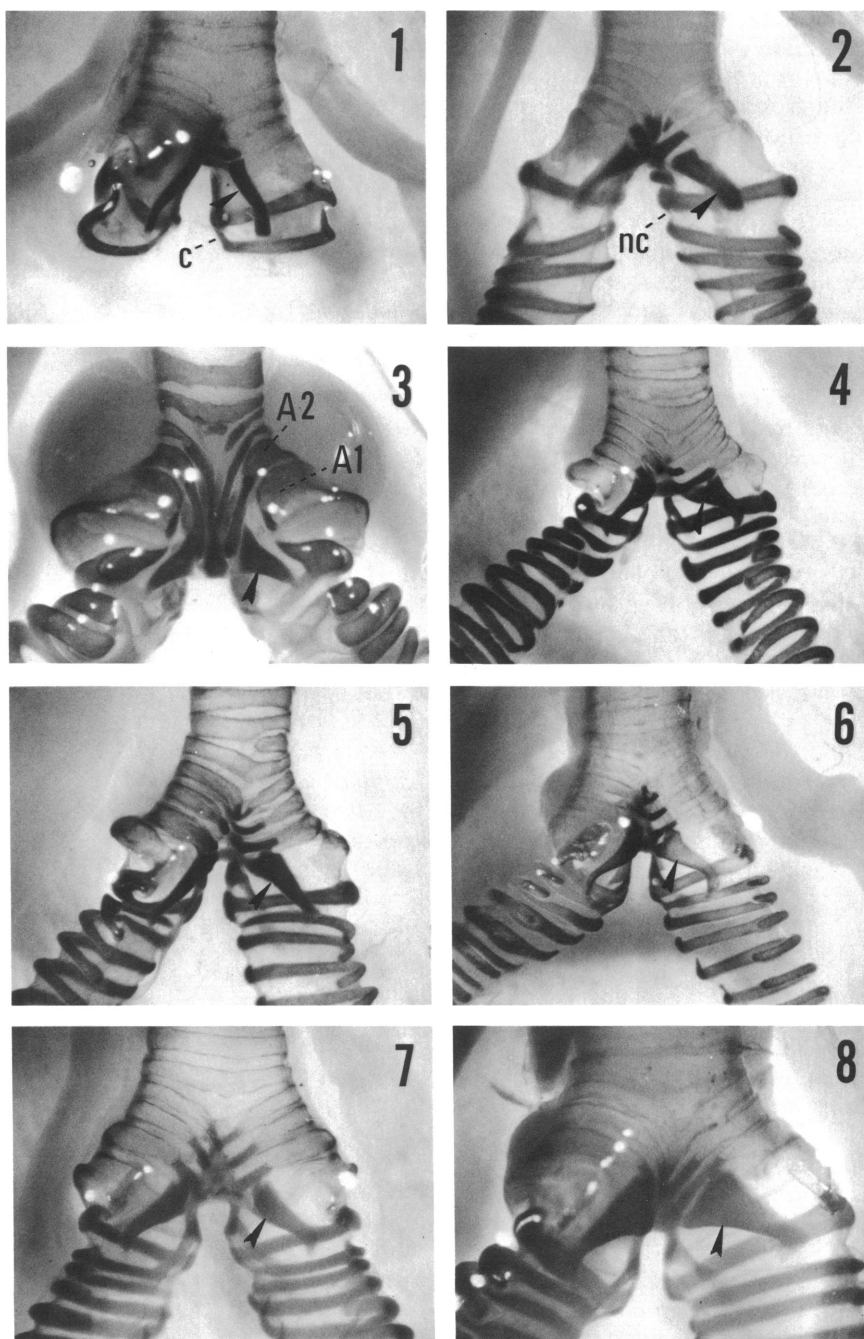


FIG. 22. The syringes of the four genera in the *Knipolegus* group (dorsal aspect; magnification = 12 \times): (1) *Lessonia rufa*, AMNH 6776; (2) *Pyrocephalus rubinus*, PMNH 2188; (3) *Hymenops perspicillata*, AMNH 2456; (4) *Knipolegus aterrimus*, AMNH 2455; (5) *K. cyanirostris*, AMNH 6791; (6) *K. poecilurus*, FMNH 290390; (7) *K. nigerrimus*, AMNH 6786; (8) *K. lophotes*, USNM 321649. Arrows indicate linear internal cartilages in *Lessonia* and *Pyrocephalus*, and triangular internal cartilages in *Hymenops* and *Knipolegus*; A1 element is twice the width of A2 in *Hymenops* (3); ventral ends of B1 and B2 elements are connected (c) in *Lessonia* and not connected (nc) in *Pyrocephalus*.

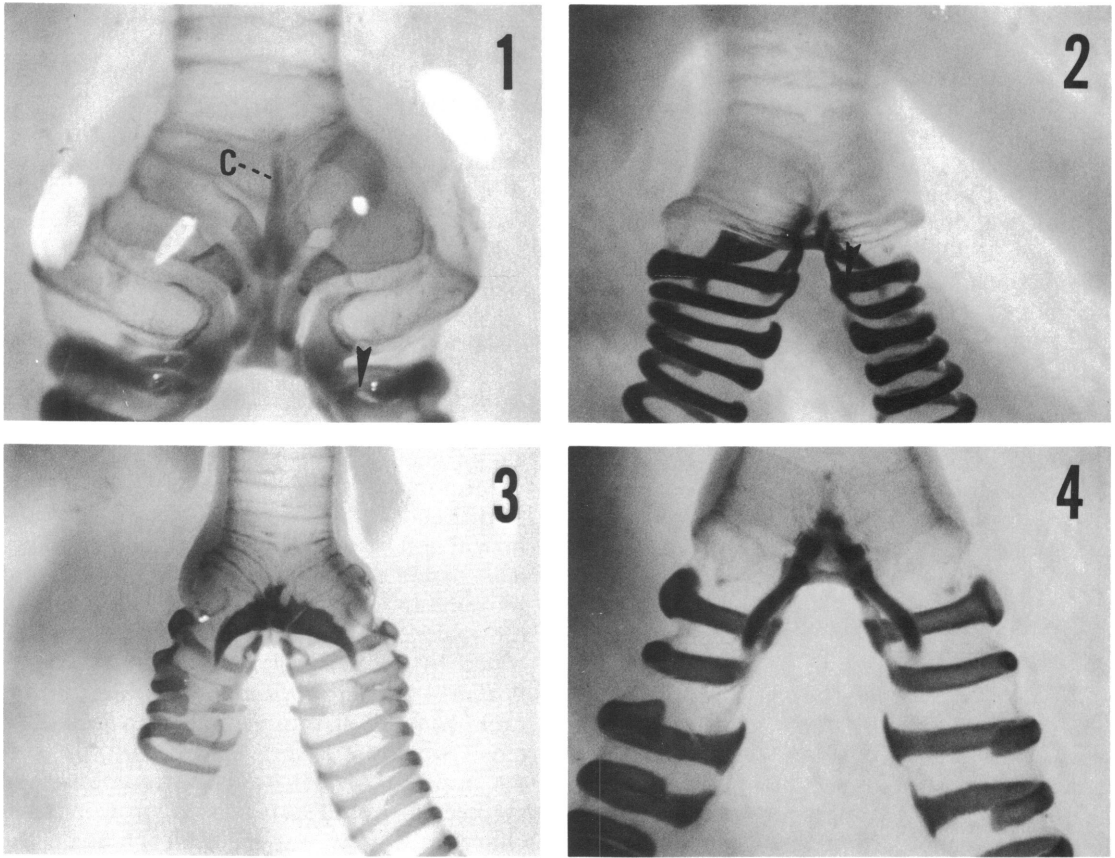


FIG. 23. Ventral aspect of the syrinxes of (1) *Hymenops perspicillata*, AMNH 6788, and (2) *Knipolegus aterrimus*, AMNH 2455, and dorsal aspect of the syrinxes of (3) *Ochthornis littoralis*, LSU 42873, and (4) *Satrapa icterophrys*, AMNH 2457. Magnification = 15 \times , except 11 \times in (3). Arrows indicate ventral end of B1 element, with unique restriction in *Hymenops* (1) and normal width in *Knipolegus* (2); c = unique strip of cartilage along medial junction of Mm. obliqui ventrales in *Hymenops*.

with *Ochthoeca* or be considered part of my *Ochthoeca* group. *Ochthornis* does not share the characters that define my *Empidonax* and *Muscisaxicola* groups but remains a member of the unresolved polychotomy in figure 13. The internal cartilages of *Ochthornis* are triangular (fig. 23: 3), as they are in *Knipolegus*, but since similar cartilages presumably have evolved independently in *Ochthoeca*, one is hesitant to use this argument for a close affinity between *Ochthornis* and *Knipolegus*. Such a relationship also would require the loss of sexual dimorphism in plumage coloration, the character used to define my *Knipolegus* group. All three of my *Ochthornis* syrinxes have the B2 and B3 elements fused together and calcified in the region just dorsal

to their ventral ends (fig. 23: 3), a curious feature that is unique within the assemblage.

I know of no report on the nest of *Ochthornis*.

Satrapa (figs. 13, 23)

The monotypic *Satrapa* has been an enigma to avian systematists and traditionally is placed among other genera of uncertain affinities near the end of the Fluvicolinae (Sclater, 1888; Berlepsch, 1907; Hellmayr, 1927; Traylor and Fitzpatrick, 1982). Zimmer (MS) and Traylor (1977) suggested a possible relationship with *Tumbezia* on the basis of similarities in plumage coloration and pattern.

Satrapa possesses a syrinx that is unlike

that of *Ochthoeca* (including *Tumbezia*) in that the A2 elements form complete rings around the bronchi and character D (figs. 12, 13; table 1) is well developed; the internal cartilages are narrow and very slightly J-shaped (fig. 23: 4). The shallow cup nest, placed in bushes or low trees, and white eggs spotted reddish-brown (AMNH collection; Barrows, 1883; Gibson, 1918; Hudson, 1920) provide no clue to relationship. The pale outer webs of the outer rectrices could be interpreted as evidence of affinity with *Muscisaxicola* and other ground tyrants, but this character is found in *Ochthoeca* and in some members of my *Knipolegus* group. I have been unable to devise any compelling argument that would ally *Satrapa* with another genus in the unresolved polychotomy within the assemblage (fig. 13).

The *Muscisaxicola* Group (fig. 24 and table 5)

My *Muscisaxicola* group is dominated numerically by *Muscisaxicola*, *Agriornis*, *Xolmis*, and *Myiotheretes*, and in addition includes *Cnemarchus*, *Neoxolmis*, *Gubernetes*, *Muscipipra*, and two new monotypic genera, *Heteroxolmis* and *Polioxolmis* (described below). I have examined the skulls and syringes of all but three species in this complex (*Agriornis andicola*, *Muscisaxicola cinerea*, and *Myiotheretes pernix*), and I lack the syrxinx of *Muscisaxicola fluviatilis*.

Though Sclater (1888) placed *Muscisaxicola* at the other end of his subfamily from *Agriornis* and *Taenioptera* (= *Xolmis*), Berlepsch (1907) and all subsequent workers consistently listed this genus among the larger group of bush and ground tyrants (the genera identified in my *Muscisaxicola* group). With the exception of *Ochthoeca*, *Gubernetes*, *Muscipipra*, and *Muscigralla*, there has been complete consensus since Sclater's time on these taxa. Systematists' views have differed only with respect to the limits and sequence of the genera, and these will be reviewed in greater detail below. I have presented arguments for maintaining *Ochthoeca* apart from the bush tyrants, based on a uniquely derived configuration of the tracheobronchial junction in the syrinx. *Gubernetes* traditionally has been considered a close relative of the

fancy-tailed tyrants *Colonia* and *Alectrurus* (Hellmayr, 1927; Zimmer, ms; Warter, 1965; Traylor, 1977), while a lack of anatomical material and information on habits has obscured the relationships of *Muscipipra*; neither *Gubernetes* nor *Muscipipra* had been thought to be allied with the bush and ground tyrants until Ames (1971) reported that their syringes possessed the cartilaginous plug typical of *Muscisaxicola* and *Xolmis*. I have previously rejected (in the section on putative relatives) the recommendation by Vuilleumier (in Smith and Vuilleumier, 1971) that *Muscigralla* be merged with *Muscisaxicola*, since the former is not in my *Empidonax* assemblage.

Monophyly of the bush and ground tyrants traditionally has been based on shared ecological and behavioral traits, the morphological correlates of a terrestrial way of life, and biogeographical considerations. Because of the real possibility of convergence, as illustrated by the alleged relationship of *Muscigralla* to this group, one would like to find more compelling morphological evidence for clustering these genera. Once again, the syrinx appears to offer the best argument. The syringes of my *Muscisaxicola* group possess character D (figs. 12, 13; table 1), as do the majority of the genera in the assemblage; but within that unresolved polychotomy, the *Muscisaxicola* group has syringes in which the upper bronchi are supported medially by cartilaginous segments of the A2 and A3 elements that are unmodified for the attachment of the internal cartilages (as they are in the *Empidonax* group), and the internal cartilages are broad and robust (character 1, fig. 24; syringes illustrated in figs. 25–27). In addition, with the exception of the monotypic *Heteroxolmis* where presumably the character has been lost secondarily, this group has the pale outer web of the outer rectrix, either white or cinnamon-rufous (character 2). This character also appears in *Alectrurus*, in six of the seven species of *Ochthoeca*, and in females of *Lessonia* and *Pyrocephalus*, but in those instances differences in syringeal morphology are considered to be more conservative than plumage pigmentation and the discordances are attributed to convergence. The appearance of character 2 in the monotypic *Satrapa* is more difficult to explain but,

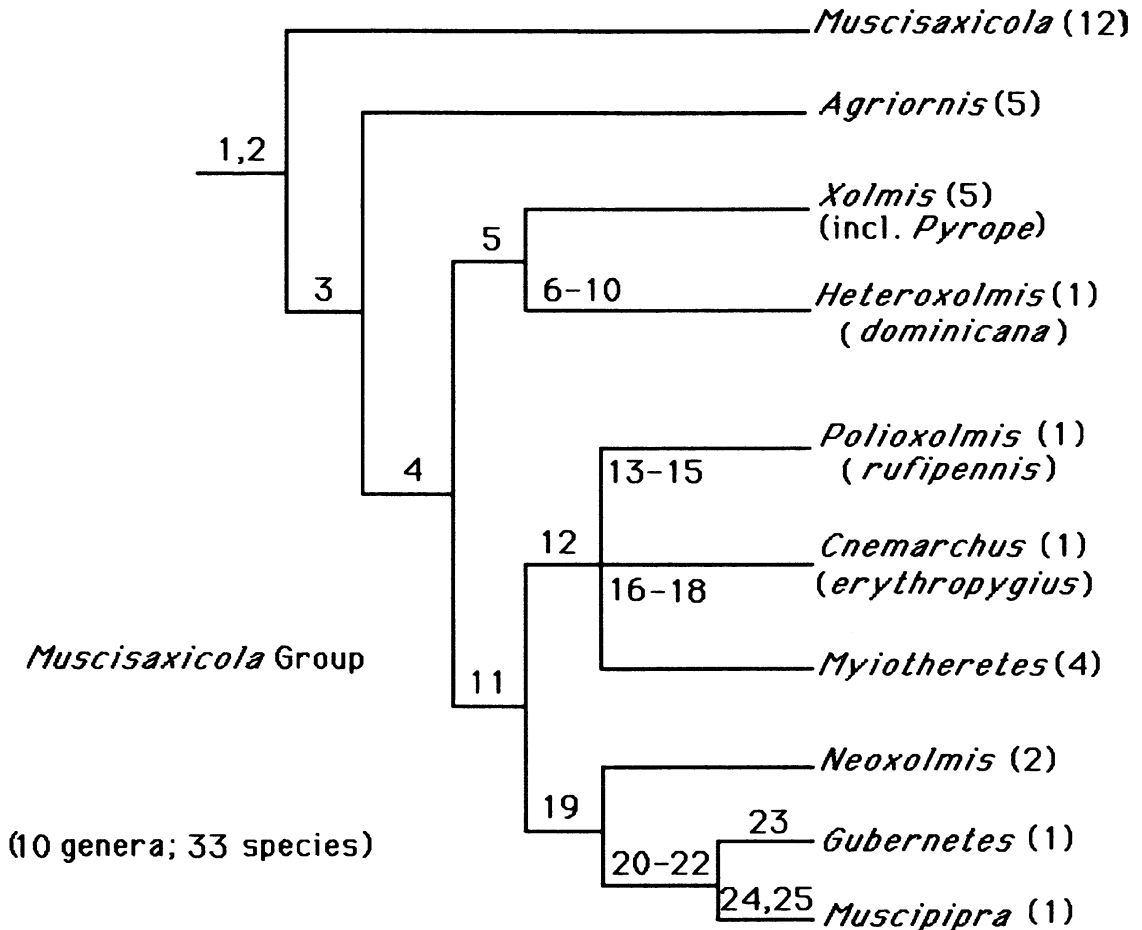


FIG. 24. Phylogenetic relationships within the *Muscisaxicola* group (10 genera; 33 species). Numbers identify diagnostic character states described in text and in table 5. Numbers in parentheses indicate number of species per genus.

in the absence of other evidence of relationship with the bush and ground tyrants, it seems best not to include *Satrapa* in the *Muscisaxicola* group.

Though unique syringeal characters are useful in determining generic diagnoses, syringeal morphology unfortunately provides few clues for clustering genera within the *Muscisaxicola* group; for this I must rely on what I perceive to be derived character states of the plumage.

As Smith and Vuilleumier (1971) have pointed out, *Muscisaxicola* is a well-defined genus and perhaps more distantly related to the other genera in this group than the latter are to each other. None of the 12 species has

a patterned wing or tail (i.e., other than a white outer web of the outer rectrix) that characterizes so many of the other ground tyrants and bush tyrants, nor are the outer primaries ever attenuated as they are in the adult males of most of the group. Some, but not all, species of *Muscisaxicola* possess a species-specific colored crown spot (not concealed as in *Myiophobus*) and a suggestion of a pale superciliary and frontal region. Many, though not all, skulls of *Muscisaxicola* show a lack of ossification of the anterior region of the nasal septum (fig. 7: 1-4), presumably a retention of the primitive state. Syringes of representative species of *Muscisaxicola* are shown in figure 25. All species, so far as

TABLE 5
Characters Used for Phylogeny of the *Muscisaxicola* Group

Character, description	Distribution by taxa
1 Internal cartilages broad and robust	All taxa in <i>Muscisaxicola</i> group except <i>Cnemarchus</i>
2 Outer web of outer rectrix pale (either white or cinnamon-rufous)	All taxa in <i>Muscisaxicola</i> group except <i>Heteroxolmis</i>
3 Outer primaries attenuated in adult males in at least 1 species in each genus	All genera in <i>Muscisaxicola</i> group except <i>Cnemarchus</i> and <i>Gubernetes</i> (reduced in <i>Polioxolmis</i>)
4 Wing patterned	All genera in <i>Muscisaxicola</i> group except <i>Muscisaxicola</i> and <i>Agriornis</i> (lost in <i>pyrope</i> and <i>Muscipipra</i>)
5 Wing patterned with white	<i>Xolmis</i> (lost in <i>pyrope</i>)
6 Uniquely shaped internal cartilages	<i>Heteroxolmis</i>
7 Fully ossified nasal capsule	<i>Heteroxolmis</i>
8 Nasal septum with narrow trabecular plate	<i>Heteroxolmis</i>
9 Loss of pale outer web of outer rectrix	<i>Heteroxolmis</i>
10 Uniquely shaped tenth primary	<i>Heteroxolmis</i>
11 Wing patterned with buff or cinnamon-rufous	<i>Myiotheretes</i> , <i>Polioxolmis</i> , <i>Neoxolmis</i> , and <i>Gubernetes</i> (reduced in <i>Cnemarchus</i> ; lost in <i>Muscipipra</i>)
12 Throat plumage streaked	<i>Polioxolmis</i> , <i>Cnemarchus</i> , and <i>Myiotheretes</i>
13 Syrinx with wide membranous areas between calcified A elements	<i>Polioxolmis</i>
14 Internal cartilages very slightly J-shaped and pointed distally	<i>Polioxolmis</i>
15 B1 elements not conspicuously broader at dorsal ends	<i>Polioxolmis</i>
16 Internal cartilages narrow and gracefully curved	<i>Cnemarchus</i>
17 Cinnamon-rufous wing pattern greatly reduced; secondaries uniquely edged with white	<i>Cnemarchus</i>
18 Trabecular plate on nasal septum not forked posteriorly	<i>Cnemarchus</i>
19 Internal cartilages very broad and J-shaped	<i>Neoxolmis</i> , <i>Gubernetes</i> , and <i>Muscipipra</i>
20 Tail elongated and forked	<i>Gubernetes</i> and <i>Muscipipra</i>
21 Ventral end of B2 is Y-shaped (forked)	As above
22 Dorsal end of B1 is bulbous (swollen)	As above
23 Nasal capsule fully ossified	<i>Gubernetes</i>
24 A1 conspicuously narrower than A2, except at expanded dorsal end	<i>Muscipipra</i>
25 Loss of wing pattern (no buff or cinnamon-rufous)	<i>Muscipipra</i>

known, nest on or very near the ground, in a slight depression, crevice, or burrow, often under or among stones; the eggs are white, sparingly to moderately spotted with reddish-brown (WFBV collection; Hellmayr, 1932; A. W. Johnson, 1967; Humphrey et al., 1970; Smith and Vuilleumier, 1971; Pettingill, 1974; Woods, 1975).

Sclater (1888) and Berlepsch (1907) included *rufipennis* Taczanowski (1874) in *Muscisaxicola*, but Hellmayr (1927) and all subsequent workers consistently placed *rufipennis* among those genera that I have iden-

tified as my *Myiotheretes* lineage, and I concur (discussed in detail below).

The remaining genera in my *Muscisaxicola* group cluster by virtue of a derived character state of the outer primaries, which are attenuated in the adult males of at least one species (usually more) in each genus (character 3). The character presumably has been lost secondarily in the monotypic *Cnemarchus* and *Gubernetes*, in one of the five species of *Xolmis*, and in three of the four species of *Myiotheretes*. Elsewhere within the *Empidonax* assemblage attenuated primaries have

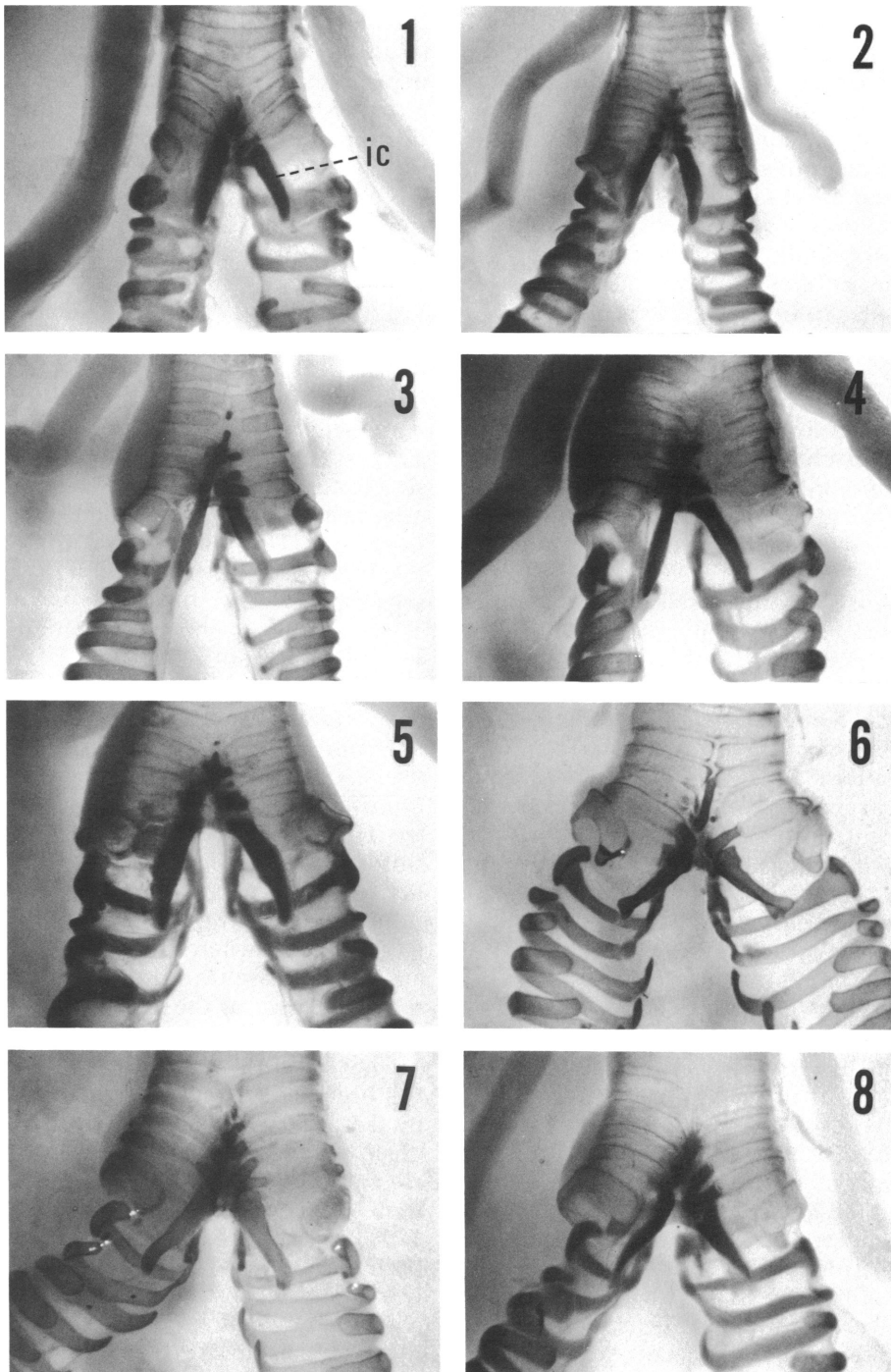


FIG. 25. The syringes of two genera in the *Muscisaxicola* group (dorsal aspect; magnification = 12 \times , except 9 \times in 2, 3, 6, 7): (1) *Muscisaxicola maculirostris*, AMNH 6670; (2) *M. macloviana*, AMNH 6668; (3) *M. albilora*, PMNH 2711; (4) *M. rufivertex*, AMNH 6664; (5) *M. frontalis*, PMNH 28; (6) *Agriornis montana*, LSU 102446; (7) *A. microptera*, LSU 102445; (8) *A. murina*, PMNH 2612. Internal cartilages (ic) broad and robust.

evolved, presumably independently, in *Arundinicola* and *Alectrurus*, in three species of *Knipolegus*, and in the two species of *Lessonia*. Traylor and Fitzpatrick (1982) have discussed the tendency for peculiarly shaped remiges to recur in all of the major flycatcher lineages and concluded that these characters are reliable only at the level of the species or subspecies. Certainly modified wing feathers are plastic, as illustrated by their presence and absence within bona fide genera. However, I have argued elsewhere (Lanyon, 1984b) that within lineages established by more conservative characters, such as syringeal morphology, modified remiges can be a useful character for clustering genera (e.g., *Tyrannus*, *Empidonomus*, and *Griseotyrannus* within a lineage of kingbird allies established on the basis of shared derived syringeal characters).

Agriornis is another well-defined genus, with dull gray or brown plumage and a white throat streaked with darker brown. Adult males of all five species have attenuated outer primaries. There is no spot of color in the crown as in some *Muscisaxicola*. The remiges are not patterned, as is characteristic of the remaining genera in this group. I agree with Vuilleumier (*in* Smith and Vuilleumier, 1971) that *murina* belongs in *Agriornis* rather than in *Xolmis*, on the basis of proportions of wing, tail, tarsus, and culmen lengths, and of color and pattern of the plumage. Syringes of representative species of *Agriornis* are shown in figure 25. Nests are known for three of the five species, and are located on the ground, in holes in the ground, in crevices of rocks or buildings, or in bushes or cacti near the ground; the eggs do not differ significantly from those of *Muscisaxicola* (WFWZ collection; Hellmayr, 1932; A. W. Johnson, 1967; Smith and Vuilleumier, 1971).

The remaining genera in the group, dominated by *Xolmis* and *Myiotheretes*, cluster by virtue of their having the wings patterned with patches of white, buff, or cinnamon-rufous (character 4). The usual pattern is for the distal portion of the remiges to be black or fuscous and for the basal portion to be white, buff, or cinnamon-rufous; however, unique patterns have evolved in three genera and two species have reverted to no pattern at all (*Xolmis pyrope* and *Muscipipra vetula*,

discussed below). Elsewhere within the assemblage, patterned wings have evolved independently in *Alectrurus*, in my *Knipolegus* group (*Knipolegus*, *Hymenops*, and *Lessonia*), and in my *Myiophobus* group (*Hirundinea* and *Pyrrhomias*).

To facilitate my review of the historical treatment of these remaining genera of bush and ground tyrants (i.e., those sharing character 4) and my reconstruction of their phylogeny, I shall refer to two clusters of genera that I believe represent sister groups. One of these is the *Xolmis* cluster, which includes the same six species (*pyrope*, *cinerea*, *coronata*, *velata*, *irupero*, and *dominicana*) that Traylor (1979) placed in his *Xolmis*. These six cluster by virtue of their having the remiges patterned with white (character 5; lost in *pyrope*). They have been considered close relatives since Sclater's catalog (1888), though separate generic status for *pyrope* was advocated by Zimmer (ms) and Meyer de Schauensee (1966). I shall refer to the other lineage as the *Myiotheretes* cluster, which includes, in addition to the monotypic *Gubernetes* and *Muscipipra*, the following eight species: *rufipennis*, *erythropygius*, *striaticollis*, *pernix*, *fumigatus*, *fuscus*, *rubetra*, and *rufiventris*. Historically these eight species have been shifted back and forth, with little consistency, between the genera *Myiotheretes*, *Cnemarchus*, *Ochthodiaeta*, *Neoxolmis*, and *Xolmis*. Regardless of where the generic boundaries are drawn, these taxa cluster together by virtue of their having the remiges patterned with buff or cinnamon-rufous (character 11).

The concept of the genus *Xolmis* frequently has been somewhat broader than that interpreted here, with taxa included that I would argue belong elsewhere. As noted above, *murina* was included in *Xolmis* by most workers until Vuilleumier (*in* Smith and Vuilleumier, 1971) recommended its transfer to *Agriornis*; both Traylor (1977) and I concur. Earlier workers (Sclater, 1888; Hellmayr, 1927) included *rubetra*, as well, and Zimmer (ms) and Meyer de Schauensee (1966) included not only *rubetra* but *rufipennis*. The broadest concept for the genus *Xolmis* is that proposed by Vuilleumier (*in* Smith and Vuilleumier, 1971), who included all of the species in my *Myiotheretes* cluster with the exception of *rufiventris*, which he maintained in a monotypic

Neoxolmis. I agree with Traylor (1977) that this lumping is too extreme:

All the species included in Hellmayr's *Myiotheretes*, *Cnemarchus* and *Ochthodiaeta* are characterized by brown, buff or rusty plumage, and are found only in brush or the edge of forest in the high Andes, from Venezuela to northwestern Argentina. The species of Hellmayr's *Xolmis*, on the other hand, are with one exception [*rubetra*, which both Traylor and I believe belongs in *Neoxolmis*, along with *rufiventris*] patterned in black, gray or white and are found in tropical to temperate lowlands from eastern Brazil and Bolivia south to Patagonia. I feel that the dichotomy between these two groups is so marked that, even though they may have had a common ancestor, their present relationship is best shown by the recognition of two genera—*Myiotheretes* (including *Cnemarchus* and *Ochthodiaeta*) and *Xolmis*.

Traylor's interpretation is compatible with my concept of two lineages, the *Xolmis* cluster and the *Myiotheretes* cluster; however, in addition, I would recognize three monotypic genera, as argued below, to acknowledge the degree of differentiation that three of these species have achieved.

My *Xolmis* includes *cinerea*, *velata*, *coronata*, *irupero*, and *pyrope*. The latter species has a syrinx that can not be distinguished from those of other *Xolmis* (fig. 26: 1–3). I do not consider that it has differentiated sufficiently to warrant separate generic status as suggested by Zimmer (ms) and Meyer de Schauensee (1966). By contrast, *dominicana*, historically an unquestioned member of *Xolmis*, differs from other *Xolmis* in a number of very significant characters, the basis for a new genus described below.

Heteroxolmis, new genus

TYPE SPECIES: *T[yrannus] dominicanus* Vieillot, 1823, p. 856; Paraguay.

INCLUDED SPECIES: The type species only.

DISTRIBUTION: Paraguay, Uruguay, northeastern Argentina from Chaco and Misiones to southern Buenos Aires, and southeastern Brazil in Paraná and Rio Grande do Sul (Traylor, 1979).

ETYMOLOGY: From the Greek *heteros* meaning different or other.

DIAGNOSIS: The syrinx of *dominicana*, though like that of other members of the

Muscisaxicola group with respect to the configuration of the tracheobronchial junction and the possession of character D (table 1) and character 1 (table 5), has internal cartilages that are unique among all flycatchers in being greatly swollen and slightly J-shaped (character 6; fig. 26: 4). This divergence is remarkable in view of the noted homogeneity of the syrinx of *Muscisaxicola*, *Agriornis*, *Xolmis*, and *Myiotheretes*. The nasal capsule of *dominicana* is fully ossified, including the alinasal walls and turbinals (character 7), and the trabecular plate that bases the nasal septum is extremely narrow (character 8; fig. 5: 2); both of these character states are unlike anything I have observed in the skulls of *Xolmis*, as represented by the nasal capsule of *X. coronata* in figure 5: 8. The divergence from *Xolmis* illustrated by characters 6 through 8 greatly exceeds intrageneric variation among tyrant flycatchers and constitutes my main argument for proposing separate generic status for this species. In addition, though inconclusive as isolated characters, supporting evidence is derived from the secondary loss of the pale outer web of the outer rectrix in *dominicana* (character 9; the only species within the *Muscisaxicola* group to have lost this character state) and from the uniquely shaped tenth primary (character 10). The latter, unlike other modified primaries in the group, is illustrated by Smith and Vuilleumier (1971, p. 189).

I know of no report on the nest of *Heteroxolmis dominicana*. The nests of four of the five species of *Xolmis* are known and are quite variable intragenerically, including ground nests located in large clumps of grass or in holes in banks, open cup nests in bushes or trees, and cavity nests in trees or old oven-bird nests; the eggs are like those of *Muscisaxicola* and *Agriornis* (AMNH collection; Barrows, 1883; Hudson, 1920; Wetmore, 1926; Ihering, 1904; Smith and Vuilleumier, 1971; Belton, 1985).

Within my *Myiotheretes* cluster, i.e., those genera sharing character 11, the following species appear to be closely related because of their streaked throat plumage (character 12): *rufipennis*, *erythropygius*, *striaticollis*, *pernix*, *fumigatus*, and *fuscus*. Historically there has been little controversy over the relatedness of the six; disagreement has

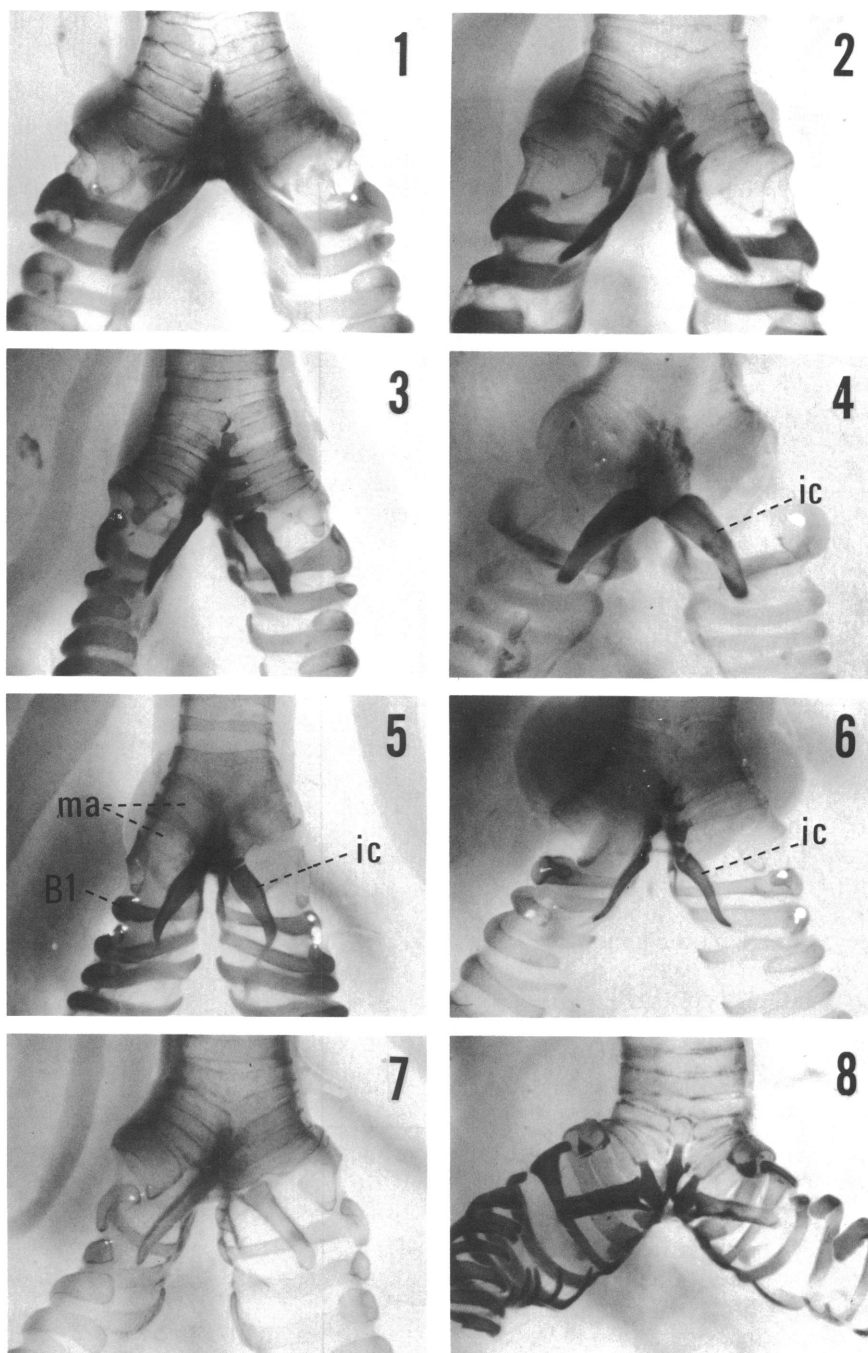


FIG. 26. The syringes of five genera in the *Muscisaxicola* group (dorsal aspect; magnification 9×): (1) *Xolmis cinerea*, AMNH 6829; (2) *X. coronata*, PMNH 2820; (3) *X. pyrope*, AMNH 2451; (4) *Heteroxolmis dominicana*, AMNH 6827; (5) *Polioxolmis rufipennis*, LSU 91519; (6) *Cnemarchus erythropygius*, LSU 91521; (7) *Myiotheretes striaticollis*, LSU 75469; (8) *M. fuscorufus*, LSU 102479. Internal cartilages (ic) broad and robust in *Xolmis* and *Myiotheretes*, but swollen and slightly J-shaped in *Heteroxolmis*, slightly J-shaped and pointed distally in *Polioxolmis*, and narrow and gracefully curved in *Cnemarchus*; membranous areas (ma) between A elements wider than the elements themselves in *Polioxolmis*; B1 elements not conspicuously broader at dorsal end in *Polioxolmis*.

centered on their generic assignment. They were distributed among three genera (*Myiotheretes*, *Cnemarchus*, and *Ochthodiaeta*) by Hellmayr (1927), placed in adjacent species groups within *Xolmis* by Vuilleumier (in Smith and Vuilleumier, 1971), and included in a single genus, *Myiotheretes* by Traylor (1977, 1979). Nothing has been reported on nesting behavior.

Taczanowski (1874) described *rufipennis* and assigned it to *Muscisaxicola*, where it was retained by Sclater (1888) and Berlepsch (1907). Hellmayr (1927) referred it to *Cnemarchus*: "... this peculiar species seems more properly referable to *Cnemarchus* than to any other genus." In unpublished notes dated August 1936, Zimmer (MS) commented on *rufipennis*: "Relationship to *Cnemarchus erythropygius* doubtful It shows some resemblance to *Xolmis* If not in *Cnemarchus* it should have a new genus erected for it. Probably near *Xolmis* In fact except for a little more slender bill, it fits best in *Xolmis*." Meyer de Schauensee (1966) included it in *Xolmis* but noted that "its generic allocation is still uncertain." Vuilleumier (in Smith and Vuilleumier, 1971) placed it in his *erythropygia* species group within *Xolmis*, while Traylor (1977, 1979) considered it part of his enlarged *Myiotheretes*.

It is understandable that Zimmer and others experienced difficulty in determining the nearest relative of *rufipennis*. Its external morphology, though useful for relating it to my *Myiotheretes* cluster within the *Muscisaxicola* group (characters 11 and 12), gives no unequivocal clues to generic alignment. Nor is syringeal morphology of any value in this regard; hence the trichotomy in figure 24. In fact, the syrinx of *rufipennis* has differentiated from those of its close relatives to a degree that exceeds intrageneric syringeal variation among tyrant flycatchers and prompts me to describe a second monotypic genus within this group.

Polioxolmis, new genus

TYPE SPECIES: *Muscisaxicola rufipennis* Taczanowski, 1874, p. 134; Maraynioc, Peru; formerly Warsaw Museum, now lost.

INCLUDED SPECIES: The type species only.

DISTRIBUTION: Subtropical, temperate, and puna zones of Peru from Lambayeque, Ca-

jamarca, and southern Amazonas southward, and Bolivia south to Potosí (Traylor, 1979).

ETYMOLOGY: From the Greek *polios* meaning ashy-gray, in reference to the predominant color of the plumage.

DIAGNOSIS: The syrinx of *rufipennis* (fig. 26: 5), though like that of other members of the *Muscisaxicola* group with respect to the configuration of the tracheobronchial junction and the possession of character D (table 1) and character 1 (table 5), differs from the syringes of all other species in the *Empidonax* assemblage in having remarkably wide membranous areas between the calcified A elements (character 13); those between the lower A elements are actually wider than the elements themselves. In addition, the internal cartilages are very slightly J-shaped and are pointed distally (character 14), unlike those of its near relatives, and the B1 elements are not conspicuously broader at their dorsal ends (character 15) as they are in all members of my *Muscisaxicola* group.

Historically there has been general agreement that *erythropygius* Sclater (1851) belongs with the bush tyrants, either in *Xolmis* (Sclater, 1851; Vuilleumier in Smith and Vuilleumier, 1971) or in *Myiotheretes* (Sclater, 1888; Berlepsch, 1907; Zimmer, MS; Meyer de Schauensee, 1966; Traylor, 1977). Ridgway (1905) created *Cnemarchus* for this species, on the strength of differences (from *Myiotheretes*) in external morphology; Hellmayr (1927) recognized *Cnemarchus* for *erythropygius*, and included *rufipennis* as a congener. This relationship between *erythropygius* and *rufipennis* is reflected also by Vuilleumier's (in Smith and Vuilleumier, 1971) treatment of the two taxa as sole members of a species group within *Xolmis*.

The long-recognized affinity between *erythropygius* and my *Muscisaxicola* group is based on overall similarity in external morphology and behavior. In developing my concept of the relationship of *erythropygius*, I have been influenced by the presence of character D (table 1) in the syrinx (fig. 26: 6), which places *erythropygius* within the unresolved polychotomy in figure 13. I stress the fact that it shares with other members of my *Muscisaxicola* group a pale outer web of the outer rectrix (character 2). Discordant with this treatment is the fact that the internal cartilages in the syrinx of *erythropygius* are

narrow and gracefully curved (character 16; fig. 26: 6), like the horns of a steer, and not at all broad and robust (character 1) as in all other members of my *Muscisaxicola* group. In view of the number of external morphological characters shared with my *Myiotheretes* cluster, I am inclined to interpret this discordance as a character loss and subsequent differentiation. This species shares with members of my *Myiotheretes* cluster a wing patterned with buff or cinnamon-rufous (character 11), though the pattern is confined only to the basal portion of the remiges. The throat is streaked (character 12) as it is in *Polioxolmis* and *Myiotheretes*. The only discordance in external morphology is the absence of attenuated outer primaries (character 3) but, as I have indicated above, this is a plastic character that has been lost or reduced in a number of the species in the *Xolmis* and *Myiotheretes* clusters.

Generic separation of *erythropygius* from *Myiotheretes* (Ridgway, 1905; Hellmayr, 1927) was based on such characters as the cinnamon-rufous rump and the proportionately longer tarsi and narrower bill. I would attach greater significance to the reduction of the cinnamon-rufous pattern in the wing and the unique white edging of the inner secondaries (character 17). The strongest evidence for generic differentiation from other members of my *Myiotheretes* cluster comes from examination of the skull and the syrinx. The posterior end of the trabecular plate (on the nasal septum), normally conspicuously forked in this assemblage, is unforked in *erythropygius* (character 18). The back-lighted skull in figure 6: 5 reveals a thinly ossified area near the posterior end of the plate, suggesting that this unforked state has been derived from the normal forked condition through progressive ossification and closure of the fork. The derived condition does not deny relationship with my *Muscisaxicola* group, of course, but indicates a degree of differentiation worthy of recognition. As noted above, the internal cartilages in the syrinx are narrow and rather gracefully curved (character 16; fig. 26: 6) and not at all broad and robust (character 1) as in all other members of my *Muscisaxicola* group. As disquieting as this discordance might seem, differences in size and shape of internal cartilages, though not

to be expected intragenerically, frequently are seen in closely related genera of tyrant flycatchers. Examples within my *Empidonax* assemblage are found between *Silvicultrix* and *Ochthoeca*, and between *Pyrrhomyias* and *Hirundinea* in the *Myiophobus* group. Among the kingbirds and their allies, I found differences of this magnitude between such pairs of closely related genera as *Pitangus* and *Philoedon*, and *Legatus* and *Myiozetetes* (Lanyon, 1984b).

I see no clear basis for determining whether *erythropygius* is more closely related to *Myiotheretes*, as maintained by some workers, or to *rufipennis*, as asserted by others. For the present I prefer to follow Ridgway (1905) and maintain *erythropygius* in *Cnemarchus*, with no congeners, as part of the unresolved trichotomy depicted in figure 24.

My *Myiotheretes* includes *striaticollis*, *pernix*, *fumigatus*, and *fuscus*, and is equivalent to Vuilleumier's *fumigata* species group (in Smith and Vuilleumier, 1971). As noted above, three of the four species have lost the attenuation of the outer primaries (character 3) that characterizes most of the genera in my *Muscisaxicola* group. The syringes of the four species are not separable from one another; all have internal cartilages that are broad, robust, and blunt distally (fig. 26: 7, 8). I see no justification, either in syringeal or external morphology, for the generic separation of the latter three species in *Ochthodiaeta* Cabanis and Heine (1859).

The clustering of the remaining three genera (*Neoxolmis*, *Gubernetes*, and *Muscipipra*) in my *Muscisaxicola* group will surprise many ornithologists, for these flycatchers have never been considered particularly closely related. My argument is based on the fact that this is only one of two examples, within my *Muscisaxicola* group, of genera sharing a significantly different syringeal morphology. All three of these genera possess internal cartilages that are very broad and J-shaped (character 19; fig. 27).

That the two species, *rubetra* and *rufiventris*, are congeners is not at once apparent from their external morphology, nor have they long been considered closely related. The terrestrial *rufiventris* had been placed in *Myiotheretes* until Hellmayr (1927) proposed a new monotypic genus, *Neoxolmis*, where it has

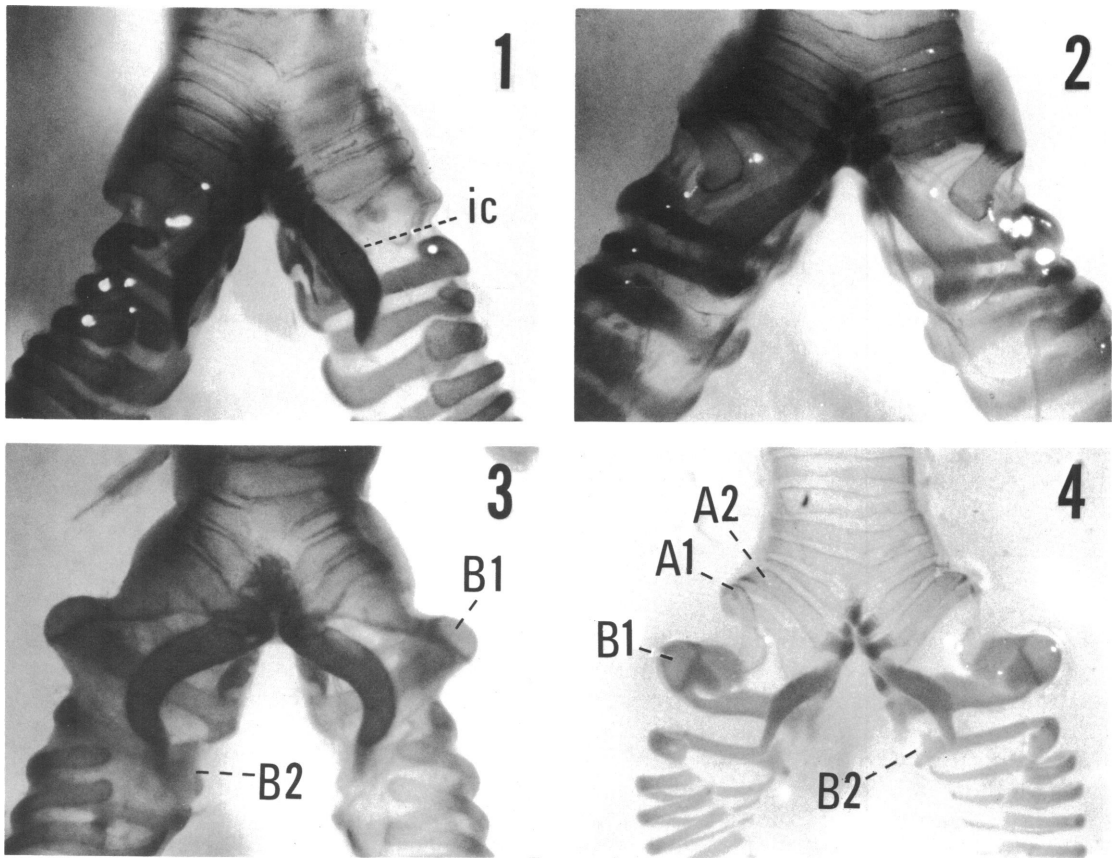


FIG. 27. The syrinxes of three genera in the *Muscisaxicola* group (dorsal aspect; magnification = 11×): (1) *Neoxolmis rubetra*, PMNH 4543; (2) *N. rufiventris*, PMNH 2859; (3) *Gubernetes yetapa*, AMNH 8237; (4) *Muscipipra vetula*, BM 1936.1.12. Internal cartilages (ic) broad and J-shaped in all three genera; ventral end of B2 Y-shaped and dorsal end of B1 bulbous or swollen in *Gubernetes* and *Muscipipra*; A1 conspicuously narrower than A2 in *Muscipipra*.

been maintained by most subsequent workers. The more arboreal *rubetra* consistently had been assigned to *Xolmis* until Traylor (1977) placed it together with *rufiventris* in *Neoxolmis*. Vuilleumier (in Smith and Vuilleumier, 1971) had *rubetra* in its own species group within his enlarged *Xolmis* and *rufiventris* in a monotypic *Neoxolmis*: “*X. rubetra* . . . appears more terrestrial than the other species of the genus [*Xolmis*]. In color, pattern, and habits, *X. rubetra* is intermediate between the other species of *Xolmis* and *Neoxolmis rufiventris*, and may represent an evolutionary transitional ‘stage’ between arboreal and terrestrial tyrants.”

While *rubetra* shares a rather typical wing pattern with the rest of my *Myiotheretes* clus-

ter (cinnamon-rufous basally and fuscous distally; character 11), *rufiventris* has a unique modification of this pattern, confined to the secondaries and with the distal segment largely white. The only reported nest of *rufiventris* (Maclean, 1969) was a cup nest located on the ground; though the eggs of *rubetra* have markings similar to those of *rufiventris* (WVZ collection), the nest is unreported. Though my samples are small, it is questionable that the syrinxes of *rubetra* and *rufiventris* can be differentiated (fig. 27: 1, 2). Until there is compelling evidence to the contrary, I support Traylor's (1977) recommendation that they be considered congeneric (in *Neoxolmis*).

That the monotypic *Gubernetes* and *Mus-*

TABLE 6
Characters Used for Phylogeny of the *Myiophobus* Group

	Character, description	Distribution by taxa
E	One or two A elements (usually A2 and A3, either fused or independently) form complete and calcified rings around bronchi, independent of tracheobronchial junction	All taxa in <i>Myiophobus</i> group
2	Plumage with concealed crown patch (lost in <i>Hirundinea</i>)	<i>Myiophobus</i> and <i>Pyrrhomias</i>
3	Trabecular plate on nasal septum not forked posteriorly	<i>Pyrrhomias</i> and <i>Hirundinea</i>
4	Narrow strand of cartilage located ventrally within internal tympaniform membrane, between ventral ends of B2 and B3	As above
5	Loss of intrinsic syringeal muscles	As above
6	Plumage with rufous underparts and wing pattern	As above
7	Nests built in niches or crevices	As above
8	Caudally pointing projection on posterior edge of each B2 element	<i>Pyrrhomias</i>
9	Internal cartilages narrow and very slightly J-shaped	<i>Pyrrhomias</i>
10	Internal cartilages broad and linear	<i>Hirundinea</i>
11	Concealed crown patch lost	<i>Hirundinea</i>

cippra are considered here to be sister taxa also will surprise many ornithologists, for this relationship is not readily apparent from external morphology, nor has it been suggested in the literature. Both have tails that are elongated and forked (character 20), but as Traylor and Fitzpatrick (1982) implied, this familiar "scissor" type tail "clearly serves to aid aerial maneuvering during long acrobatic sallies after flying prey," and could well be convergence. Syringeal morphology provides a more convincing argument for their close relationship, however, for here we have the second of two examples, within my *Muscisaxicola* group, of genera sharing syringeal characters that are unique for the group at large. In the syringes of both of these genera (fig. 27: 3, 4) the ventral end of the B2 element is Y-shaped or forked (character 21) and the dorsal end of the B1 element is bulbous or swollen (character 22). The nest of *Gubernetes* is reported to be a cup, located on the ground (Chubb, 1910); unfortunately the nest of *Muscipipra* is unreported.

I am not clear as to the basis for Warter's (1965, p. 130) tribal status for *Gubernetes* and two other long-tailed tyrants (*Colonia*, and *Yetapa* = *Alectrurus risora*), for I can find no details in his thesis other than his report that all of these taxa possess a "fluvicoline" skull. I have already discussed my reasons for omitting *Colonia* from my *Empidonax* assem-

blage—it lacks the character states of the nasal septum that define this assemblage—and I have argued in an earlier section that *Alectrurus* (including *Yetapa*) belongs in my *Ochthoeca* group. Warter does mention that *Gubernetes* has a fully ossified nasal capsule, but this is part of the generic diagnosis (character 23; fig. 6: 1, 2) that differentiates it from *Muscipipra*; this fully ossified condition has evolved independently in a number of genera within the assemblage, including *Alectrurus* and its close relatives, *Arundinicola* and *Fluvicola*.

Traylor (1977) noted some similarities between *Muscipipra* and the kingbirds (*Tyrannus*) and their allies, both in plumage and proportions, but cautiously retained the genus in his Fluvicolinae; Warter (1965) did not have access to a skull for his study. I have reported elsewhere (Lanyon, 1984b) on a skull of *Muscipipra* obtained from the Rijksmuseum in Leiden, which demonstrates that the genus can not be a member of the kingbird assemblage; the nasal septum of *Muscipipra* has a conspicuous anterior notch and is based by a large trabecular plate that is forked anteriorly, and thus has all of the derived character states characteristic of my *Empidonax* assemblage.

My only whole specimen of a *Muscipipra* syrinx (fig. 27: 4) lacks an obvious cartilaginous plug, which it should have (character

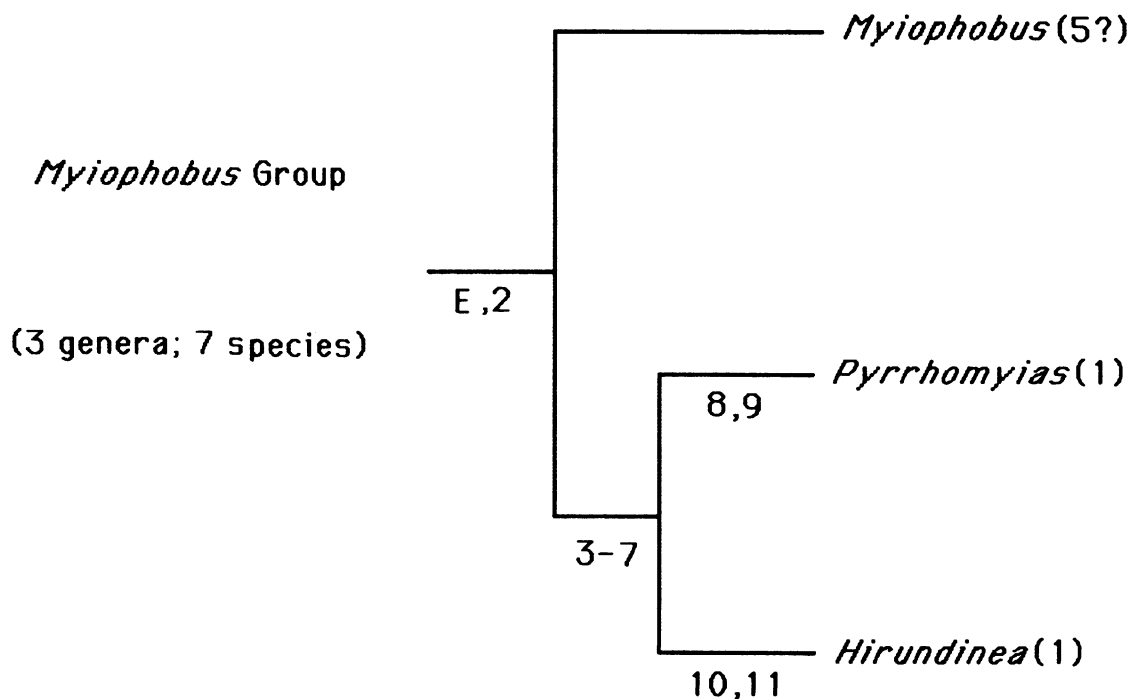


FIG. 28. Phylogenetic relationships within the *Myiophobus* group (3 genera; 7 species). Numbers identify diagnostic character states described in text and in table 6. Numbers in parentheses indicate number of species per genus.

D; table 1) to be a member of my *Muscisaxicola* group. Ames (1971) implied that his specimen did have this plug; his specimen had been damaged by shot, however, and by the time I obtained and stained it, there was no plug visible. The inclusion of *Muscipipra* within my *Muscisaxicola* group must be provisional, pending confirmation of this point in additional specimens when available.

The syrinx of *Muscipipra* is unique within the assemblage in having the A1 element conspicuously narrower than the A2, except at the expanded dorsal end (character 24; fig. 27: 4). It is the only genus within the *Myiotheretes* lineage that has apparently lost the buff or cinnamon-rufous pattern in the wing (character 25).

The *Myiophobus* Group (fig. 28 and table 6)

My *Myiophobus* group consists of *Myiophobus* and the two monotypic genera *Pyrrhomyias* and *Hirundinea*, an arrangement

consistent with that proposed by Hellmayr (1927), Zimmer (MS), and Meyer de Schauensee (1966). Warter (1965) considered *Pyrrhomyias* and *Myiophobus fasciatus* to have a type 6, fluvicoline septum, but he lacked a skull of *Hirundinea*. Traylor (1977) placed *Myiophobus* at the beginning of his Fluvicolinae, and included *Hirundinea* among "other peculiar monotypic genera" at the end of that subfamily; *Pyrrhomyias* was allied with *Mitrephanes* and *Contopus* on the basis of similarities in form, coloration, and habits.

A close relationship of *Pyrrhomyias* and *Hirundinea*, though not expressed in Traylor's classification (1977, 1979), was advocated by Fitzpatrick (in Traylor and Fitzpatrick, 1982): "The two genera share similar and unusual rufous wing patterns, calls, and 'pinched' bill tips; and both build the same style of nest. Furthermore, the peculiar swallow-like proportions of *Hirundinea* (tiny short tarsi and long pointed wings) make sense in light of the species' unparalleled specialization on aerial hawking from perches on cliff

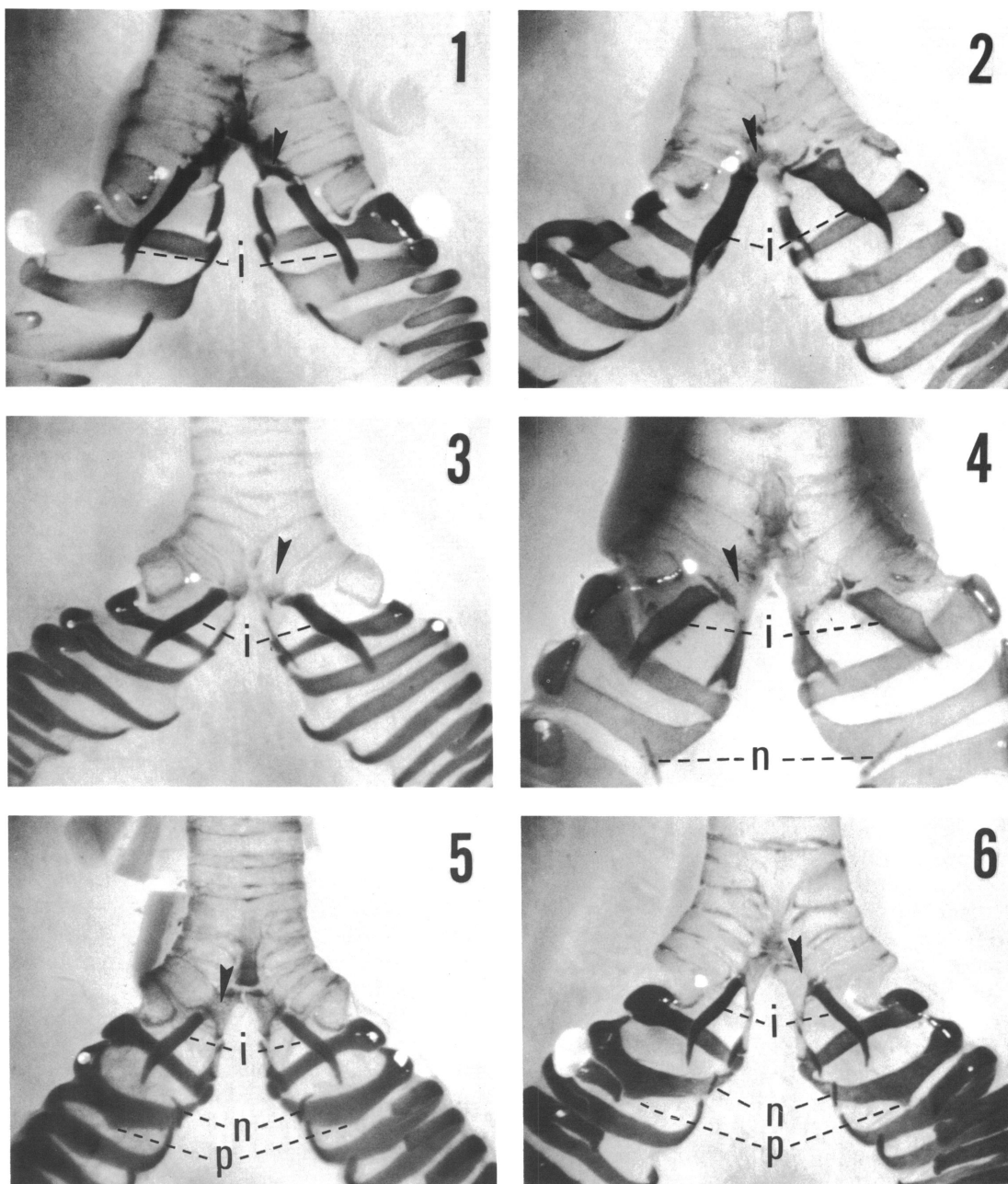


FIG. 29. The syringes of the three genera in the *Myiophobus* group (dorsal aspect; magnification = 15×): (1) *Myiophobus fasciatus*, LSU 102584; (2) *M. flavicans*, LSU 107656; (3) *M. inornatus*, LSU 98045; (4) *Hirundinea ferruginea*, USNM 504581; (5) *Pyrrhomys cinnamomeus*, PMNH 2057; (6) *P. cinnamomeus*, PMNH 2014. Arrows indicate calcified A element forming a complete ring around bronchus; i = internal cartilage; n = narrow strand of cartilage between ventral ends of B2 and B3 elements; p = caudally pointing projection on posterior edge of B2 element.

faces; this morphology is easily achieved from a *Pyrrhomys*-like ancestor."

I have argued in the section on putative relatives that *Myiophobus*, as constituted by

Traylor (1979), is polyphyletic. Species of *Myiophobus* known to possess a nasal septum characteristic of the *Empidonax* assemblage are *fasciatus*, *flavicans*, and *inornatus*. The only skull of *pulcher* examined was too badly preserved to be useful, and I have not seen a skull of *cryptoxanthus*; the latter two species are included in *Myiophobus* provisionally. I lack syringes of these two species as well.

These three genera (*Myiophobus*, *Pyrrhomyias*, and *Hirundinea*) cluster by virtue of their sharing the third basic type of syrinx discussed in my overview of syringeal morphology within the assemblage: one or two A elements (usually A2 and A3, either fused or independently) form complete and calcified rings around the bronchi (character E in figs. 12, 13, and 28; syringes illustrated in fig. 29). In some instances it is clear that it is the A3 element; rarely it is the A2 element or the A4 element that is complete; more commonly both the A2 and the A3 are fused in varying degrees to form a single complete ring around each bronchus. This variation seems not to be correlated with generic boundaries, though the only examples of a complete A4 element in my sample were in one specimen of *Pyrrhomyias* and one of *Hirundinea*. The calcified pessulus in all specimens from this group is probably a correlate of the greater degree of calcification and completeness of the A elements described above. There is no sign of a plug of tissue just caudal to the tracheo-bronchial junction and between the medial segments of the A2 elements (i.e., character D, figs. 12 and 13, is lacking).

Concordant with this clustering on the basis of syringeal morphology is the concealed crown patch in the plumage of *Myiophobus* and *Pyrrhomyias*, also unique within the assemblage (character 2). *Hirundinea* is presumed to have lost this character.

The monotypic *Pyrrhomyias* and *Hirundinea* are considered closest relatives because they share derived characters in the nasal septum, syrinx, plumage, and nesting behavior. The trabecular plate along the ventral edge of the nasal septum, though it has the anterior notch characteristic of this assemblage (fig. 4: 2), is not conspicuously forked posteriorly in either species (character 3; fig. 6: 3, 4). This character state, involving a greater degree of ossification in that region, is presumed to be derived. In the syrinx there is a narrow strand

of cartilage located ventrally within the internal tympaniform membrane, between the ventral ends of the B2 and B3 elements (character 4; fig. 29: 4–6); I have not seen this elsewhere within the assemblage. In addition, my specimens of *Pyrrhomyias* and *Hirundinea* lack intrinsic syringeal muscles (character 5). Ames (1971) reported the absence of these muscles in *Pyrrhomyias* but did not have access to a specimen of *Hirundinea*. He found that most tyrant flycatchers possess a single intrinsic muscle, M. obliquus ventralis; most of the genera that he found lacking it were brought together in his “*Myiobius*” group, including *Pyrrhomyias*. I think it more likely that the M. obliquus ventralis has been lost independently at least twice during evolution of this family, and that one of these losses occurred in the ancestor of *Pyrrhomyias* and *Hirundinea*. The plumage in both species is largely cinnamon-rufous, with concentrations of this pigmentation on the underparts and in the remiges (character 6).

The two species of *Myiophobus* for which I have nest records (*cryptoxanthus* and *fasciatus*) suspend their cup nest in a horizontal fork of a bush or tree, in the manner of a vireo; the eggs are white, sparingly to moderately blotched with reddish-brown (AMNH and WFVZ collections; Taczanowski, 1884; Ihering, 1904; Gilliard, 1959; Herklots, 1961; Haverschmidt, 1968; Skutch, 1977; Belton, 1985). By way of contrast, though their eggs are marked like those of *Myiophobus*, both *Pyrrhomyias* and *Hirundinea* build cup nests that are partially hidden in niches or crevices or located on a sheltered ledge or beam (character 7; AMNH collection; Euler, 1900; Dinelli, 1918; Ewert, 1975; Belton, 1985), presumably a derived behavior pattern.

Generic distinction between *Pyrrhomyias* and *Hirundinea* is suggested by differences in their syringeal morphology: in the syrinx of *Pyrrhomyias* the posterior edge of each B2 element is not parallel to the anterior edge, as in *Hirundinea*, but possesses a conspicuous caudally pointing projection (character 8; fig. 29: 5, 6); the internal cartilages of *Pyrrhomyias* are narrow and very slightly J-shaped (character 9; fig. 29: 5, 6), while those of *Hirundinea* are broad and linear (character 10; fig. 29: 4). In addition, the concealed crown patch is presumed to have been lost in *Hirundinea* (character 11).

APPENDIX

List of anatomical specimens (352 skulls, 282 syringes) examined for developing a phylogeny of the *Empidonax* assemblage of flycatchers. Genera and species, including putative relatives, 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
<i>Aechmolphus mexicanus</i> . See <i>Xenotriccus mexicanus</i>		
<i>Agriornis andicola</i> (<i>albicauda</i>)	Lacking	Lacking
<i>A. livida</i>	USNM 227782, 318400– 318402	PMNH 19
<i>A. microptera</i>	USNM 227506	LSU 102445
<i>A. montana</i>	AMNH 7152, 7153	LSU 102446
<i>A. murina</i>	UK 78224	PMNH 2612
<i>Alectrurus risora</i>	AMNH 6658, 14473; UMMZ 158768, 158770, 158771	USNM 227318
<i>A. tricolor</i>	Lacking	Lacking
<i>Aphanotriccus audax</i>	LSU 108927	LSU 108498, 108499, 108927
<i>A. capitalis</i>	Lacking	AMNH 8244
<i>Arundinicola</i> <i>leucocephala</i>	AMNH 6703; USNM 321637, 346037	CM 1344; LSU 110632, 111084, 120096; USNM 227314, 227315
<i>Cnemarchus</i> <i>erythropygius</i>	LSU 113675	LSU 91521
<i>C. rufipennis</i> . See <i>Polioxolmis rufipennis</i>		
<i>Cnemotriccus</i> <i>fuscatus</i>	AMNH 6685; USNM 344187, 346049, 346050, 347165, 491831	LSU 68605, 101499, 114499; USNM 505993
<i>Colonia colonus</i>	AMNH 11612, 11613; USNM 346044–346046	AMNH 6757, 8096, 8097, 8239, 8240; LSU 102552
<i>Colorhamphus</i> <i>parvirostris</i>	FMNH 316920	FMNH 316920; USNM 511875, 536383
<i>Contopus albogularis</i>	Lacking	Lacking
<i>C. borealis</i>	AMNH 5670, 5904; USNM 224519, 498870, 499685	AMNH 6709; CM 2177; LSU 103450
<i>C. caribaeus</i>	PMNH 12124; USNM 553329, 553395, 555836, 555837	AMNH 8026–8028
<i>C. cinereus</i>	UMMZ 153236; USNM 288860–288862	LSU 101497, 102566
<i>C. fumigatus</i>	AMNH 8472; USNM 226729, 428867, 499360	AMNH 6763, 8585; LSU 102567
<i>C. latirostris</i>	USNM 487944, 488001, 501770, 501876, 501898	ROM 111691
<i>C. nigrescens</i>	LSU 117185	Lacking
<i>C. ochraceus</i>	Lacking	Lacking
<i>C. sordidulus</i>	AMNH 8389, 8434, 11394; USNM 499684	AMNH 6761, 6762
<i>C. virens</i>	AMNH 5636, 5693, 5790– 5792, 5913	AMNH 8379; UK 45187, 56733
<i>Empidonax affinis</i>	UMMZ 159156	USNM 506408

APPENDIX (*Continued*)

	Skulls	Syringes
<i>E. albigularis</i>	UK 69672	PMNH 9036
<i>E. alnorum</i>	AMNH 12873; USNM 290160, 491185	AMNH 12873
<i>E. atriceps</i>	AMNH 12692, 12693, 12698, 12701, 12706, 12722, 12723, 12725–12729, 12736, 12739, 12740; UMMZ 153239	AMNH 8780, 12701
<i>E. difficilis</i>	AMNH 14234; UMMZ 208993; USNM 498991	AMNH 8036; UK 66993
<i>E. euleri</i> . See <i>Lathrotriccus euleri</i>		
<i>E. flavescens</i>	AMNH 12785–12787, 12789, 12790; UMMZ 156488	PMNH 9045
<i>E. flaviventris</i>	AMNH 5476, 5768–5776, 8281, 10329, 12939	AMNH 6770, 6771, 12939
<i>E. fulvifrons</i>	LSU 31944; USNM 499797	MVZ 3825; ROM 112940
<i>E. griseipectus</i>	Lacking	Lacking
<i>E. hammondii</i>	AMNH 13884; FMNH 288099; USNM 554135	MVZ 4139; ROM 112165
<i>E. minimus</i>	AMNH 5562, 9999, 11055; USNM 492645, 499682, 557836	AMNH 6774, 6775, 8217
<i>E. oberholseri</i>	UMMZ 155406	PMNH 9516; UK 51240
<i>E. traillii</i>	AMNH 7178, 8483, 8805, 10238, 10240, 10245, 11031	AMNH 6765–6767
<i>E. virescens</i>	FMNH 289465; LSU 105277; USNM 321002, 498567, 498572	CM 2738; FMNH 106509
<i>E. wrightii</i>	UMMZ 159155; USNM 346504, 346505, 554718	UK 51239; PMNH 6661
<i>Fluvicola nengeta</i>	AMNH 14625	AMNH 6781
<i>F. pica</i>	AMNH 11603, 12068; USNM 344204	AMNH 2297, 2298, 11603
<i>Gubernetes yetapa</i>	AMNH 14469; UMMZ 200837, 202199–202201; USNM 488695	AMNH 8237; LSU 123024; USNM 227280; PMNH 2657
<i>Heteroxolmis dominicana</i>	AMNH 6652; UMMZ 158766	AMNH 6827
<i>Hirundinea ferruginea</i>	LSU 118266; UMMZ 200850	LSU 64809; USNM 504581
<i>Hymenops perspicillata</i>	AMNH 6646; UMMZ 157080; USNM 227514, 345139, 499369	AMNH 2456, 6788–6790
<i>Knipolegus aterrimus</i>	AMNH 7167; LSU 48835; USNM 227520	AMNH 2455, 6785
<i>K. cyanirostris</i>	AMNH 11474; LSU 95272	AMNH 6791
<i>K. hudsoni</i>	Lacking	USNM 227585
<i>K. lophotes</i>	USNM 321628	USNM 321649
<i>K. nigerrimus</i>	Lacking	AMNH 6786, 6787
<i>K. orenocensis</i>	LSU 116241	LSU 114490

APPENDIX (*Continued*)

	Skulls	Syringes
<i>K. poecilocercus</i>	Lacking	Lacking
<i>K. poecilurus</i>	FMNH 290299; ROM 114971; USNM 428693, 428721	FMNH 290390
<i>K. signatus</i>	Lacking	Lacking
<i>K. striaticeps</i>	USNM 227410	USNM 227317
<i>Lathrotriccus euleri</i>	AMNH 6934; LSU 73119, 91174; UMMZ 200848, 200849; USNM 556421	LSU 102571, 102573; USNM 227323, 512281
<i>Lessonia oreas</i>	LSU 42889	AMNH 3674, 6778
<i>L. rufa</i>	AMNH 14468; USNM 227779, 343092, 343094	AMNH 6776, 6777, 6779; USNM 227563
<i>Machetornis rixosus</i>	AMNH 6657; LACM 93329; PMNH 2705; UMMZ 157085–157087, 158792, 202203, 202204; USNM 499048	AMNH 6799, 6800; PMNH 2705, 2706
<i>Mecocerculus calopterus</i>	LSU 94087	Lacking
<i>M. leucophrys</i>	AMNH 10704	AMNH 4636, 6743, 6744, 8241, R. D. 17078, R. D. 17079; FMNH 319352
<i>M. poecilocercus</i>	LSU 84039	LSU 107665
<i>M. stictopterus</i>	LSU 84040	LSU 102653, 107667
<i>Mitrephanes olivaceus</i>	LSU 95428	LSU 108479
<i>M. phaeocercus</i>	AMNH 14475; USNM 429799	UK 51246
<i>Muscigralla brevicauda</i>	AMNH 7169; LSU 48837, 90009; UMMZ 156848	AMNH 3530, 6794–6796; LSU 113829
<i>Muscipipra vetula</i>	LMa	AMNH 6792; BM 1936.1.12
<i>Muscisaxicola albifrons</i>	UMMZ 202730	LSU 102461, 102464, 102466
<i>M. albilora</i>	LSU 90008	PMNH 2711, 2713
<i>M. alpina</i>	AMNH 6928, 6929	AMNH 6673; LSU 101486, 102466
<i>M. capistrata</i>	LSU 114268; UMMZ 212733	LSU 102457; PMNH 2710
<i>M. cinerea</i>	Lacking	Lacking
<i>M. flavinucha</i>	UMMZ 212734	LSU 113997; USNM 508337
<i>M. fluviatilis</i>	AMNH 7156; LSU 84029	Lacking
<i>M. frontalis</i>	LSU 101480	LSU 102460; PMNH 28, 30
<i>M. juninensis</i>	LSU 101478	LSU 101478, 102449, 102453, 113996
<i>M. macloviana</i>	UMMZ 136211	AMNH 6668, 6669
<i>M. maculirostris</i>	AMNH 5352, 5353, 7159	AMNH 6670, 6671
<i>M. rufivertex</i>	AMNH 7154, 7155, 7157	AMNH 6664, 6665
<i>Myiobius atricaudus</i>	AMNH 14157; LSU 48615, 108929; USNM 347711, 429195, 429785	LSU 108475; USNM 343906
<i>M. barbatus</i>	LSU 111552, 111557; UK 71554, 71848; UMMZ 133967, 153246, 153247, 156492, 219224, 219225; USNM 432171	AMNH 6661, R. D. 16986, R. D. 17009; LSU 75470; PMNH 2144, 6680

APPENDIX (*Continued*)

	Skulls	Syringes
<i>M. villosus</i>	LSU 99419, 99420, 99590, 107298	LSU 108473
<i>Myiophobus cryptoxanthus</i>	Lacking	Lacking
<i>M. fasciatus</i>	AMNH 7181; LSU 81265, 81266; USNM 318764, 346032, 347155	AMNH 4321; LSU 102584, 113850
<i>M. flavicans</i>	AMNH 14156; UMMZ 203823	LSU 107656
<i>M. inornatus</i>	LSU 99424	LSU 98045
" <i>Myiophobus</i> " <i>ochraceiventris</i>	AMNH 14155; LSU 74894, 74895	LSU 102581, 107658, 113743
" <i>M.</i> " <i>phoenicomitra</i>	LSU 86568	LSU 85982
<i>Myiophobus pulcher</i>	Lacking	ROM 118777
" <i>Myiophobus</i> " <i>roraimae</i>	FMNH 319446; LSU 107313	AMNH R. D. 17109; LSU 118050; USNM 504572, 504574, 504577
<i>Myiotheretes erythropygius</i> . See <i>Cnemarchus erythropygius</i>		
<i>M. fumigatus</i>	LSU 74885	CM 1789
<i>M. fusciorufus</i>	LSU 99397	LSU 102477, 102479, 102481
<i>M. pernix</i>	Lacking	Lacking
<i>M. rufipennis</i> . See <i>Polioxolmis rufipennis</i>		
<i>M. striaticollis</i>	AMNH 8459; USNM 289423, 428791	LSU 75469, 102476
<i>Myiotriccus ornatus</i>	AMNH 14158; FMNH 288172; LSU 86414, 90046	LSU 85983, 85984, 117203
<i>Neoxolmis rubetra</i>	USNM 227509	PMNH 4543
<i>N. rufiventris</i>	USNM 158053	PMNH 2746, 2859
<i>Nesotriccus ridgwayi</i>	AMNH 9210; LSU 42902	AMNH 8067, 8068
<i>Nuttallornis borealis</i> . See <i>Contopus borealis</i>		
<i>Ochthoeca cinnamomeiventris</i>	LSU 94055; UMMZ 203822; USNM 428926	LSU 104351
<i>O. diadema</i> . See <i>Silvicultrix diadema</i>		
<i>O. frontalis</i> . See <i>Silvicultrix frontalis</i>		
<i>O. fumicolor</i>	AMNH 9507, 9508; LSU 79820; USNM 428073, 428282, 428871	AMNH 4642, 4643, 7890, 8229
<i>O. leucophrys</i>	LSU 94052	AMNH 6666, 6707; LSU 75025
<i>O. oenanthoides</i>	AMNH 6931, 7162	AMNH 6706; LSU 102484, 102486, 102488
<i>O. parvirostris</i> . See <i>Colorhamphus parvirostris</i>		
<i>O. piurae</i>	Lacking	LSU 97546
<i>O. pulchella</i> . See <i>Silvicultrix pulchella</i>		
<i>O. rufipectoralis</i>	AMNH 7164; LSU 79823; USNM 428681	AMNH 3991; LSU 102491, 102492
<i>O. salvini</i>	LSU 81272	LSU 91523, 113835
<i>Ochthornis littoralis</i>	AMNH 14152; LSU 64864; USNM 429379	LSU 42873, 91222; USNM 504530
<i>Onychorhynchus coronatus</i>	AMNH 14163; LSU 50817; USNM 288900, 344910	AMNH 8781; LSU 102588, 110697, 115912

APPENDIX (*Continued*)

	Skulls	Syringes
<i>Polioxolmis rufipennis</i>	AMNH 7161	AMNH 4658; LSU 91519
<i>Polystictus pectoralis</i>	UMMZ 218535	
<i>Pyrocephalus rubinus</i>	AMNH 6701, 7168, 8049, 8416	AMNH 6724, 6727; PMNH 2188, 4820; USNM 20546, 20552, 20578, 504529
<i>Pyrope pyrope</i> . See <i>Xolmis pyrope</i>		
<i>Pyrrhomys cinnamomea</i>	AMNH 7179; LSU 74891, 79825; USNM 428730	LSU 107652; PMNH 2014, 2057
<i>Satrapa icterophrys</i>	AMNH 14477	AMNH 2457, 2458, 6718; USNM 227927
<i>Sayornis nigricans</i>	UMMZ 73948; USNM 492520, 492705, 498795, 555323, 555324	AMNH 4158, 6735; LSU 102550; PMNH 4695
<i>S. phoebe</i>	AMNH 2449, 5668, 5708, 5810, 6175, 6183, 6223, 11376, 13460	AMNH 6732, 6733, 8199
<i>S. saya</i>	AMNH 8477; USNM 492699, 553956, 554132, 554133	AMNH 824924
<i>Silvicultrix diadema</i>	LSU 84151	CM 1793; LSU 112839, 112842
<i>S. frontalis</i>	LSU 74887; UK 80547; UMMZ 203820	LSU 102500, 102527, 102529
<i>S. pulchella</i>	AMNH 6930; UMMZ 203821	AMNH 3521; LSU 79595, 81151, 86222
<i>Terenotriccus erythrurus</i>	AMNH 5799; LSU 42891, 111566, 111570; UMMZ 153244, 153245, 214047, 214048; USNM 347158	AMNH 8261, R. D. 16972; LSU 108469; UK 65481
<i>Tumbezia salvini</i> . See <i>Ochthoeca salvini</i>		
<i>Xenotriccus callizonus</i>	AMNH 11392	AMNH 4161
<i>X. mexicanus</i>	UMMZ 210532	AMNH 8789; ROM 109631
<i>Xolmis cinerea</i>	USNM 227697	AMNH 6829; BM 1969.13.54
<i>X. coronata</i>	UMMZ 158765	PMNH 2818, 2820
<i>X. dominicana</i> . See <i>Heteroxolmis dominicana</i>		
<i>X. irupero</i>	AMNH 6687; USNM 227449, 499081	AMNH 2450, 6822, 6823, 6825, 6826
<i>X. murina</i> . See <i>Agriornis murina</i>		
<i>X. pyrope</i>	USNM 322958, 490885, 490884, 491017	AMNH 2451; PMNH 14, 2832; USNM 227960, 227982
<i>X. velata</i>	FMNH 105656; USNM 321646	FMNH 106070; USNM 321645
<i>Yetapa risora</i> . See <i>Alectrurus risora</i>		
<i>Zimmerius bolivianus</i>	LSU 99434	FMNH 291668; LSU 70641
<i>Z. vilissimus</i>	AMNH 14553; UMMZ 133958	LSU 108939
<i>Z. viridiflavus</i>	USNM 344216	PMNH 1725, 1741

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