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A Phylogeny of the Kingbirds and Their Allies

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ABSTRACT

A phylogeny is developed for those genera of tyrant flycatchers known as the kingbirds and their allies: *Pitangus*, *Megarynchus*, *Myiozetetes*, *Conopias*, *Myiodynastes*, *Legatus*, *Empidonomus*, *Tyrannopsis*, and *Tyrannus*. Monophyly of the assemblage is established by two shared derived character states of the skull. Three putative relatives are excluded from this group: *Sirystes sibilator*, *Machetornis rixosus*, and *Muscipipra vetula*.

Generic limits and relationships are determined primarily on the morphology of the syrinx, and secondarily on nesting behavior and external morphology. The enigmatic *luteiventris* of Sclater (1858) is retained in *Myiozetetes* on the basis of syringeal morphology and nesting behavior. Al-

though possessing some unique morphological and behavioral characteristics, *Legatus* is shown to be closely allied with *Myiozetetes*. Three new monotypic genera are recognized: *Phelpsia* for *Conopias inornata*, *Philohydor* for *Pitangus lictor*, and *Griseotyrannus* for *Empidonomus aurantioatrocrisatus*.

A classification of the 12 genera recognized in this assemblage might reasonably follow this sequence, based on the relationships demonstrated here: *Tyrannus*, *Empidonomus*, *Griseotyrannus*, *Tyrannopsis*, *Megarynchus*, *Conopias*, *Myiodynastes*, *Myiozetetes*, *Legatus*, *Philohydor*, *Pitangus*, and *Phelpsia*.

RESUMEN

Se elabora una filogenia para los géneros de tiránidos atrapamoscas conocidos como pitirres y sus géneros relacionados: *Pitangus*, *Megarynchus*, *Myiozetetes*, *Conopias*, *Myiodynastes*, *Legatus*, *Empidonomus*, *Tyrannopsis* y *Tyrannus*. Se establece la monofilia de este conjunto, basándose

en dos estados de características derivadas craneales que ellos poseen. Tres putativas especies relacionadas están excluidas de este grupo: *Sirystes sibilator*, *Machetornis rixosus*, y *Muscipipra vetula*.

Los límites y relaciones genéricas se han deter-

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minado, basándose principalmente en la morfología de la siringe y, secundariamente, en el comportamiento de anidación y morfología externa. El enigmático *luteiventris* de Sclater (1858) está retenido en *Myiozetetes* basándose en la morfología de la siringe y comportamiento de anidación. Aunque *Legatus* muestra algunas características únicas de morfología y del comportamiento, el género está íntimamente relacionado con *Myiozetetes*. Se reconocen tres nuevos géneros mono-

típicos: *Phelpsia* para *Conopias inornatus*, *Philohydor* para *Pitangus lictor*, y *Griseotyrannus* para *Empidonomus aurantioatrocristatus*.

Basándose en las relaciones demostradas en el presente trabajo, una clasificación de los doce géneros incluidos en este conjunto, sigue la siguiente secuencia: *Tyrannus*, *Empidonomus*, *Griseotyrannus*, *Tyrannopsis*, *Megarynchus*, *Conopias*, *Myiodynastes*, *Myiozetetes*, *Legatus*, *Philohydor*, *Pitangus*, and *Phelpsia*.

INTRODUCTION

The tyrant flycatchers (Tyrannidae) whose relationships are discussed here are those that Hellmayr (1927) assigned exclusively to his subfamily Tyranninae, with the exception of *Sirystes*, now considered to belong to the myiarchine assemblage (Lanyon and Fitzpatrick, 1983; Lanyon, in press). They are the kingbirds (*Tyrannus*) and their allies—33 species of medium to large-sized, open country tyrants having relatively short tarsi and medium to long wings. Traylor (1977) placed them in his kingbird group, but synonymized three of Hellmayr's genera, thereby reducing the number of genera to nine: *Pitangus*, *Megarynchus*, *Myiozetetes*, *Conopias* (incl. *Coryphotriccus*), *Myiodynastes*, *Legatus*, *Empidonomus*, *Tyrannopsis*, and *Tyrannus* (incl. *Muscivora* and *Tolmarchus*). In the present study I recognize all of Traylor's genera, but create three new monotypic genera, thus raising the number of genera to 12. To the best of my knowledge no one previously has presented a phylogeny for this group.

I ask three questions: Is the group monophyletic? What are the limits of the various genera? What are the presumed genealogical relationships among the genera? The primary emphasis of these questions is on a comparative study of the skull and the syrinx, and a secondary consideration of nesting behavior and external morphology. This approach has proved effective in addressing similar questions with regard to the myiarchine flycatchers (Lanyon, in press) and holds promise for the eventual determination of a meaningful phylogeny of the family Tyrannidae (Traylor, 1977; Traylor and Fitzpatrick, 1982).

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METHODOLOGY

In developing my concepts of relationships among the tyrant flycatchers I have been influenced greatly 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. I accept the tyrant flycatchers (Tyrannidae) as being a monophyletic group on the basis of their possession of internal cartilages in the syrinx, structures uniquely derived within all suboscine birds; the exact limits of the Tyrannidae, particularly with respect to *Oxyruncus* and certain genera of manakins (Pipridae) have yet to be determined (Ames, 1971; Lanyon, ms; McKittrick, ms). For my outgroup comparisons I have examined the skulls of 129 of the 139 genera of New World Tyrannoidea (Tyrannidae, Pipridae, Cotingidae, Oxyruncidae, and Phytotomidae), and the syringes of 132 of these genera. Within the Tyrannidae (*sensu* T aylor, 1979), I have examined over 600 skulls of 88 of the 90 genera (*Culicivora* and *Xenopsaris* lacking), over 700 syringes of all 90 genera, and have data on the nesting behavior for 81.

Monophyly and the limits of the assemblage of kingbirds and their allies are determined by a consideration of shared derived character states of the skull. The nasal capsule is remarkably uniform in its morphology throughout this assemblage.

The syrinx is less conservative and its morphology is my principal basis for determining the limits of genera and relationships within the assemblage. 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." Whether it will ever be possible to establish transformation series for the variety of character states apparent in the morphology of the tyrannid syrinx remains to be demonstrated. At the present state of our knowledge we must rely on uniqueness of distribution of the character state as an indicator of 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). Secondary considerations are given to differentiation in nesting behavior and in external morphology, within groups whose monophyly has been established with syringeal characters. As character states are identified by which a genus or cluster of genera is separable, these character states are assigned numbers in the text that correspond to the numbers in the phylogenetic diagram in figure 1 and table 1.

In addition to the anatomical collections at the American Museum of Natural History (AMNH), New York, I borrowed specimens from the British Museum (Natural History) (BM), Tring; the Carnegie Museum of Natural History, Pittsburgh; the Conner Zoological Museum at Washington State University, Pullman; Field Museum of Natural History, Chicago; the Los Angeles County Museum of Natural History (LACM), Los Angeles; the Museu Ciencias Naturais in Rio Grande do Sul, Brazil; the Museu Paraense Emilio Goeldi 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, Ann Arbor; the Museum of Vertebrate Zoology at the University of California (MVZ), Berkeley; the National Museum of Natural History, Smithsonian Institution (USNM), Washington, D.C.; the Peabody Museum of Natural History at Yale University (PMNH), New Haven; the collection of Peter L. Ames, the collection of Pierce Brodkorb (PB), the Rijksmuseum van Natuurlijke Historie, Leiden; the Royal Ontario Museum in Toronto (ROM), Canada; and the Western Foundation of Vertebrate Zoology in Los Angeles. Specimens cited here are identified to collection by the abbreviations given above.

MONOPHYLY AND THE LIMITS OF THE ASSEMBLAGE

The kingbirds and their allies traditionally have been regarded as a natural assemblage since Berlepsch (1907) formally assigned them to a single subfamily, the Tyranninae, the arrangement later adopted by Hellmayr (1927) and all subsequent authors. Following the practice of the time, this clustering of

TABLE 1
Characters Used in Constructing Phylogeny

Character	Description	Distribution by Taxa
1	Ossified nasal septum, lacking transverse trabecular plate and conspicuous internal supporting rod	All kingbirds and their allies
2	Medial ridge in frontal region of skull	Same as above
3	A2 element alone forms complete ring around each bronchus	<i>Myiodynastes</i> , <i>Conopias</i> , <i>Megarynchus</i> , <i>Tyrannopsis</i> , <i>Tyrannus</i> , <i>Empidonomus</i> , and <i>Griseotyrannus</i>
4	Ventral connections of B1 and B2 elements symmetrically rounded	Same as above
5	Nest in cavities or crevices	<i>Myiodynastes</i> and <i>Conopias</i>
6	Ventral connections of B1 and B2 elements virtually touching one another	<i>Megarynchus</i> , <i>Tyrannopsis</i> , <i>Tyrannus</i> , <i>Empidonomus</i> , and <i>Griseotyrannus</i>
7	Build open, shallow, rather loosely constructed bowl or saucer-shaped nests	Same as above
8	J-shaped internal cartilages broader and more robust than in other genera	<i>Megarynchus</i> and <i>Tyrannopsis</i>
9	Outer primaries conspicuously notched	<i>Tyrannus</i> , <i>Empidonomus</i> , and <i>Griseotyrannus</i>
10	B elements below B5 form complete rings around each bronchus	<i>Griseotyrannus</i>
11	Internal cartilages located close to midline of syrinx, not splayed laterally	<i>Griseotyrannus</i>
12	Bronchi uniformly tubular	<i>Griseotyrannus</i>
13	Plumage uniformly smoky-gray below	<i>Griseotyrannus</i>
14	A3 element provides greater support for each bronchus, initially through fusion with A2 but ultimately as complete and independent ring	<i>Myiozetetes</i> , <i>Legatus</i> , <i>Philohydor</i> , <i>Pitangus</i> , and <i>Phelpsia</i>
15	Ventral connections of B1 and B2 elements flattened, not rounded	Same as above
16	A2 and A3 elements fuse medially to form one complete calcified ring around each bronchus	<i>Myiozetetes</i> and <i>Legatus</i>
17	Possession of second pair of intrinsic syringeal muscles	Same as above
18	Use untidy globular nests of grass	Same as above
19	Calcified pessulus continuous dorsally with dorsomedial ends of A4 and/or A5 elements	<i>Myiozetetes</i>
20	B1 element significantly shorter than B2	<i>Myiozetetes</i>
21	B1 and B2 diverge dorsally, forming a V configuration	<i>Myiozetetes</i>
22	Internal cartilages J-shaped, with ventrally directed arm extending nearly to ventral ends of B2 elements	<i>Legatus</i>
23	Pair of winglike plates project laterally from nasal septum	<i>Legatus</i>
24	Piratic nesting habits, using globular or pensile nests of other species	<i>Legatus</i>
25	A3 element forms complete ring around each bronchus	<i>Philohydor</i> , <i>Pitangus</i> , and <i>Phelpsia</i>
26	Both A2 and A3 elements form complete and independent rings around each bronchus	<i>Philohydor</i> and <i>Pitangus</i>

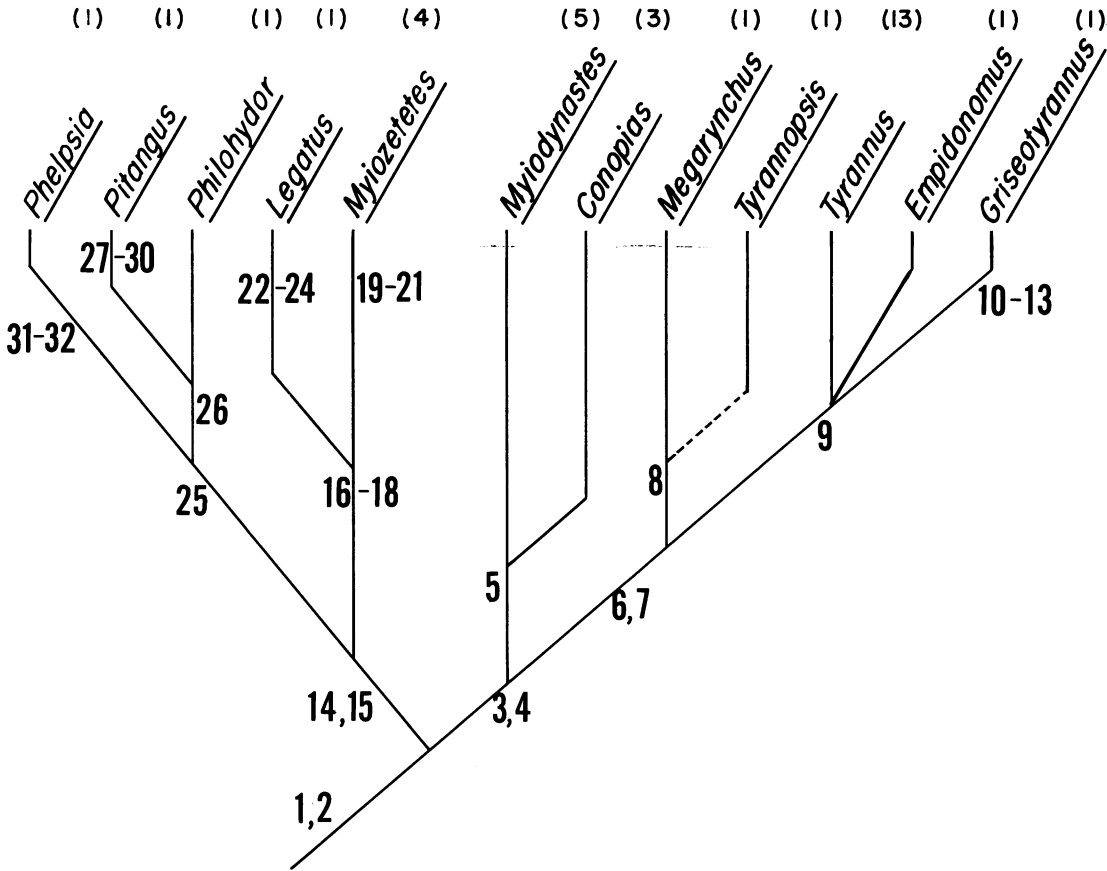


FIG. 1. Phylogenetic relationships among kingbirds and their allies. Numbers identify diagnostic character states described in text and in table 1. Numbers in parentheses indicate number of species per genus.

TABLE 1—(Continued)

Character	Description	Distribution by Taxa
27	Three A elements (A2, A3, A4) and sometimes four (A5) form complete rings around each bronchus	<i>Pitangus</i>
28	Internal cartilages broad, relatively short, truncated	<i>Pitangus</i>
29	Curvature of B2 element ventrally parallels that of B1, resulting in unique configuration	<i>Pitangus</i>
30	Nest large, untidy domed structure of twigs and coarse grasses, with side entrance	<i>Pitangus</i>
31	Internal cartilages attached to incomplete A2 elements	<i>Phelpsia</i>
32	Nest an open cup, saddled on branch and containing lichens and cobwebs	<i>Phelpsia</i>

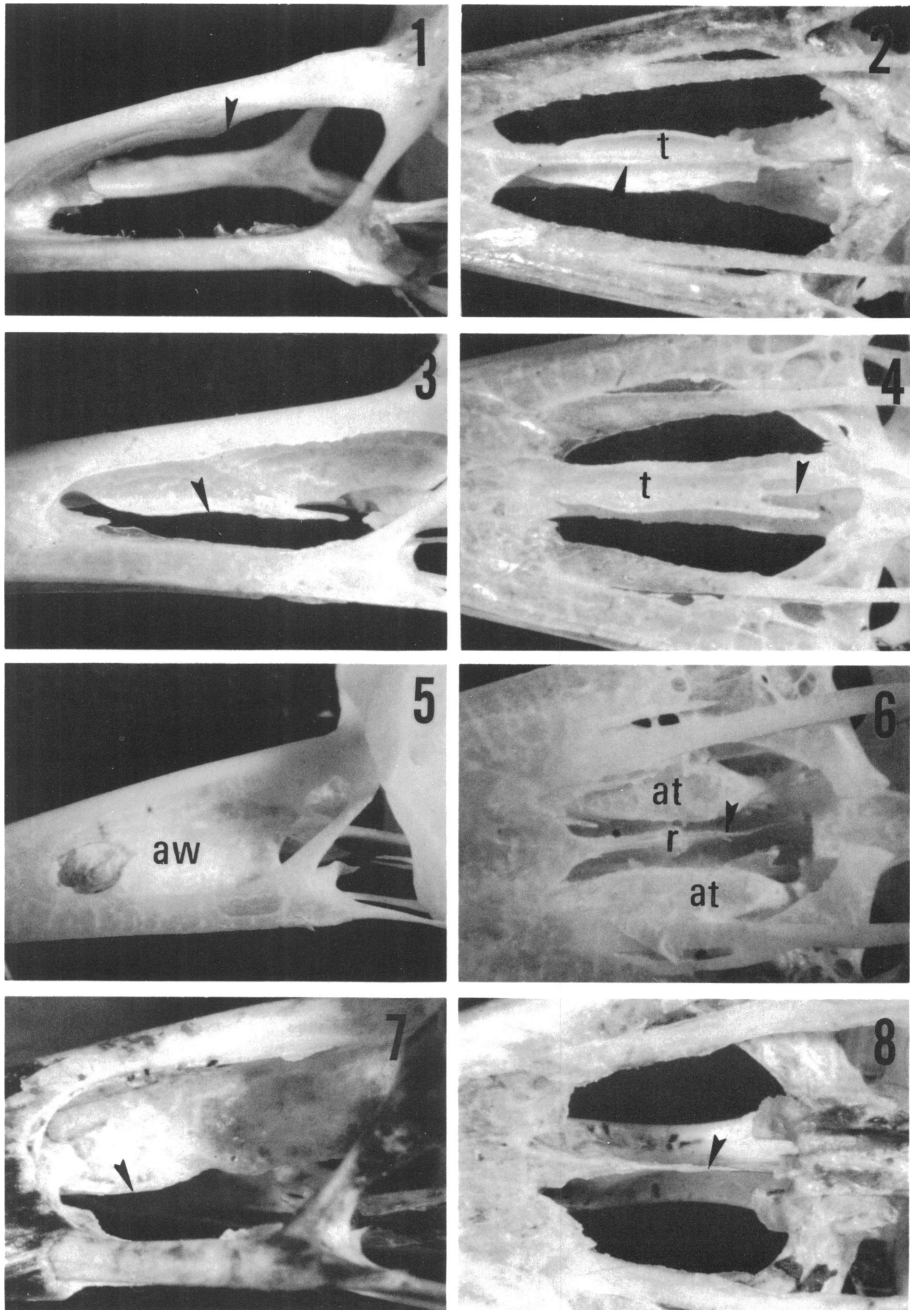


FIG. 2. Variation in appearance of nasal region of various tyrant flycatchers (anterior end of skull to left; magnification = $7\times$, except $12\times$ in 1): (1) *Lophotriccus pileatus*, USNM 428688, lateral view; (2) *Euscarthmus meloryphus*, AMNH 7183, ventral view; (3, 4) *Sayornis phoebe*, AMNH 6183, lateral and ventral views; (5, 6) *Myiarchus yucatanensis*, ROM 112155, lateral and ventral views; (7, 8) *Tyrannopsis sulphurea*, AMNH 11605, lateral and ventral views. Arrows indicate ventral edge of nasal septum; t = transverse trabecular plate; aw = alinasal wall; at = alinasal turbinals; r = internal supporting rod.

genera was based 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 (Ihering, 1904; Meise, 1949). But as Traylor (1977) noted, to derive an effective diagnosis of the assemblage based on mensural or external morphological characters is an exercise in futility.

Traylor (1977) was willing to adopt Hellmayr's treatment of this group after finding supporting data in the unpublished dissertation of Warter (1965) that suggested a remarkable uniformity in the cranium of these genera. It wasn't until this observation of Warter's that we had even the beginnings of a valid argument for monophyly.

Among the cranial complexes examined by Warter (1965), the one that offers the greatest potential for revealing phylogenetic relationships within the Tyrannidae is the nasal capsule (Lanyon, in press). As Warter has 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 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. Tyrant flycatchers exhibit a great array of character states of the nasal capsule, ranging from 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 (as in *Lophotriccus pileatus*, fig. 2:1), to virtually complete septa replete with transverse trabecular plates (as in *Euscarthmus meloryphus*, fig. 2:2 and *Sayornis phoebe*, fig. 2:3 and 4). In the myiarchine flycatchers the nasal capsule is even more fully ossified; the bony outer alinasal wall obscures the medially located nasal septum when the skull is viewed in the lateral aspect, as in figure 2:5. In addition, the myiarchines have a conspicuous internal supporting rod within the nasal septum and ossified alinasal turbinals on each side of the septum (fig. 2:6).

In kingbirds and their allies the nasal capsule as a whole is rather poorly ossified, compared to the myiarchines, but the nasal septum is usually fully ossified and occupies virtually the entire mid-sagittal plane of the nasal region, as seen in the lateral view of the skull of *Tyrannopsis sulphurea*, figure 2:7. When this same skull is viewed ventrally it is seen that (fig. 2:8) the septum lacks the transverse trabecular plates found on the septa of more than half of the tyrant genera (as in fig. 2:2 and 4) and also lacks the conspicuous internal supporting rod that characterizes the septa of the myiarchines (compare ventral edge of septum in fig. 2:8 with ventral edge of septum in fig. 2:6).

All genera of kingbirds and their allies share this character state: a well-ossified nasal septum, lacking a transverse trabecular plate and a conspicuous internal supporting rod (character 1). They are separable from all other tyrant flycatchers on this character alone. Figure 3 illustrates the kinds of variation that I have found in my sample of 70 skulls from these genera. The ventral half of the septum may be less well-ossified and thereby not preserved in some museum specimens, as seen in the *Pitangus sulphuratus* skull in figure 3:1. The alinasal turbinals may become partially ossified, as seen in the *Myiozetetes granadensis* skull in figure 3:4. The only significant variant of this basic kingbird septum is found in *Legatus leucophaius*, a monotypic genus in which the septum is fully ossified (as seen in the lateral view in fig. 3:7) but possesses a pair of winglike plates that project laterally from the septum (fig. 3:8). No other tyrant genus has this type of modification of the septum. These plates are not transverse as in the trabecular plates of such genera as *Euscarthmus* and *Sayornis* (fig. 2), but instead are located in a plane running diagonally through the septum, as illustrated in figure 3:7 and 8.

I was delighted to discover an additional cranial character, heretofore unreported in the literature, that is shared by all the genera under consideration here. This is a medial ridge in the frontal region of the skull (character 2). There is much variation in the length and height of this ridge, both within species (fig. 4) and between species and genera (fig. 5).

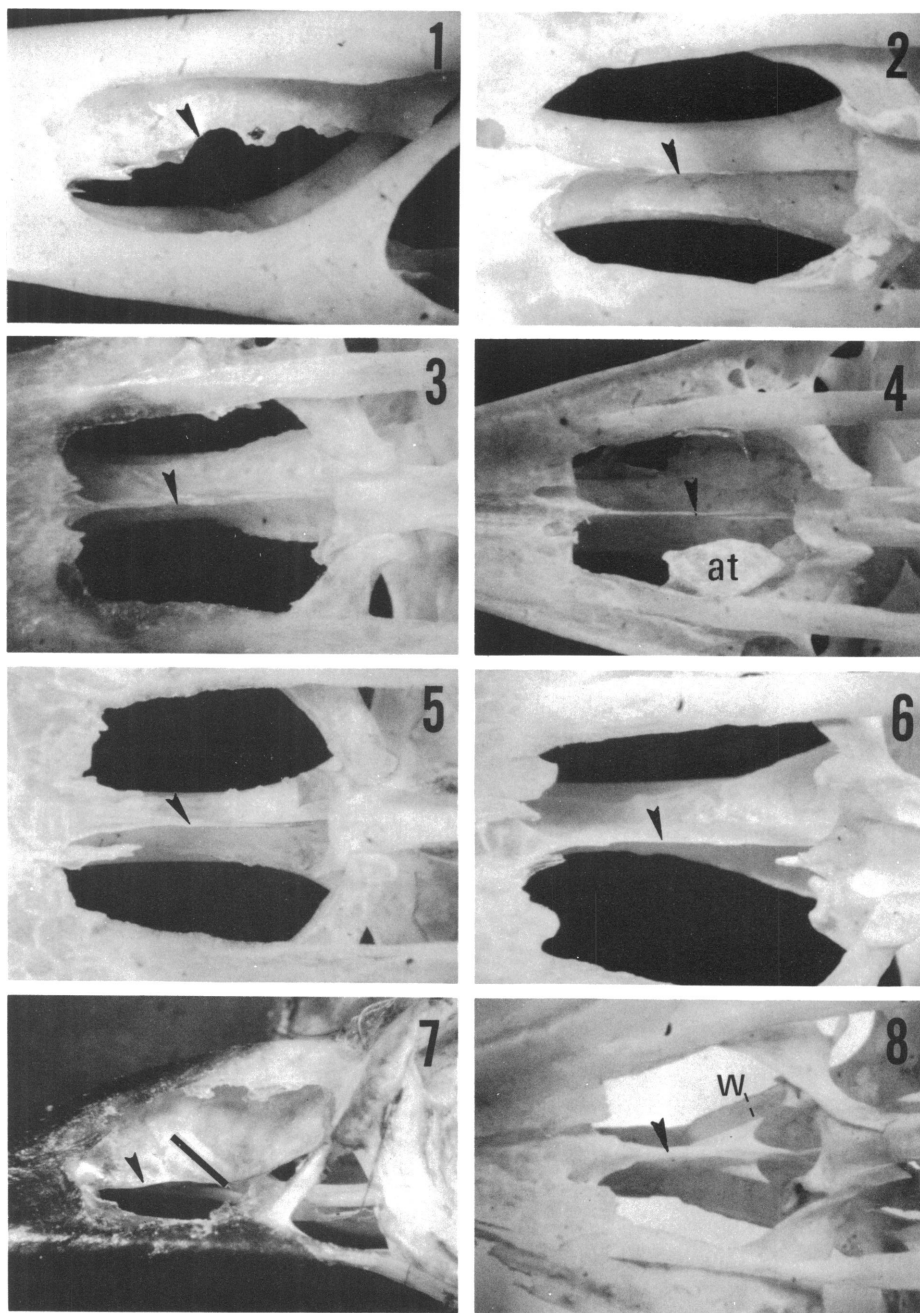


FIG. 3. Variation in appearance of nasal region of various genera within kingbird assemblage (anterior end of skull to left; magnification = $7\times$): (1, 2) *Pitangus sulphuratus*, AMNH 2823, lateral and ventral views; (3) *Tyrannus niveigularis*, LSU 100538, ventral view; (4) *Myiozetetes granadensis*, USNM 432167, ventral view; (5) *Myiodynastes luteiventris*, AMNH 11388, ventral view; (6) *Empidonomus varius*, USNM 346039, ventral view; (7) *Legatus leucophaius*, AMNH 11389, lateral view; (8) *L. leucophaius*, PB 26565, ventral view. Arrows indicate ventral edge of nasal septum; at = remnant of alinasal turbinals; w = winglike plates projecting laterally from the septum; bold line in 7 indicates diagonal plane of winglike plate.

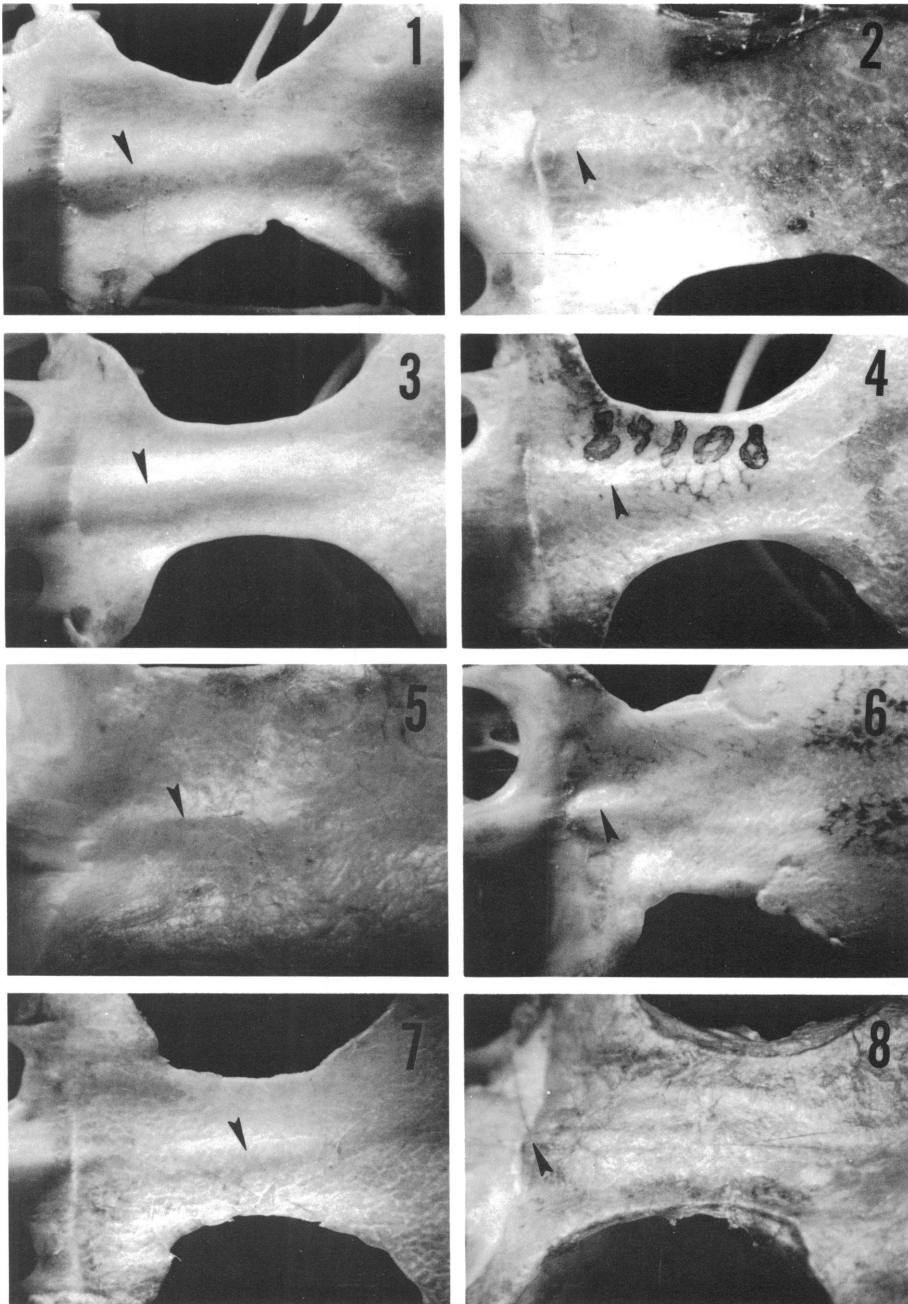


FIG. 4. Intraspecific variation in medial frontal ridge (indicated by arrows) in four species of kingbird allies (anterior end of skull to left; magnification = $5\times$): (1) *Pitangus sulphuratus*, AMNH 2823; (2) *P. sulphuratus*, AMNH 12574; (3) *Myiozetetes similis*, AMNH 7173; (4) *M. similis*, AMNH 10168; (5) *Megarynchus pitangua*, AMNH 11595; (6) *M. pitangua*, AMNH 8800; (7) *Legatus leucophaius*, AMNH 11389; (8) *L. leucophaius*, AMNH 11599.

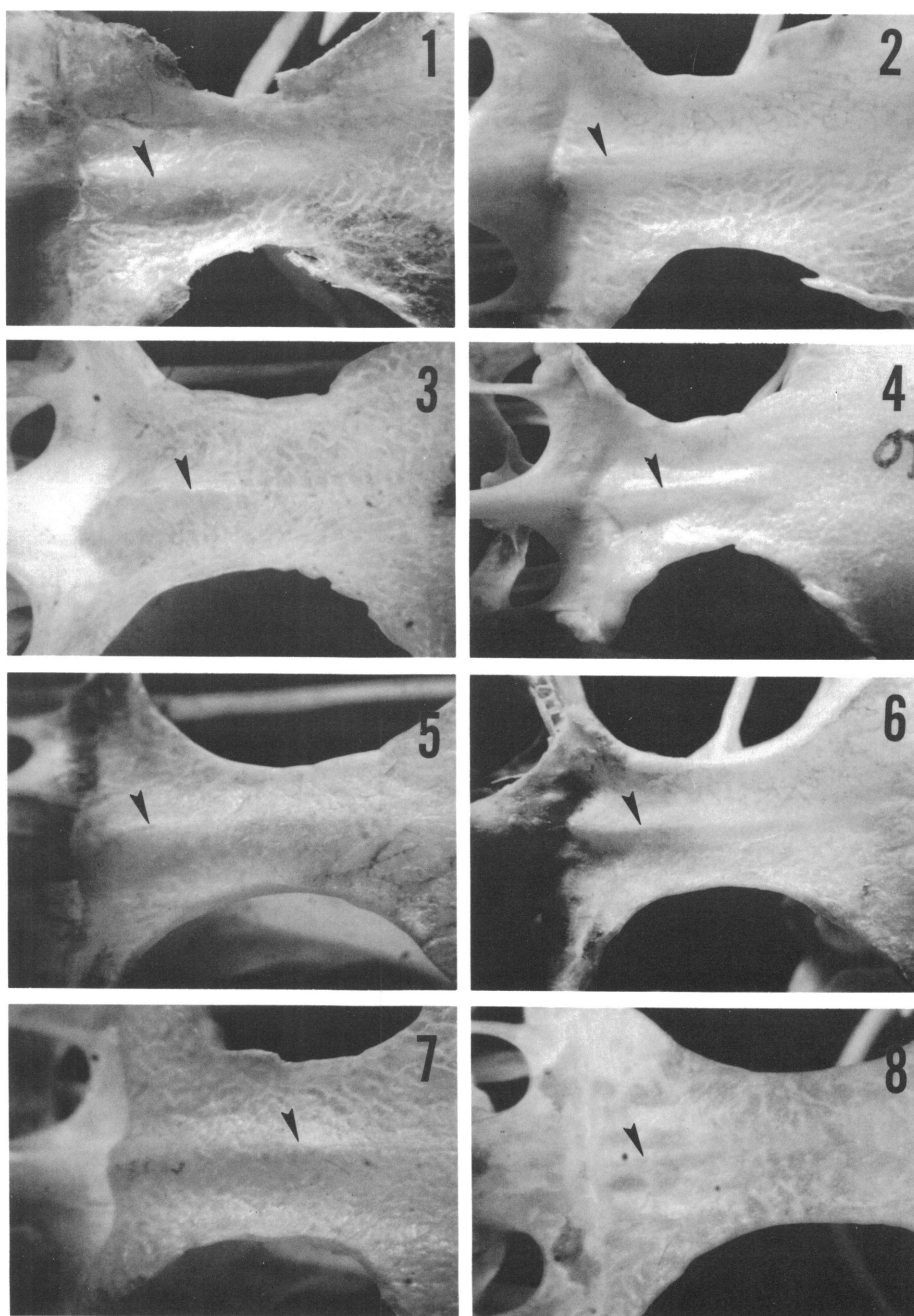


FIG. 5. Variation in medial frontal ridge (indicated by arrows) in six genera within kingbird assemblage (anterior end of skull to left; magnification = $5\times$): (1) *Tyrannus melancholicus*, AMNH 11600; (2) *T. tyrannus*, AMNH 5958; (3) *Myiodynastes luteiventris*, AMNH 11388; (4) *M. maculatus*, AMNH 6676; (5) *Philohydor lictor*, AMNH 12046; (6) *Conopias parva*, AMNH 11602; (7) *Griseotyrannus aurantioatrocristatus*, AMNH 6933; (8) *Myiozetetes luteiventris*, LSU 94068.

Within the assemblage it is least well-developed in *Legatus leucophaius*. In my sample of 12 *Legatus* skulls, the most conspicuous medial ridge was that illustrated in figure 4:7; but in four of these skulls there was only minimal suggestion of this character, in the form of a small, inconspicuous bulge or promontory just caudal to the nasal-frontal hinge (fig. 4:8, and in PB 26565, UMMZ 218960, USNM 428684, and 344909). The character appears to be derived within the Tyrannoidea and I have yet to find it in any tyrant genus outside of the kingbird assemblage with the single exception of the genus *Machetornis*, in which its presence is equivocal. A detailed discussion of the position of this putative relative of the kingbirds is given below.

In speculating on the function of this character, one is tempted to relate the frontal ridge to the special musculature that might be required to raise the coronal crests that are a feature of the plumage of nearly all species in this assemblage. Such a theory is less attractive, however, when one considers the presence of the ridge in the few species within the assemblage that lack these crests and especially the absence of any such cranial structure in many other tyrant genera that possess conspicuous crests.

In spite of the disquieting diversity of bill shapes and sizes and of plumage coloration and pattern among kingbirds and their allies, and the "array of foraging habits unparalleled in any other flycatcher group" (Fitzpatrick, 1978), I believe characters 1 and 2 provide a strong argument for monophyly.

We can now address the question of those genera whose close relationship to the kingbirds has been suggested in the literature. I am aware of three such putative relatives, all in monotypic genera: *Sirystes sibilator*, *Machetornis rixosus*, and *Muscipipra vetula*.

Ihering (1904), Berlepsch (1907), and Hellmayr (1927) included *Sirystes* within their assemblages, but Meise (1949) expressed uncertainty about this relationship. It was not until Warter's (1965) study of cranial anatomy that there was a suggestion of a closer affinity of *Sirystes* to *Myiarchus*, a recommendation later followed by Wetmore (1972) and Traylor (1977). In addition to having a

typically myiarchine nasal capsule, a fact that Warter appreciated and reported, *Sirystes* lacks the medial frontal ridge that diagnoses the kingbird group. Nesting and foraging behavior and syringeal morphology indicate unequivocally that *Sirystes* is a close relative of *Myiarchus* (Lanyon and Fitzpatrick, 1983), and I have placed it in a generic cluster with *Myiarchus*, *Casiornis*, and *Rhytipterna* in my phylogeny of the myiarchines (Lanyon, in press).

Fitzpatrick (1978) argued that *Machetornis* be placed in this kingbird group on the basis of behavior and external morphology, and I have acknowledged (Lanyon, in press) that the eggs of *Machetornis* are remarkably similar to those of the myiarchine flycatchers, which Traylor (1977) places in the same subfamily as the kingbirds and their allies. My observation reported above, that *Machetornis* has a somewhat equivocal expression of the medial ridge character that I use to define the kingbird assemblage, is a more compelling reason for a critical reexamination of this genus. All 10 skulls in my sample of *Machetornis* possessed a rather broad, raised area just caudal to the nasal-frontal hinge (fig. 6:1, 2); not ridgelike as in members of the kingbird assemblage, but similar enough to raise the specter of discordance. In fact, I suspect that some skulls of *Machetornis* would be more likely characterized as possessing a medial frontal ridge than those of *Legatus* in which the ridge is only minimally developed (as in fig. 4:8).

But *Machetornis* differs unequivocally from all members of the kingbird assemblage with respect to its nasal septum, which possesses a well-developed transverse trabecular plate located along the ventral edge of the septum (fig. 6:3), in the manner of most members of the tyrant subfamily Fluvicolinae (*sensu* Traylor, 1977; compare with fig. 2:2). In lateral view, the septum has an anterior notch (fig. 6:4) that is suggestive of fluvicoline septa (compare with fig. 2:3; Lanyon, ms). Moreover, the syrinx of *Machetornis* (fig. 6:5) has none of the derived characters that help to define the kingbirds and their allies, as discussed below. Instead, the calcified supporting elements of each bronchus are reduced to

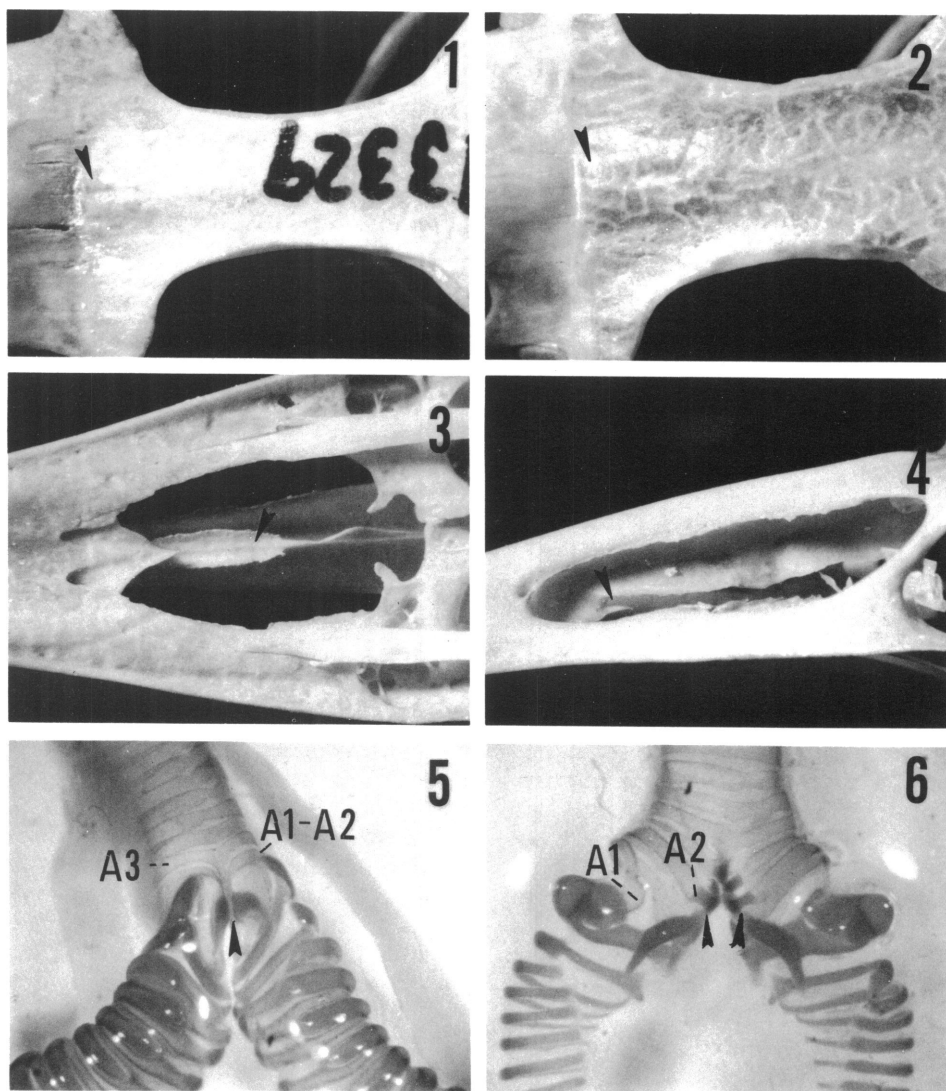


FIG. 6. Skulls and syringes of putative relatives of kingbirds and their allies (anterior ends of skulls to the left, magnification = 7 \times ; syringes viewed from dorsal aspect, magnification = 10 \times): (1) frontal region of *Machetornis rixosus*, LACM 93329; (2) frontal region of *M. rixosus*, AMNH 6657; (3) ventral view of nasal septum of *M. rixosus*, LACM 93329; (4) lateral view of nasal septum of *M. rixosus*, LACM 93329; (5) syrinx of *M. rixosus*, PMNH 2705; (6) syrinx of *Muscipipra vetula*, BM 1936.1.12. Arrows indicate broad raised area just caudad to the nasal-frontal hinge in 1 and 2, transverse trabecular plate in 3, anterior notch in nasal septum in 4, pair of internal cartilages located close to one another in 5, and attachment of internal cartilages to cartilaginous segments of A2 elements in 6. A elements as numbered in 5 and 6.

a single complete ring formed by the fusion of the A1 and A2 elements. The A3 element is a single complete ring around the trachea, from which a calcified projection extends into the tracheo-bronchial junction. Since the

bronchi are not splayed laterally as in the kingbird assemblage, the pair of small internal cartilages lie very close to one another medially. As Ames (1971) has reported, *Machetornis* lacks intrinsic syringeal mus-

cles, whereas all kingbirds and their allies possess at least one pair, the Mm. obliqui ventrales.

Muscipira is a little known tyrant restricted to southeastern South America; its nest is unknown (Traylor and Fitzpatrick, 1982). Hellmayr (1927) included it with his fluvicolines. Traylor (1977) noted some similarities with the kingbirds, both in plumage and proportions, but cautiously retained it in his Fluvicolinae, adding that it "may well prove to be a Tyrannine." Warter (1965) did not have access to a skull for his study. In the absence of any skeletal specimens in North America, I selected a study skin (AMNH 495581) that lacked data and removed skin and feathers from the frontal region. There was no suggestion of a medial frontal ridge on this specimen. Subsequently, G. F. Mees of the Rijksmuseum in Leiden lent me what may be the only extant skeletal specimen of this species, and I was able to examine and photograph both the frontal and nasal regions. In the Leiden specimen there is no suggestion of a medial frontal ridge either, and the nasal septum is typically fluvicoline in that there is a conspicuous anterior notch (as in fig. 2:3) and a large trabecular plate located along the ventral edge of the septum (as in fig. 2:4). The syrinx of *Muscipira* (fig. 6:6) is unlike the syringes of the kingbirds and their allies, as described below; the dorsomedial segments of the A2 elements, to which the internal cartilages are attached, are cartilaginous rather than calcified, and the A1 elements are widely separated from the A2s dorsally. *Muscipira* is a fluvicoline flycatcher, not a member of the kingbird assemblage.

Traylor (1977) placed the myiarchine flycatchers with Hellmayr's Tyranninae because of "identical cranial characters" noted by Warter (1965). Monophyly of Traylor's enlarged Tyranninae rests on the assumption that the myiarchine nasal septum, with its conspicuous internal supporting rod, has been derived from the somewhat simpler septum of the kingbird assemblage, or that both groups derived their septa from a common ancestor. Although one or the other of these assumptions may be true, this remains to be demonstrated. I would feel more comfortable if there were a uniquely derived character that linked the two lineages. For the present

I prefer to avoid the use of the subfamilial term, Tyranninae, either in the limited sense used by Berlepsch (1907) and Hellmayr (1927) or the more inclusive category adopted by Traylor (1977). Since *Tyrannus* is the oldest name and largest of the genera included in this group, it is appropriate to refer to the assemblage as consisting of the kingbirds and their allies.

GENERIC LIMITS AND RELATIONSHIPS

The syringes of the 12 genera in this assemblage have these anatomical features in common: the bronchi are splayed laterally and the internal tympaniform membranes oriented dorsally, so that the internal cartilages are easily observed; there is only one pair of internal cartilages, located dorsally within the internal tympaniform membranes, and these cartilages are attached to the dorsomedial segment of the calcified A2 elements (as labeled in fig. 7:1). These are features found elsewhere in the family Tyrannidae and not indicative of monophyly. But there are significant differences in syringeal morphology that occur in clusters of genera within the assemblage, and I hypothesize that these clusters represent natural groups.

More than two-thirds of the species of kingbirds and their allies (25 of 33) cluster together in what I consider to be a monophyletic group within the assemblage (the *Tyrannus* group; *Myiodynastes* through *Griseotyrannus* in fig. 1). They share the same basic syringeal morphology and none of the seven genera (with the exception of *Griseotyrannus*, a new genus described below) can be diagnosed unequivocally on the basis of the syrinx. There are two syringeal character states not found elsewhere in the assemblage that I presume to be derived and evidence for the monophyly of this *Tyrannus* group. In the first of these, only the A2 element forms a complete ring around each bronchus (character 3; as labeled in fig. 7:2); A1 and A3 are incomplete, i.e., do not form unbroken rings around each bronchus (as labeled in fig. 7:2), and A4 is incomplete in some specimens (seen clearly in fig. 7:1, 5, and 8). Secondly, this *Tyrannus* group is characterized by having the cartilaginous B1 and B2 elements

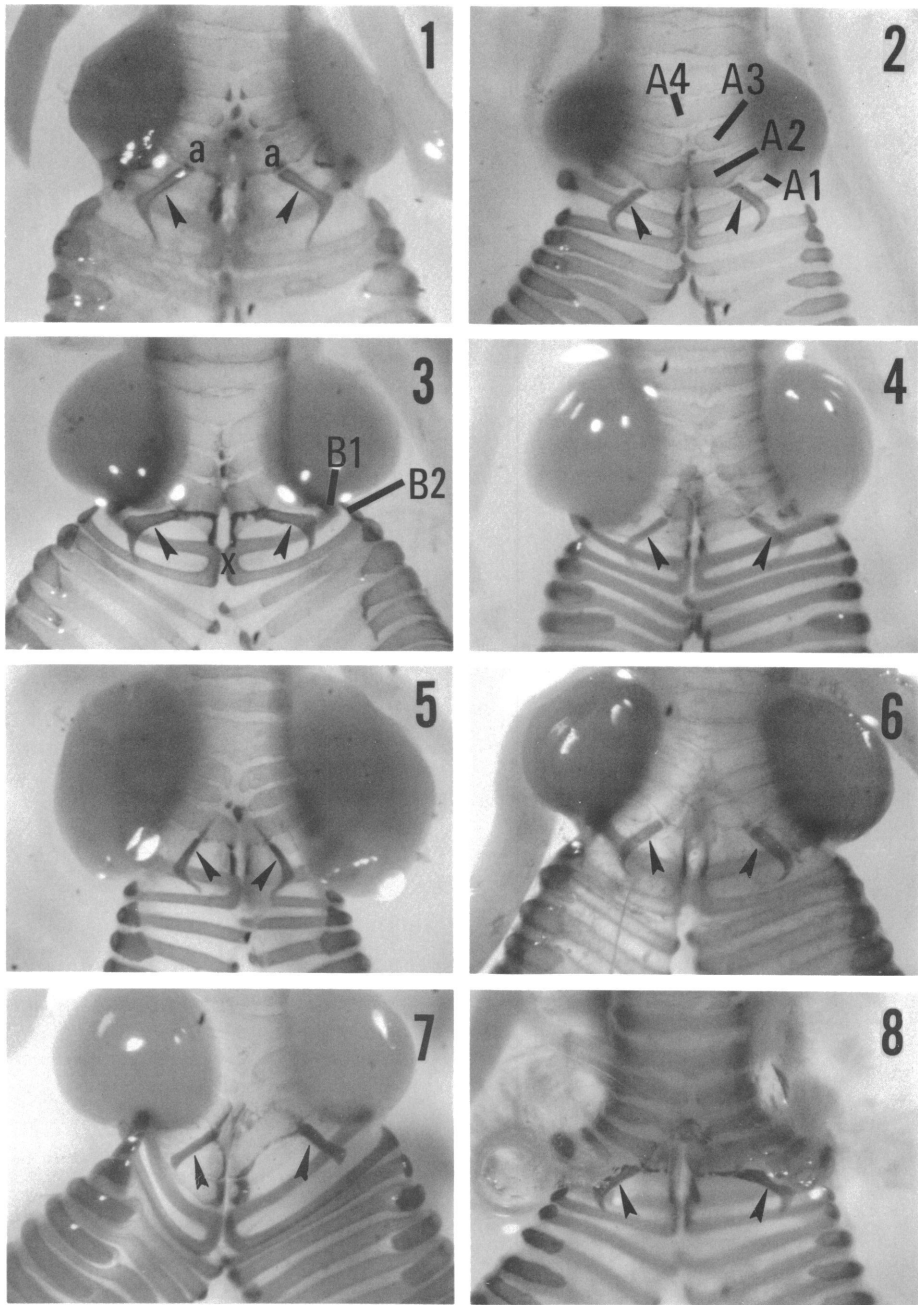


FIG. 7. Intrageneric variation in syrinxal morphology of eight species of *Tyrannus* (dorsal aspect; magnification = 10×): (1) *vociferans*, ROM 110113; (2) *melancholicus*, AMNH 6828; (3) *verticalis*, PMNH 12606; (4) *dominicensis*, AMNH 7968; (5) *forficatus*, PMNH 7422; (6) *caudifasciatus*, AMNH 8552; (7) *crassirostris*, UK 42008; (8) *cubensis*, AMNH 7972. Arrows indicate internal cartilages; a = attachment of cartilages to dorsomedial segment of A2 element; A1–A4 = calcified A elements; B1–B2 = cartilaginous B elements; x indicates rounded ventral connection of B1 and B2 elements.

attached to one another ventrally via a rather symmetrically rounded connection (character 4; as labeled in fig. 7:3). The internal cartilages are basically J- or L-shaped, a configuration that has evolved independently in a number of genera in other tyrant lineages. There is some variation between and within genera with regard to the length and width of these cartilages.

Within this *Tyrannus* group, two genera (*Myiodynastes* and *Conopias*) cluster together by virtue of their nesting in cavities or crevices (character 5), a derived behavior unlike that of any other genus in the entire assemblage. References for *Myiodynastes* include the following: *chrysocephalus*—in a niche of a vertical rock surface of a road cut (Ewert, 1975); *bairdii*—in holes or crevices (Marchant, 1960); *maculatus* and *luteiventris*—in natural tree cavities, abandoned woodpecker holes, niches at the bases of large palm fronds, bird boxes, and crevices in buildings (Bent, 1942; Gross, 1950; Skutch, 1960; Ligon, 1971; Wetmore, 1972); and *hemichrysus*—in the niches and recesses of epiphytes (Skutch, 1960). *Conopias* is less well known behaviorally, and I know of nesting reports for only one of the three species as the genus is constituted here; *parva* uses old woodpecker holes (Haverschmidt 1957, 1968) and, on one occasion, the deserted baglike nest of a cacique (*Cacicus*; Haverschmidt, 1973). The nesting behavior of *Conopias inornata* is uniquely derived and part of my reasoning for assigning this species to a new genus described below.

The syringes of *Myiodynastes* and *Conopias* (fig. 8:1–6) differ from those of the other genera within this group only by having the connections between the B1 and B2 elements further apart ventrally. The approximation of the ventral ends of the B1 and B2 elements is marked with an x in each of the syringes in figure 8; note that these elements are farther apart in photographs 1 through 6 (*Myiodynastes* and *Conopias*) than in photographs 7 and 8 (*Megarynchus* and *Tyrannopsis*) and in all photographs in figures 7 (*Tyrannus*) and 10 (*Tyrannus*, *Empidonotus*, and *Griseotyrannus*). I have examined syringes from four of the five species of *Myiodynastes* (12 specimens; *hemichrysus* lacking) and find little

intrageneric variation except in the length of the internal cartilages (fig. 8:1–4). The syringes of two of the three species of *Conopias* (seven specimens; *cinchoneti* lacking) also are very similar to one another; *inornata*, sometimes placed in *Conopias*, has a very distinctive syrinx and is assigned to a new genus described below.

Monophyly of the genus *Conopias* rests on the similarity in the syringes of *parva* and *trivirgata*, and cannot be argued further without knowledge of the syrinx of *cinchoneti* and the nesting behavior of *cinchoneti* and *trivirgata*. Ridgway (1906) created the monotypic genus *Coryphotriccus* for *parva*, on the basis of the bill being relatively longer than in other *Conopias*, and the fact that the crown of *parva* has a large concealed patch of yellow (Ridgway, 1907), unlike *trivirgata* and *cinchoneti*. Hellmayr (1927) and Wetmore (1972) followed Ridgway, whereas Meyer de Schauensee (1966), Haverschmidt (1968), and Traylor (1977) retained *parva* in *Conopias*. Generic separation of *Conopias* and *Myiodynastes* is readily effected by substantial differences in body size and in plumage pattern.

The remaining genera (*Megarynchus* through *Griseotyrannus*) in the *Tyrannus* group have syringes in which the ventral connections of the B1 and B2 elements virtually touch one another (character 6; fig. 8:7 and 8; figs. 7 and 10), unlike the syringes of other genera in this assemblage and of nearly all tyrant flycatchers in other lineages. Furthermore, these genera (*Megarynchus* through *Griseotyrannus*) all build open, shallow, and rather loosely constructed bowl or saucer-shaped nests (character 7), a type of nest not found elsewhere in this assemblage and presumably derived within the Tyrannidae. References to nesting in these genera include the following: *Megarynchus*—broad, shallow cup (Skutch, 1960; Haverschmidt, 1968; Wetmore, 1972); *Tyrannopsis*—frail, open cup (Herklots, 1961; Haverschmidt, 1968; French, 1973); *Tyrannus*—broad, shallow cup (Bent, 1942; Haverschmidt, 1968; Bond, 1971; Wetmore, 1972); *Empidonotus*—flimsy, saucer-shaped nest (Naumburg, 1930; Haverschmidt, 1968); and *Griseotyrannus*—“a rather careless structure of twigs and roots” (Barrows, 1883).

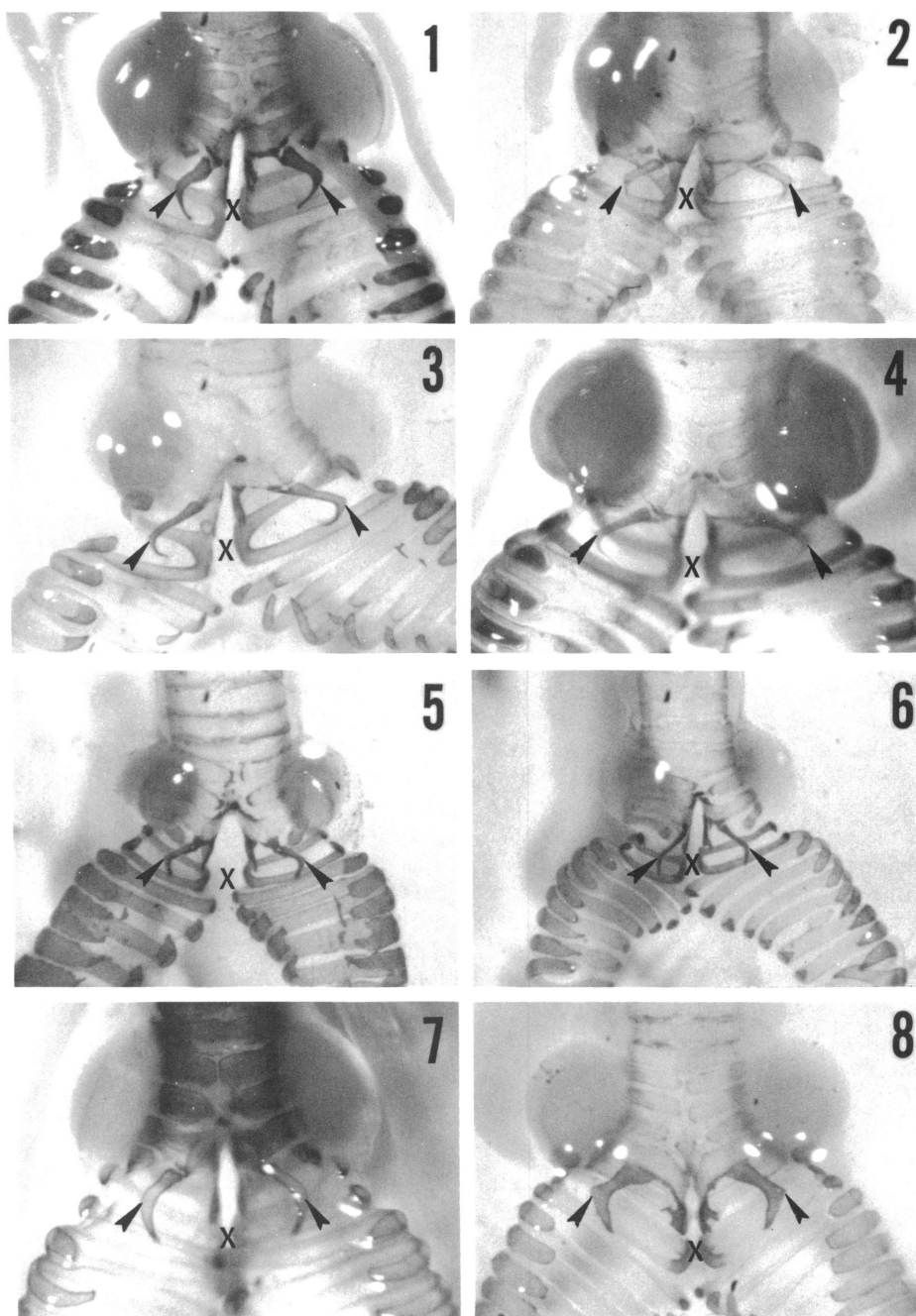


FIG. 8. Syringes of these four genera have a basic morphology similar to that of *Tyrannus* in figure 7 (dorsal aspect; magnification = 10 \times): (1) *Myiodynastes chrysocephalus*, MVZ 155007; (2) *M. bairdii*, P. L. Ames; (3) *M. maculatus*, LSU (SML 781); (4) *M. luteiventris*, UK 40654; (5) *Conopias parva*, LSU 108454; (6) *C. trivirgata*, PMNH 2683; (7) *Megarynchus pitangua*, AMNH 8317; (8) *Tyrannopsis sulphurea*, AMNH 8119. Arrows indicate internal cartilages; x indicates approximation of ventral ends of B1 and B2 elements.

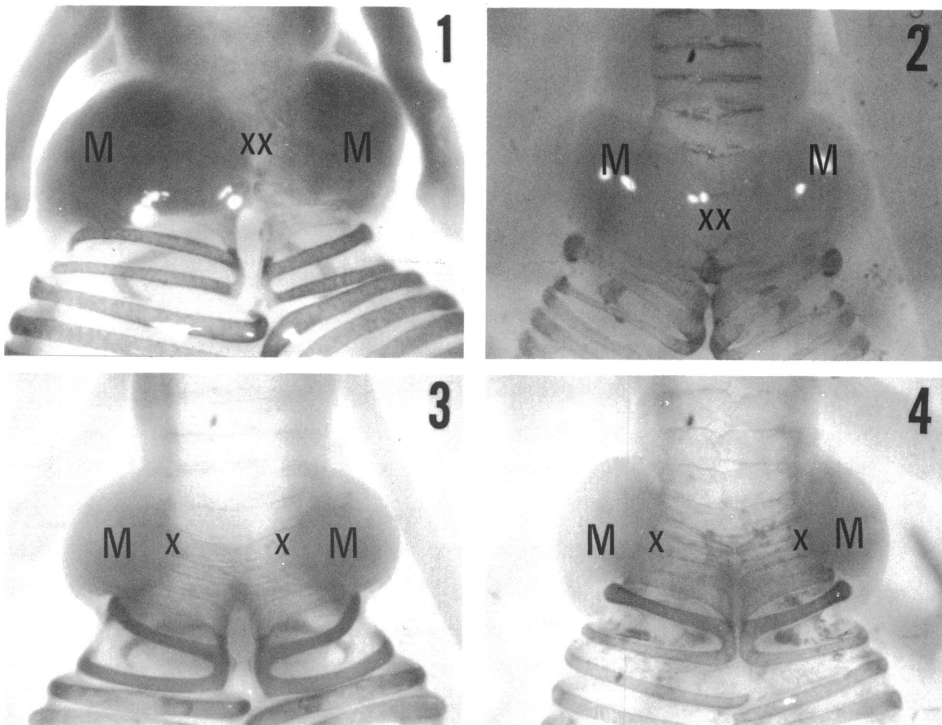


FIG. 9. Single pair of intrinsic syringeal muscles, Mm. obliqui ventrales (M), meet at ventral midline (medioventral contours indicated by x) in (1) *Megarynchus pitangua*, AMNH 4165, and (2) *Tyrannopsis sulphurea*, AMNH 8118, but are located more laterally in near relatives such as (3) *Myiodynastes luteiventris*, UK 40654, and (4) *Tyrannus caudifasciatus*, USNM 505724 (ventral aspect; magnification = 10 \times).

Megarynchus and *Tyrannopsis* may be each other's closest relatives by virtue of their sharing one syringeal character that is unique within the *Tyrannus* group, though this affinity is not obvious in terms of external morphology. In these two monotypic genera (four specimens of *Megarynchus* and two specimens of *Tyrannopsis* examined) the J-shaped internal cartilages are noticeably broader and more robust than those found in the other genera in the *Tyrannus* group (character 8; fig. 8:7 and 8, as compared with the internal cartilages in fig. 8:1–6 and in figs. 7 and 10).

There is a second syringeal character shared by *Megarynchus* and *Tyrannopsis* that is unique within this group, but its presence in all genera within the other branch of the assemblage and sporadically elsewhere in the family make it difficult to evaluate, and the polarity is unknown. All kingbirds and their

allies have a pair of intrinsic syringeal muscles, the Mm. obliqui ventrales (the short, broad, laterally bulging muscle masses seen in the syringes in figs. 7 and 8), and these muscles are present in one form or another in nearly all flycatchers (Ames, 1971). They are located laterally in the other five genera within the *Tyrannus* group, whereas they meet at the ventral midline in *Megarynchus* and *Tyrannopsis* (fig. 9). However, these muscles are located ventrally in all the genera in the other branch of this assemblage and their use for establishing relationships is equivocal at best.

Very distinctive differences in bill size and plumage pattern readily provide the generic diagnoses for *Megarynchus* and *Tyrannopsis*. *Tyrannopsis sulphurea* had been placed in *Myiozetetes* by most authors until Ridgway (1905) created a new genus for it, on the basis

of its "much larger and stouter bill, shorter and more rounded wing, shorter tail, and shorter tarsus." Hellmayr (1927) and subsequent authors have followed Ridgway, but have acknowledged a close affinity with *Myiozetetes*. As will be seen shortly, however, *Myiozetetes* has a syrinx and nesting habits that are very different from *Tyrannopsis* and the other members of this monophyletic *Tyrannus* group. The recommendation of Meise (1949) to merge *Tyrannopsis* with *Tyrannus* has found little favor, though Traylor (1977) considered *Tyrannus* to be its closest relative.

Although the monotypic *Empidonomus* and *Griseotyrannus* have plumage patterns not represented in *Tyrannus*, these three genera cluster together on the basis of their having the inner webs of the outer primaries conspicuously notched (character 9). As indicated earlier, I have avoided clustering genera on the basis of external morphology, which may be extremely plastic and equivocal. In this one instance, however, I feel justified that we are dealing with a derived state, for it is unique within the assemblage and only seven or eight tyrant genera in other subfamilies have evolved similarly modified outer primaries.

My sample of syringes of *Tyrannus*, the largest and most successful genus in this assemblage (40 specimens of 12 species examined; *couchii* lacking) is large enough to demonstrate the degree of intrageneric variation one may expect in syringeal morphology (fig. 7). The syringes of *T. forficata* and *T. savanna* (both formerly placed in *Muscivora*) and of *T. caudifasciatus* (formerly placed in *Tolmarchus*) do not differ from those of other kingbirds (fig. 7:5 and 6). Smith (1966) has reviewed *Muscivora* behaviorally and morphologically and concluded that the differences between *Muscivora* and *Tyrannus* are those that permit the former to exploit unusually open, savanna habitat; he argued for merger of the two genera and Traylor (1977) concurred. The merger of *Tolmarchus* with *Tyrannus* had been recommended by Meise (1949) and Bond (1956) and followed by Traylor (1977). The outer primaries of *caudifasciatus* lack the notching of the inner webs that characterize all other species of *Tyrannus*, but *T. crassirostris* is variable in this

respect, with some specimens lacking the notching altogether.

The plumage of *Empidonomus varius* is prominently streaked above and below, unlike *Tyrannus*, but similarities in the syrinx (fig. 10), nest (Naumburg, 1930), and foraging behavior (Fitzpatrick, 1978) are the basis for the traditional argument that the two genera are closely related. Furthermore, Meise (1949) has interpreted *Laphyctes apolites* Cabanis and Heine to be a hybrid between *E. varius* and *T. melancholicus*. I am unable to resolve whether *varius* is a sister group of *Tyrannus* or of *Griseotyrannus*, hence the trichotomy in figure 1.

The species *aurantioatrocristatus*, described 19 years after Vieillot described *varius*, is rather plain brown above and virtually uniformly gray throughout the underparts, quite unlike *varius* or any species in *Tyrannus*. Although originally assigned to *Tyrannus*, *aurantioatrocristatus* was aligned with *varius* by most workers soon after the genus *Empidonomus* was created for the latter (by Cabanis and Heine in 1859). Of *varius* and *aurantioatrocristatus* Traylor (1977) writes: "They are an obvious species pair, being almost identical in measurements, and having a long blackish crest with bright yellow vertex." No one in this century, to my knowledge, has questioned that they are congeneric, hence my surprise with the discovery that the syrinx of *aurantioatrocristatus* (four specimens examined) differs from that of *varius* (three specimens) in three notable characteristics. These differences in syringeal morphology are of a much greater magnitude than I have found within the genera of tyrant flycatchers examined thus far, and, when viewed together with the marked differences in plumage coloration and pattern, provide the basis for my proposing a new genus, named and diagnosed below.

GRISEOTYRANNUS, NEW GENUS

TYPE SPECIES: *T(yrannus) aurantio-atrocristatus* D'Orbigny and Lafresnaye (1837, p. 45)—Valle Grande, Santa Cruz, Bolivia; Paris Museum.

INCLUDED SPECIES: The type species only.

DISTRIBUTION: East-central and southern South America; see more detailed range for the species in Traylor (1979).

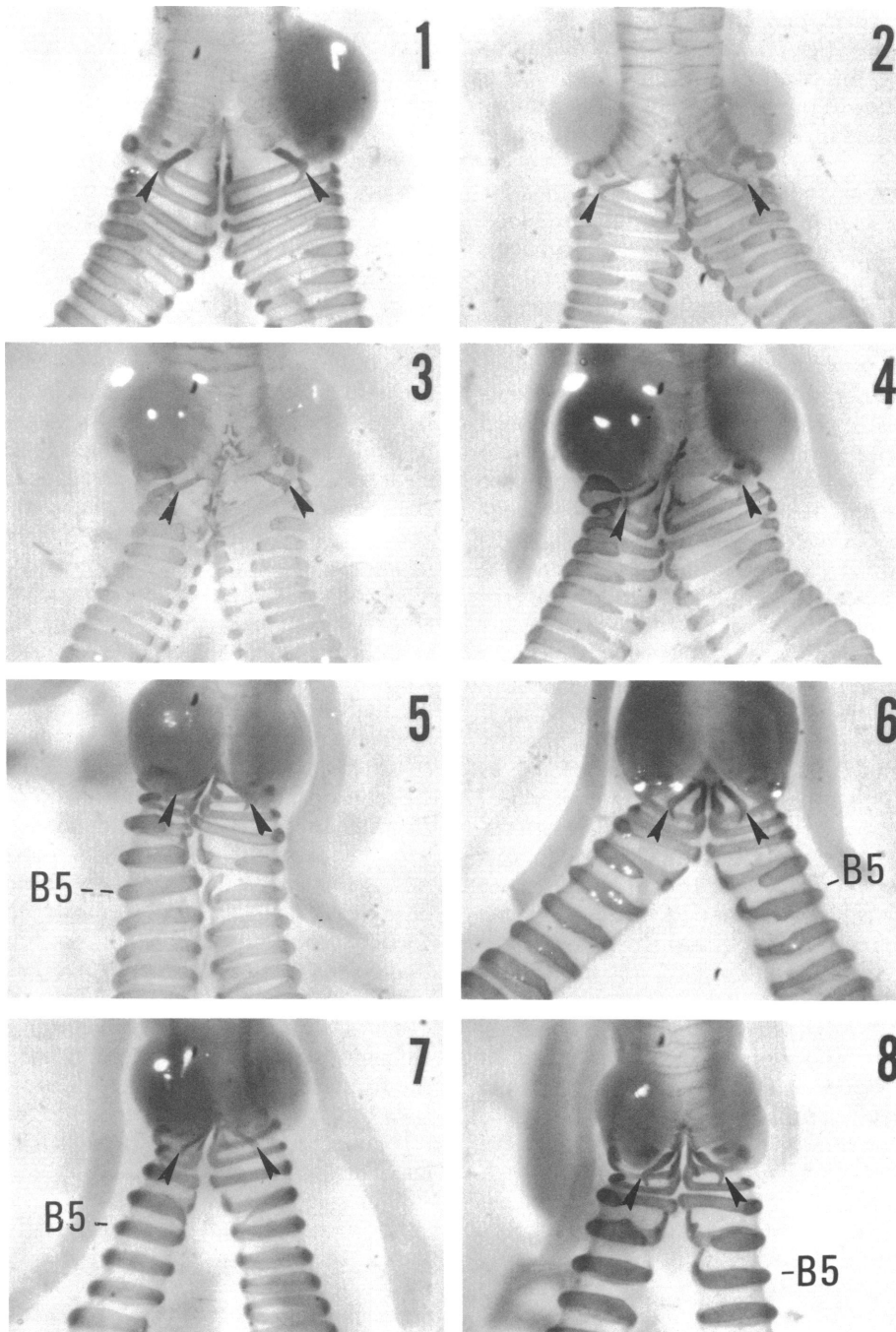


FIG. 10. Syrinx of *Empidonomus varius* (2–4) is like that of *Tyrannus* (1), whereas syrinx of *Griseotyrannus aurantioatrocristatus* (5–8) differs in that B elements below B5 form complete bronchial rings, internal cartilages (indicated by arrows) are more medial, and bronchi are more uniformly tubular throughout (dorsal aspect; magnification = 10×): (1) *Tyrannus albogularis*, PMNH 1788; (2) *Empidonomus varius*, AMNH 8122; (3) *E. varius*, AMNH 8123; (4) *E. varius*, USNM 505991; (5) *Griseotyrannus aurantioatrocristatus*, AMNH 6769; (6) *G. aurantioatrocristatus*, AMNH 6768; (7) *G. aurantioatrocristatus*, USNM 227215; (8) *G. aurantioatrocristatus*, AMNH 2462.

ETYMOLOGY: The Latin adjective *griseus*, pertaining to the smoky-gray or sooty plumage below, in combination with *tyrannus*, meaning tyrant or ruler as well as the generic name for the kingbirds, to which there is close affinity.

DIAGNOSIS: Separable from *Tyrannus* by its smaller size, more slender build, and black crown (semiconcealed yellow patch), and from both *Tyrannus* and *Empidonomus* by its smoky-gray throat, breast, and abdomen.

Griseotyrannus shares with *Tyrannus* and *Empidonomus* a basic syringeal morphology, notched inner webs of the outer primaries, similar nesting behavior (Barrows, 1883), and a similar method of foraging for food, wherein repeated sallies for aerial prey are made from exposed perches (Barrows, 1883; Fitzpatrick, 1978, 1980). That it deserves separate generic status is suggested by three syringeal characteristics illustrated in figure 10. The B elements below B5 form complete cartilaginous rings around each of the bronchi (character 10), whereas in all other genera in this assemblage (all tyrant flycatchers?) the B elements are always incomplete. Secondly, the internal cartilages are located closer to the midline of the syrinx (character 11), not splayed out laterally as they are in *Tyrannus*, *Empidonomus*, and all other genera in this assemblage. Thirdly, the bronchi are more uniformly tubular in shape throughout their length (character 12), without the expansion near the tracheal junction that characterizes the syringes of other genera of kingbirds and their allies. Furthermore, the uniformly smoky-gray underparts of the plumage of *Griseotyrannus* (character 13) are unique within this assemblage.

I have pointed out that the seven genera in the *Tyrannus* group (*Myiodynastes* through *Griseotyrannus* in fig. 1) share two syringeal character states: only the A2 element forms a complete ring around each bronchus (character 3) and the B1 and B2 elements have a rounded ventral connection (character 4). The remaining five genera (the *Myiozetetes* group; *Myiozetetes* through *Phelpsia* in fig. 1) form a sister group by virtue of their sharing two very different states of these syringeal characters. In these genera the A3 element provides greater support for each bronchus (character 14), initially through fusion with the A2 element but ultimately as a complete

and independent ring around each bronchus. Secondly, in these five genera the B1 and B2 elements in each bronchus have a *flattened* rather than rounded connection ventrally (character 15; fig. 11).

Within this remaining group of five genera, *Myiozetetes* and *Legatus* cluster together by virtue of their having the A3 element fuse medially with the A2 to form one complete calcified ring around each bronchus (character 16; fig. 11:1–5). In addition, Ames (1971) reports that these two genera possess a second pair of intrinsic syringeal muscles, the Mm. obliqui laterales, a derived character in the Tyrannidae (character 17). I am unable to confirm this with my syringes, which were cleared and stained to reveal supporting structures. The affinity between these two genera is supported by nesting habits as well, in that both use large, rather untidy globular nests of grass, having side entrances (character 18; Mitchell, 1957; Skutch, 1960; Haverschmidt, 1968; Wetmore, 1972; personal commun. with Mark Robbins). The four species of *Myiozetetes* construct their own nests, though the abandoned cup-shaped nests of other birds may be taken as a base of construction (Skutch, 1960; Wetmore, 1972). *Legatus*, the Piratic Flycatcher, does not build its own nest but appropriates the globular nests of *Myiozetetes* and *Pitangus* or the pendant nests of such genera as *Tolmomyias* and *Cacicus* (Naumburg, 1930; Skutch, 1960; Haverschmidt, 1968; Wetmore, 1972). The tendency for some *Myiozetetes* to utilize the nests of other birds in constructing their enclosed nests suggests a possible transition to the piratic behavior of *Legatus* in which the nest-building instinct has been reduced to lining stolen nests with a loose litter of dead leaves (Skutch, 1960).

The syrinx of *Myiozetetes* (14 specimens examined, from all four species) is unique within the entire assemblage with respect to the structure of the tracheo-bronchial junction, in which the calcified band (the pessulus) that is the principal support for the junction is continuous dorsally with the dorsomedial ends of the A4 and/or A5 elements (character 19; fig. 11:1–4). The B1 element is significantly shorter than the B2 (character 20), and these two elements are not parallel to one another but instead diverge prominently as they extend around to

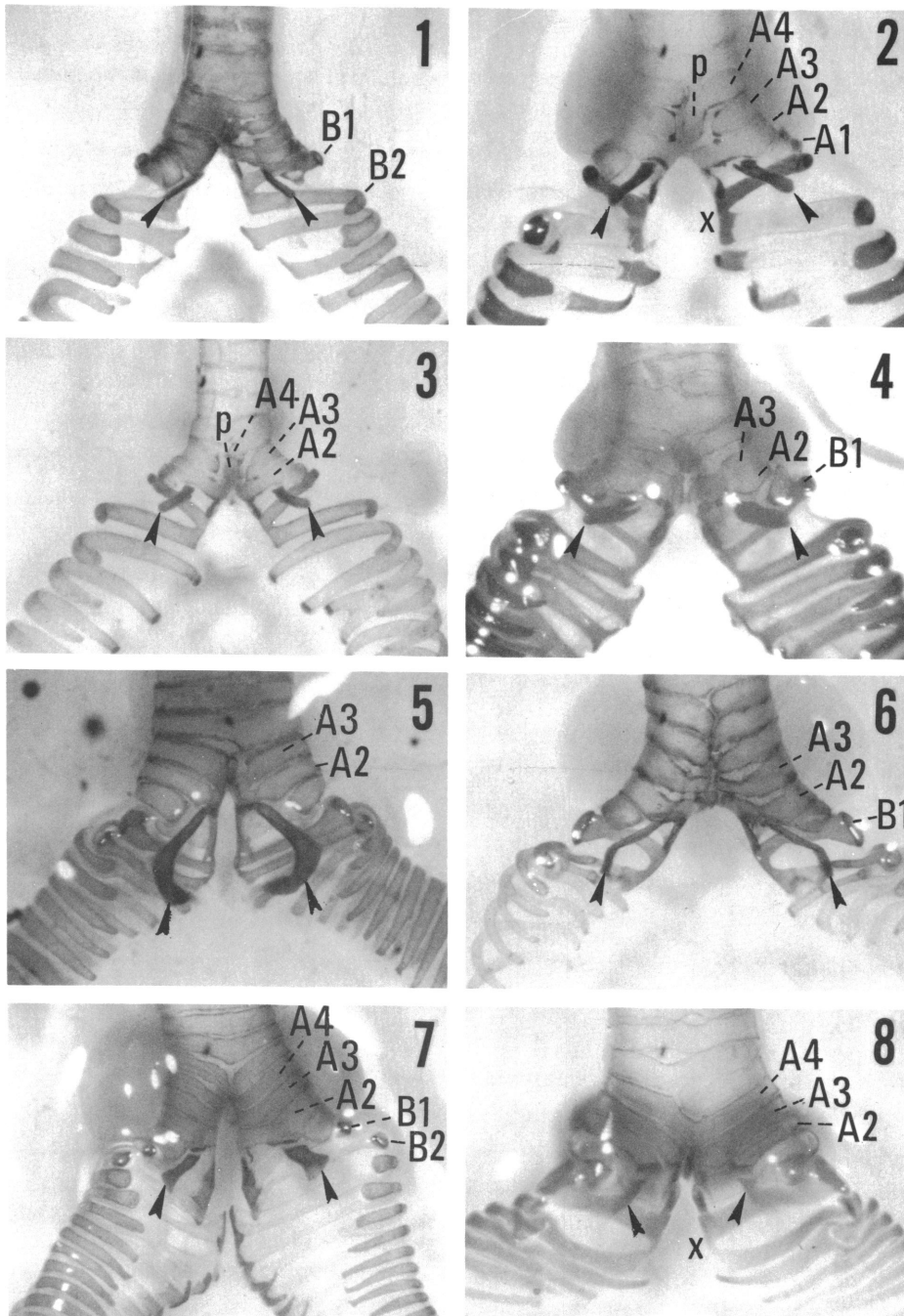


FIG. 11. Five genera of kingbird allies form a monophyletic group by virtue of their having other than solely the A2 element contributing to a complete ring around each bronchus and B1 and B2 elements with a flattened rather than rounded connection ventrally (indicated by x in 2 and 8): (1) *Myiozetetes cayanensis*, AMNH 8103; (2) *M. similis*, AMNH 6717; (3) *M. granadensis*, AMNH 8233; (4) *M. luteiventris*, LSU (DLD 497); (5) *Legatus leucophaeus*, AMNH 8131; (6) *Philohydor lictor*, AMNH 8100; (7) *Pitangus sulphuratus*, AMNH 7885; (8) *Phelpsia inornata*, AMNH 8391. A and B elements as labeled; p = pessulus, continuous with A4; arrows indicate internal cartilages (dorsal aspect; magnification 10×, except 6× in 7).

the dorsal side of each bronchus, thus forming a V configuration (character 21; fig. 11: 1–4). The internal cartilages of all four species are straight bars, somewhat variable in width.

The case of *Myiozetetes luteiventris* is an excellent illustration of the equivocal evidence that external morphology, particularly size and plumage coloration and pattern, brings to bear on generic relationships within this and other assemblages within the Tyrannidae. An external resemblance between this enigmatic species and other *Myiozetetes* is superficial at best. *Myiozetetes luteiventris* is smaller in size, darker above, and lacks any suggestion of a white superciliary line and frontal region. Virtually nothing has been published on its natural history, it is relatively scarce in museum collections, and it has a spotty and very localized distribution throughout much of Amazonia (Remsen, 1977). Although originally assigned to *Elaenia* by Sclater (1858), the same author transferred it to *Myiozetetes* without comment (Sclater, 1871) and most subsequent authors have maintained it there (Blake, 1961). Hellmayr (1927) had raised a question, however: "A very characteristic species of peculiar coloration and with very short bill, probably not congeneric with *Myiozetetes*. Its structure should be carefully reinvestigated." John T. Zimmer (unpubl. notes, dated 1937) originally assigned it to *Myiozetetes*, with these comments: "Females lack the orange red [crown] patch though may have some pale yellow edges in area. Bill is short and feet proportionally shorter than in other *Myiozetetes*, but appears to be no closer genus. Lack of superciliary and presence of pectoral streaking also abnormal for genus. On whole, goes here as well as elsewhere." But in notes added later, at an unknown date, Zimmer wrote: "Pattern closely resembles *Tyrannopsis* and details agree mostly with Ridgway's diagnosis . . . [Bill] more like that of *Tyrannopsis* than *Myiozetetes*. Size small." Meyer de Schauensee (1966) found Zimmer's unpublished notes persuasive and transferred *luteiventris* to *Tyrannopsis*, giving it the common name Dusky-chested Flycatcher in recognition of the dark chest band not found in the other three species of *Myiozetetes*. Traylor (1977) noted: "*Luteiventris* is a miniature (*Tyrannopsis*) *sulphurea* in coloration, even

smaller than the smallest *Myiozetetes*, and it is identical with the latter in proportions; its nest is not known. I feel, as did Blake (1961), that *luteiventris* should remain in *Myiozetetes*."

The nest of *luteiventris* was found by a field party from the Academy of Natural Sciences in Philadelphia, working in the Department of Loreto, Peru, in August 1983. Mark B. Robbins kindly sent me his field notes relating to this very significant discovery:

One or both birds kept flying to the crown of a large tree at the edge (along the path) of the forest. Within a few minutes I spotted the reason why they were returning to the tree. There was a large, bulky nest not more than a meter from the uppermost part of the tree. The nest appeared to be constructed of grasses—it reminded me of a nest of *Myiozetetes similis* that I have seen elsewhere. Estimating the dimensions of the nest—length about 12 inches by 6 inches—this does not include some of the long strands of grass that hung below the main part of the nest. One or both birds kept flying to nest and disappearing into it for about 3–4 seconds before reappearing then flying into the primary forest. It appeared that they were entering the nest at an entrance (on southeastern side of the nest) on the side at the upper third of the nest. I never saw what the birds were bringing (if anything) to the nest. There was no obvious nesting material brought to the nest—they may have been bringing food to nestlings (?). I watched the birds for about 15 minutes. One or more birds made several trips to the nest during this period.

A field party from Louisiana State University at Baton Rouge took an alcoholic specimen of *luteiventris* in the Department of Loreto, Peru, in 1983. In light of the admitted ambiguity of external morphology, I was impressed with the fact that the syrinx of this specimen (fig. 11:4) possessed all the derived characters (19–21) that characterize the syrinx of *Myiozetetes*. The most obvious difference is that the internal cartilages of this unique specimen are somewhat wider than those in my specimens of the other three species. I have no hesitancy in retaining *luteiventris* in *Myiozetetes*.

The syrinx of the monotypic *Legatus* (four specimens examined; fig. 11:5) is like that of *Myiozetetes* with respect to the fusion of the A2 and A3 elements to form a single calcified

band around the medial section of each bronchus (character 16). There is a calcified pes-sulus, but it is only marginally if at all continuous with any of the A elements in the manner of *Myiozetetes*. The most obvious difference between the syringes of *Legatus* and *Myiozetetes* is in the shape of the internal cartilages; in *Legatus* these are large, J- or L-shaped structures in which the ventrally directed arm is well-developed and extends nearly as far as the ventral ends of the B2 elements (character 22).

I have already indicated that *Legatus* differs from all genera within this assemblage (and from all other tyrant flycatchers) by having a remarkable variant of the basic kingbird nasal septum: a pair of winglike plates that project laterally from the septum (character 23; fig. 3:7 and 8). Likewise, I have noted that *Legatus* is aberrant with respect to its unique piratic nesting habits (character 24).

One might argue that the unique nasal septum of *Legatus* (character 23) is sufficiently divergent to warrant giving this monotypic genus the status of sister group to the rest of the assemblage. However, such a treatment would result in discordance with respect to the distribution of what I perceive to be the derived characters shared between *Legatus* and *Myiozetetes* (characters 16–18). The similarities in their syringeal morphology and in the type of nests used are too impressive, I think, not to regard these two genera as a monophyletic group within the assemblage (fig. 1).

The remaining three genera in the *Myiozetetes* group (*Philohydor*, *Pitangus*, and *Phelp-sia* in fig. 1) have syringes in which the A3 element forms a complete and independent ring around each bronchus (character 25; fig. 11:6–8).

The relationship of the Great and Lesser Kiskadees, *Pitangus sulphuratus* and *P. lictor*, has been a concern of avian systematists for some time. This represents another classic case wherein consideration of similarities in plumage coloration and pattern commanded the attention of early workers but gradually was denigrated in the face of growing evidence of substantial differences in ecology and behavior, particularly with regard to nest construction (Haverschmidt, 1957; Smith, 1962; Wetmore, 1972). Traylor (1977) com-

mented: "Wetmore (1972:422) says *lictor* should probably be placed in a separate genus, but considering my imperfect knowledge of this and related groups, I cannot see creating a new genus at this time. I shall leave *lictor* in *Pitangus*, but only for lack of a better place to put it."

After noting some remarkable differences between the syringes of *sulphuratus* and *lictor* and reviewing the equally marked differences in their nesting behavior, and after comparing these differences to the degree of variation in these character complexes that one finds at the generic level among tyrant flycatchers, I am compelled to propose a new genus for *lictor*, named and diagnosed below.

PHILOHYDOR, NEW GENUS

TYPE SPECIES: *L(anius) lictor* Lichtenstein (1823, p. 49)—Pará (=Belém), Brazil; Berlin Museum.

INCLUDED SPECIES: The type species only.

DISTRIBUTION: Panama southward through northern and eastern South America; see more detailed range for the species in Traylor (1979).

ETYMOLOGY: The Greek prefix *philo*, meaning loving or fond of, in combination with *hydor*, water, referring to observations that the species is generally found near water.

DIAGNOSIS: Separable from *Pitangus*, its closest relative, by smaller size, and from both *Pitangus* and *Myiozetetes* by the relatively long and slender bill.

Philohydor (three specimens examined) and *Pitangus* (eight specimens examined) have syringes in which both the A2 and A3 elements form complete and independent rings around each bronchus, a feature by which they are separable from all other genera in the assemblage (character 26; fig. 11:6 and 7). But as Ames (1971) reported, there are striking differences in their syringeal morphology. I have identified three fundamental differences which far exceed intrageneric variation in syringeal morphology among tyrant flycatchers. In *Philohydor* (fig. 11:6) only the A2 and A3 elements form complete rings around each bronchus, the internal cartilages are narrow and J-shaped and the B1 and B2 elements do not parallel one another and the B1s are noticeably expanded dorsally. The

unique alternate states to these characters, found in *Pitangus*, are discussed below.

Haverschmidt (1957), Smith (1962), and Willis (1962) have reviewed the controversy in the literature regarding the nesting behavior of *lictor* and conclude that the nest normally is shallow and cup-shaped consisting of small twigs and grasses, lined with finer rootlets, grasses and leaves, unlike the unique nest of *Pitangus* discussed below.

It is not clear what Wetmore (1972) had in mind when he said that *lictor* and *sulphuratus* differ widely in "details of form in the palatal region of the skull." Wetmore's references to cranial features of the Tyrannoidea generally were based on Warter's (1965) findings, but Warter's only reference (p. 36) to these two species was that they "differ interspecifically to a degree greater than any other congeneric flycatchers examined. *P. lictor* has the most slender skull of any tyrannine examined." Warter's observation is reflected in the narrowness of the bill of *lictor*, compared to that of *sulphuratus*.

As in *Philohydor*, the monotypic *Pitangus sulphuratus* has the A2 and A3 elements forming complete rings around each bronchus, but in addition the A4 element is also complete. In two of my eight specimens the A5 elements formed narrow but complete rings as well. This species is unique within the entire assemblage in having three (and sometimes four) A elements forming complete rings around each bronchus (character 27; fig. 11:7). It is also unique with respect to the shape of the internal cartilages, which are broad, relatively short, and truncated (character 28; fig. 11:7). Furthermore, the curvature of the B2 element, ventrally, parallels that of the B1, resulting in a configuration of these elements not found elsewhere among the kingbirds and their allies (character 29; fig. 11:7).

The nest of *Pitangus sulphuratus* differs from that of all other genera in the assemblage in that it is typically a large, untidy, domed structure of twigs and coarse grasses, lined with finer grasses and having a side entrance (character 30; Van Rossem, 1914; Hudson, 1920; Naumburg, 1930; Smith, 1962; Wetmore, 1972). But Smith (1962) cites reports in the literature of three *sulphuratus* nests that were in the form of a large, open

cup; two of these were in sheltered situations, which may help to explain this rare variation in nest form. That *sulphuratus* may begin egg-laying while the nest is but a shallow cup is suggested by an observation of John W. Fitzpatrick (personal commun.) that a pair continued to construct and eventually complete a typical domed structure during laying and incubation.

The remaining species in the *Myiozetetes* group was described as *Myiozetetes inornatus* by Lawrence in 1869, but many subsequent authors have preferred to assign it to *Conopias* (Sclater, 1871; Cherrie, 1916; Phelps and Phelps, 1963; Traylor, 1977). Hellmayr (1927) wrote: "somewhat aberrant. Count Berlepsch . . . was inclined to refer it to *Myiozetetes*, and it may eventually deserve generic separation." John T. Zimmer (unpubl. notes) was inclined to leave it in *Myiozetetes*, and Meyer de Schauensee (1966) concurred. A comparison of the syrinx of *inornatus* with that of *Myiozetetes* and *Conopias*, as well as a review of their nesting behavior, has convinced me that *inornatus* is generically distinct from both of these genera. Consequently, a new genus is named and diagnosed below.

PHELPSIA, NEW GENUS

TYPE SPECIES: *Myiozetetes inornatus* Lawrence (1869, p. 268)—Valencia, Carabobo, Venezuela; American Museum of Natural History.

INCLUDED SPECIES: The type species only.

DISTRIBUTION: Endemic to northern and central Venezuela; see more detailed range for the species in Phelps and Phelps (1963).

ETYMOLOGY: It is appropriate that this unique Venezuelan endemic be named for the Phelps family (the late William H., the father; Billy, the son; and Billy's wife, Kathy) in recognition of their monumental contribution to our understanding of the ornithology of Venezuela, a tribute long overdue.

DIAGNOSIS: Superficially similar in coloration and size to *Philohydor*, *Myiozetetes*, and *Conopias* but separable from those genera by having the throat white, a nearly black patch across the cheeks and through the eye, and a nearly black crown (no concealed patch of color) bordered by a prominent white border;

much smaller than *Pitangus* and *Megarynchus*.

Phelpsia belongs to that branch of the assemblage (with *Myiozetetes*, *Legatus*, *Philohydor*, and *Pitangus*) characterized by having the A3 element involved in greater support of each bronchus (character 14) and by having a flattened connection for the B1 and B2 elements ventrally (character 15). The A3 elements (with some contribution from the A4s) form complete rings around the bronchi (character 25). But the syrinx of *Phelpsia* (four specimens examined; fig. 11:8) differs from all other genera in this assemblage by having the A2 element incomplete, i.e., not forming a complete ring around each bronchus. Since it is the A2 elements to which the internal cartilages are attached in all kingbirds and their allies, the attachment of these cartilages to the incomplete A2 elements in *Phelpsia* (character 31) is in striking contrast to their attachment to the complete A2 elements that encircle each bronchus in all other genera in the assemblage.

The internal cartilages of *Phelpsia* are most similar to those of *Myiozetetes*, in being straight rather than J-shaped as in *Legatus* and *Philohydor*, or club-shaped as in *Pitangus*. In my specimens these cartilages did not retain the stain as well as in other genera, and the basically straight cartilages appear somewhat amorphous distally.

That the nest of *Phelpsia inornata* is very different from that of any other member of the assemblage was first reported by Cherrie (1916): "an open, cup-shaped affair, closely resembling that of our wood-pewee It was saddled on to the forks of a good sized limb The nest walls seem to be composed almost entirely of grey lichens that are bound together by cobwebs The whole is neat and trim in appearance." Thomas (1979) confirmed the structure of the nest of this species. This nesting behavior (character 32), unique within the Tyrannidae, is in concordance with the differences in syringeal morphology and argues for separate generic status for *inornata*.

DISCUSSION

The wisdom of recognizing three new monotypic genera in this assemblage has been

questioned by several colleagues, partly because of their concern for the lack of information on the functional significance of the relevant syringeal characters and partly because of a suspicion that a study of another character complex might reveal species that exhibit a similar degree of divergence from their respective congeners. Would those species be entitled to elevation to monotypic genera as well? My response to the first concern is that it has been over a century since Müller and Garrod established the taxonomic value of syringeal morphology; we are no closer now than we were then to an understanding of a relationship, if any, between the function of syringeal characters and their application to systematics. To repudiate the clues that the syrinx reveals regarding the evolutionary history of a taxon or group of taxa, until such time as functional morphology has closed the gap, would be tantamount to ignoring such characters as the modifications in the shape of flight feathers until we know their effects on aerodynamics, or the variations in the distribution of feather tracts until we appreciate their significance in plumage maintenance.

The second concern is more difficult to assuage. The generic limits of tyrant flycatchers traditionally have been based on gaps in external morphology (size, shape, pattern, and color), and the literature abounds with the contrary views of systematists as to the requisite size of these gaps and with commentary on their equivocal nature. Early in my studies I noted that the syrinx is more conservative than external morphology and that it is not unusual for uniquely derived syringeal characters to be shared by a cluster of closely related genera: e.g., *Myiarchus*, *Sirystes*, *Casiornis*, and *Rhytipterna* among the myiarchines (Lanyon, in press), and *Empidonax*, *Contopus*, *Sayornis*, *Xenotriccus*, *Aphanotriccus*, and *Mitrephanes* among the fluvicolines (Lanyon, MS). In view of the conservative nature of the syrinx, one cannot ignore the species that differs from its presumed congeners in a whole suite of syringeal characters. In such cases I have examined the variant for evidence of equivalent evolutionary divergence in at least one other character complex, e.g., a derived pattern of nesting behavior or of external morphology. The

variant(s) found to differ not only in syringeal morphology but in derived patterns of nesting behavior and external morphology should be given separate generic status, in recognition of the diagnostic value of these derived conditions and in the interest of achieving some degree of consistency in our concept of the genus. Arbitrary, certainly, but less capricious than genera based on external morphology alone. I hope other investigators who find variation within genera, whether it be anatomical or biochemical, will adopt similar procedures and standards.

Derived syringeal characters and nesting behavior function as indicators of relationship as well as having diagnostic value at the generic level. Within this monophyletic assemblage of kingbirds and their allies, as defined by two shared derived cranial characters, there is a general concordance between clustering of genera by shared derived syringeal character states and clustering by derived patterns of nesting behavior. In the *Tyrannus* branch, in which seven genera share the same basic type of syrinx, a cluster of five genera (*Megarynchus* through *Griseotyrannus*) build loosely constructed saucer-shaped nests, whereas two genera nest in cavities or niches (*Myiodynastes* and *Conopias*). But the syringes in the five genera within the *Myiozetetes* branch differ substantially in that they all have greater involvement of the A elements in support of the bronchi. Within this branch the two genera (*Myiozetetes* and *Legatus*) with fused A2 and A3 elements use domed nests of grasses; the two genera (*Pitangus* and *Philohydor*) with complete and independent A2 and A3 elements build rough stick nests lined with grasses, which in *Pitangus* are usually domed over and entered through the side; and *Phelpsia*, with fusion of its A3 and A4 elements but incomplete A2s, builds a lichen-covered cup-shaped nest saddled on a branch.

It is this concordance between syringeal characters and nesting behavior, also observed in my analysis of relationships among the myiarchine flycatchers (Lanyon, in press), that gives me confidence in the phylogenetic hypothesis presented in figure 1. Alternatively, one might rely on external morphology to establish affinities and generic limits within this assemblage, but problems arise

with this procedure (reviewed by Traylor, 1977). Particularly aggravating to systematists are the multiple alignments that might be made among the five genera that share a more or less distinctive plumage pattern: *Pitangus*, *Myiozetetes*, *Myiodynastes*, *Conopias*, and *Megarynchus*. Which criteria should be given priority? Body size, relative bill length, relative tarsal length, plumage pattern and coloration, or some combination of any of the above? After a full discussion of the possibilities, Traylor concludes: "I recognize the above five genera, not because I consider them satisfactory, but because at the moment I have nothing better to suggest." An argument might be made for a close relationship between *Legatus* and *Empidonomus* because of the similarities in their plumage coloration and pattern, the latter being but a slightly larger example of the former. Moreover, the use of external morphological characters is equivocal at best in revealing taxa that have differentiated in unique ways from their putative congeners, such as *inornatus* from *Conopias*, and *lictor* from *Pitangus*. The converse might also apply—plumage coloration and pattern may obfuscate natural affinities, as seen above in the example of *Myiozetetes luteiventris*. Such are the dilemmas posed by an emphasis upon external morphology among tyrant flycatchers. In developing the phylogeny in figure 1, I used external morphology only once as a means of clustering genera, when I was convinced that the character state (notching of the outer primaries) was indeed derived and unique within the assemblage.

Having excluded plumage patterns and coloration in the initial development of my phylogeny, I was impressed that the resulting arrangement of genera is compatible with the observed distribution of external morphological characters, providing certain assumptions are made as to the primitive states of these characters. I hypothesize that the primitive kingbird stock must have had yellow underparts, a concealed crown patch, a dark band through the eye, and lacked streaking in the plumage. These are characteristics now found in all the polytypic genera and in most of the monotypic genera. That these primitive plumage characters are plastic and subject to secondary loss or modification is il-

lustrated by: (1) the reduction in yellow underparts in some *Myiodynastes*, and the reduction and loss of yellow in *Tyrannus*, *Empidonomus*, and *Griseotyrannus*; (2) the reduction or loss of the concealed crown patch in some *Conopias* and the loss of this character in *Phelpsia*; (3) the reduction of the dark band through the eye in *Griseotyrannus* and in some *Myiozetetes* and *Tyrannus*, and the loss of that character in *Tyrannopsis*; and by (4) the development of streaking (and concomitant paling of yellow) in some *Myiodynastes* and in the monotypic *Legatus* and *Empidonomus*. The presence of a more or less complete ring of white or yellow around the darker crown may also be the primitive condition. This character is well developed in all five genera in the *Myiozetetes* branch of the assemblage (secondarily reduced and lost in the genus *Myiozetetes*) and in the first three genera of the *Tyrannus* branch (secondarily reduced in some *Myiodynastes* and some *Conopias*), and reduced or lost altogether in the last four genera.

Whether additional anatomical or biochemical data will be equally compatible remains to be demonstrated; there is now a hypothesis available for testing.

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