

AMERICAN MUSEUM *Novitates*

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, N.Y. 10024
Number 2915, pp. 1-11, figs. 1-5

March 11, 1988

The Phylogenetic Affinities of the Flycatcher Genera *Myiobius* Darwin and *Terenotriccus* Ridgway

WESLEY E. LANYON¹

ABSTRACT

The genera *Myiobius* and *Terenotriccus* were excluded from the *Empidonax* assemblage of tyrant flycatchers due to the lack of one cranial character and to deviant variations in two other cranial characters used to argue for monophyly of that assemblage (Lanyon, 1986). Subsequent reexamination of anatomical specimens of these taxa has led to a recommendation for their removal from

incertae sedis and their allocation to the *Myiophobus* group in the *Empidonax* assemblage, with which they share derived character states of syringeal morphology. The sister taxa appear to be *Pyrrhomyias* and *Hirundinea*. The sharing of derived character states of cranial and syringeal morphology and specialized nesting biology argue for the merger of *Terenotriccus* with *Myiobius*.

INTRODUCTION

Sclater (1888) and Berlepsch (1907) perceived the tyrant flycatcher genus *Myiobius* as including not only the three species now recognized in that genus but also species that Hellmayr (1927), Zimmer (ms), and Traylor (1979) later assigned to *Terenotriccus*, *Myiophobus*, *Pyrrhomyias*, and *Myiotriccus*. In my studies of phylogenetic relationships within the flycatcher family Tyrannidae, I have already presented arguments for the systematic

position of the last three of these genera. I believe *Myiophobus*, as constituted by all recent authors, to be polyphyletic, with representatives in two distinct tyrant lineages. One segment of this genus, including at least *fasciatus* (the type species), *flavicans*, and *inornatus*, possesses the derived character states of the nasal septum that are shared by the members of my *Empidonax* assemblage, and among this segment's closest relatives is *Pyr-*

¹ Lamont Curator of Birds, Department of Ornithology, American Museum of Natural History.

rhomyias (Lanyon, 1986). The other segment, including at least *phoenicomitra*, *ro-raimae*, and *ochraceiventris*, is a member of my *Elaenia* assemblage by virtue of its sharing the derived character states of the nasal septum that characterize that major lineage of tyrant flycatchers. I have refrained from proposing a new generic name for the species in this latter segment until we know more about their nesting behavior and have anatomical specimens of *lintoni*. The closest relative of this segment of "*Myiophobus*" is *Myiotriccus* (Lanyon, 1988). Though they possess some of the derived character states that I have used to argue for monophyly of the *Empidonax* assemblage, *Myiobius* and *Terenotriccus* were excluded from that assemblage (Lanyon, 1986) due to the lack of one character in particular and to deviant variations in two other characters. Subsequently I have reexamined anatomical specimens of these taxa, and the following report is my recommendation for their removal from incertae sedis and their allocation to the *Myiophobus* group in my *Empidonax* assemblage.

ACKNOWLEDGMENTS

I am grateful to the many individuals who arranged for the loan of specimens. In addition to the anatomical collections at the American Museum of Natural History (AMNH), I borrowed specimens from the Field Museum of Natural History (FMNH), Chicago; 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 National Museum of Natural History, Smithsonian Institution (USNM), Washington, D.C.; the Peabody Museum of Natural History at Yale University (PMNH), New Haven; and the Royal Ontario Museum (ROM) in Toronto, Canada. Specimens cited in the text, figure captions, and in the Appendix are identified to collection by the abbreviations given above.

The photographs of skulls and syringes were made with equipment in the laboratory of Dr. C. W. Myers. I am indebted to Mr. M. A. Traylor, Jr. for his encouragement and

comments on the manuscript. This research was supported by the Sanford Fund of the American Museum of Natural History.

CRANIAL EVIDENCE FOR ASSIGNMENT TO THE *EMPIDONAX* ASSEMBLAGE

In reconstructing the evolution of the tyrant flycatchers I have relied heavily on shared derived character states of the nasal capsule for establishing monophyly of each of several assemblages of genera (Lanyon, 1984, 1985, 1986, 1988). In the *Empidonax* 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, the plate typically is forked at its posterior end, and in lateral view the plate curves dorsally at its anterior end, with the septum beneath this anterior portion remaining unossified, creating an illusion that the septum bears an anterior notch. There is much variation in the length and conspicuousness of the posterior forking and in the size and shape of the anterior notch, as I have documented previously (Lanyon, 1986). This configuration of the septum is equivalent to Warter's (1965) "type 6," in which he notes that the trabecular plate "bases the septum."

Occasionally, in this assemblage, the trabecular plate at the base of the nasal septum is not forked posteriorly, or only barely so. I noted that the monotypic *Pyrrhomyias* and *Hirundinea* are sister taxa because they share derived character states in the syrinx, plumage, and nesting behavior, and in neither species is the trabecular plate conspicuously forked (Lanyon, 1986). The 12 specimens of the monotypic *Terenotriccus* and 28 specimens of the three species of *Myiobius* that I examined all have trabecular plates that are tapered gradually at the caudal ends, not forked (figs. 1, 2). The plates are located along the ventral edge of the nasal septum, as in all members of the *Empidonax* assemblage, except in two specimens of *Myiobius atricaudus* (LSU 108929, USNM 429195) where the plate appears to be elevated somewhat above the ventral edge, creating a suggestion of a sagittal ridge when the plate is viewed from

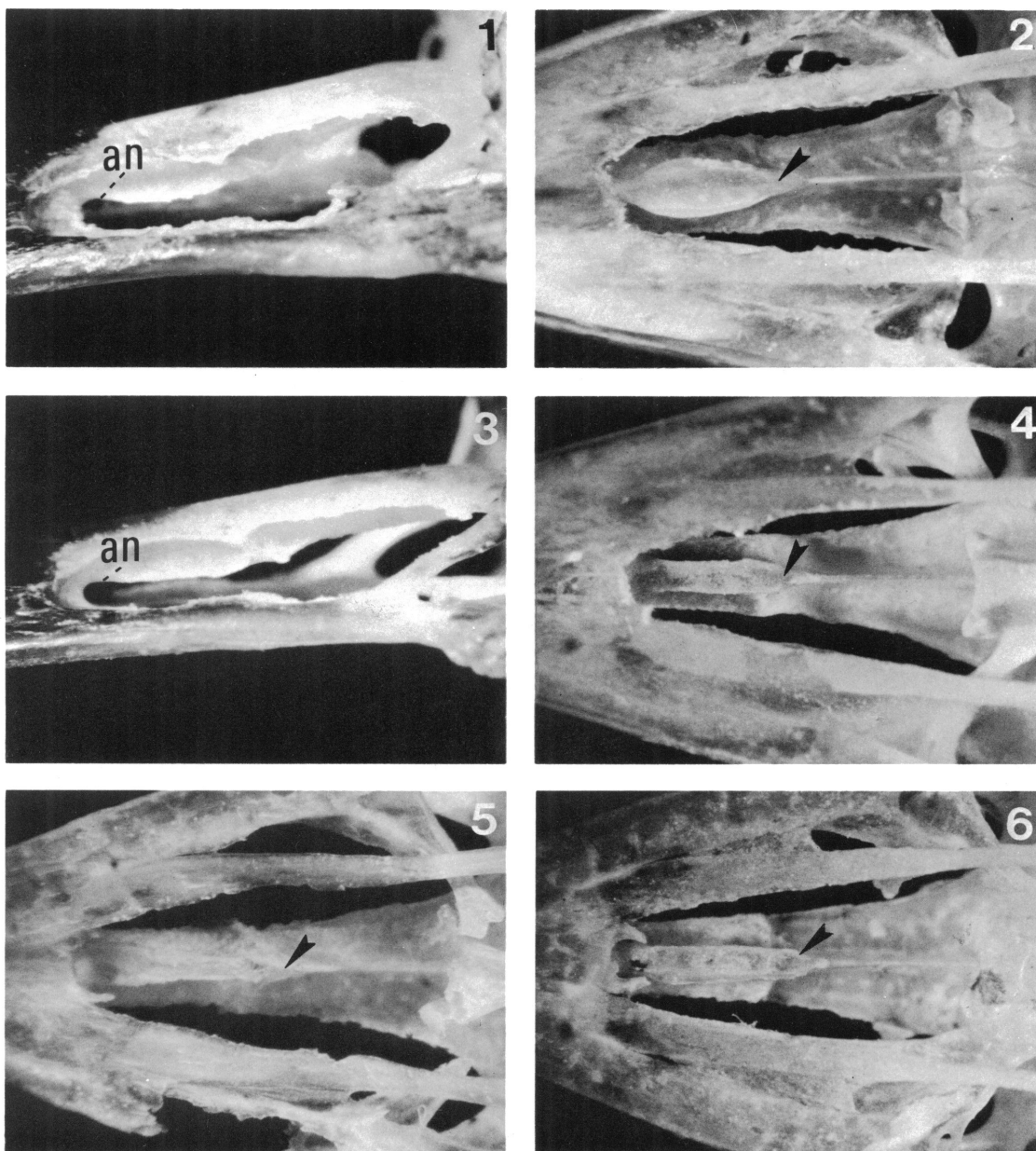


Fig. 1. Nasal capsules of *Terenotriccus erythrurus* (anterior end of skull to left; magnification $\times 12$). (1, 2) LSU 111570, lateral and ventral views; (3, 4) LSU 42891, lateral and ventral views; (5) USNM 347158, ventral view; (6) UMMZ 214048, ventral view. Arrows indicate tapered caudal end of trabecular plate; an = anterior notch in nasal septum.

the ventral aspect (fig. 2: 5, 6). All specimens of *Terenotriccus* and most specimens of *Myiobius* have a septum with an anterior notch (figs. 1, 3), the character state that is

so diagnostic of the *Empidonax* assemblage. However, some of the specimens of *Myiobius* (UK 71554, LSU 108929) have this character poorly developed (fig. 3: 5, 6).

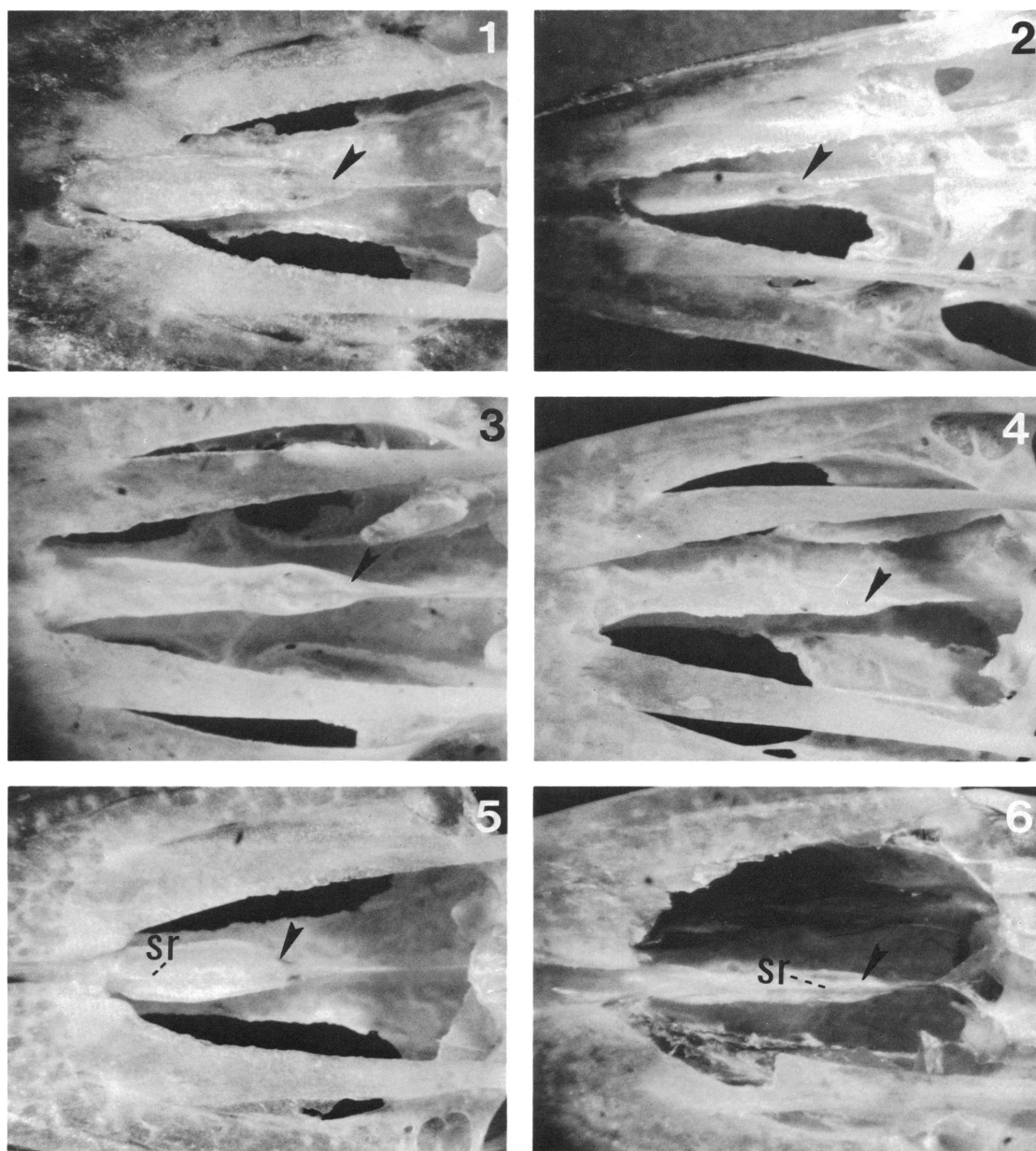


Fig. 2. Ventral aspect of the nasal capsule of *Myiobius* (anterior end of skull to left; magnification $\times 12$). (1) *M. villosus*, LSU 99590; (2) *M. villosus*, LSU 99419; (3) *M. barbatus*, USNM 432171; (4) *M. barbatus*, UK 71848; (5) *M. atricaudus*, LSU 108929; (6) *M. atricaudus*, USNM 429195. Arrows indicate tapered caudal end of trabecular plate; sr = suggestion of a sagittal ridge on trabecular plate.

It was these deviations from the normal appearing nasal capsule, taken collectively, that made me reluctant to admit *Myiobius* and *Terenotriccus* to the *Empidonax* assemblage, though I speculated that they might

“well have evolved from or be related to a form ancestral to this assemblage” (Lanyon, 1986). Further reflection on this matter has revealed no other tyrant lineage to which *Myiobius* and *Terenotriccus* can more appro-

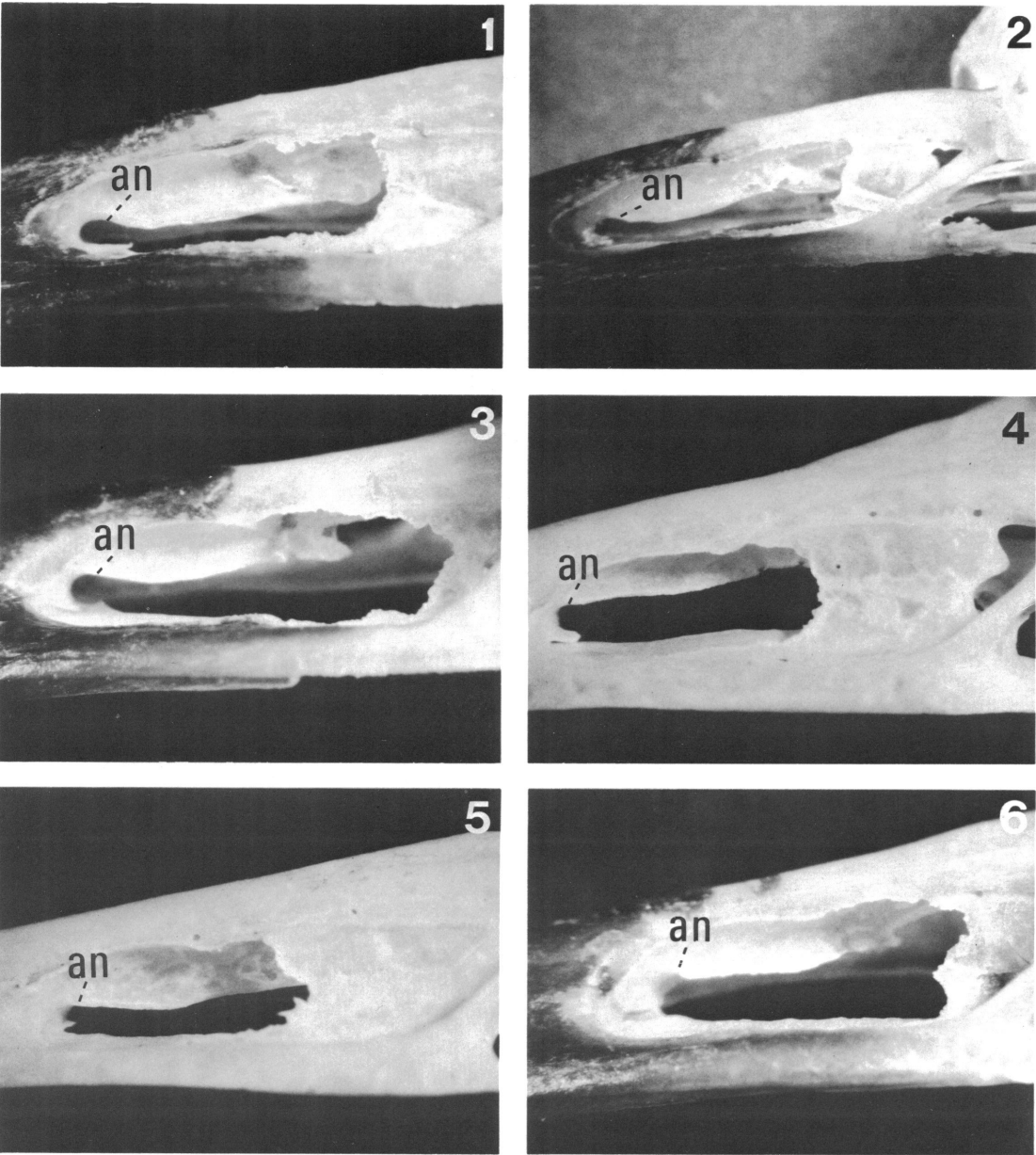


Fig. 3. Lateral aspect of the nasal capsule of *Myiobius* (anterior end of skull to left; magnification $\times 12$). (1) *M. villosus*, LSU 99590; (2) *M. villosus*, LSU 99419; (3) *M. barbatus*, LSU 111552; (4) *M. barbatus*, UK 71848; (5) *M. barbatus*, UK 71554; (6) *M. atricaudus*, LSU 108929. an = anterior notch in nasal septum.

priately be assigned. It seems prudent to make allowances for a somewhat more variable nasal septum and associated trabecular plate than I had visualized initially for the *Empidonax* assemblage, in order that these taxa

can be admitted. As I will indicate below, there is convincing evidence from syringeal morphology that *Myiobius* and *Terenotriccus* do indeed have close relatives within this assemblage, most of which were included in the

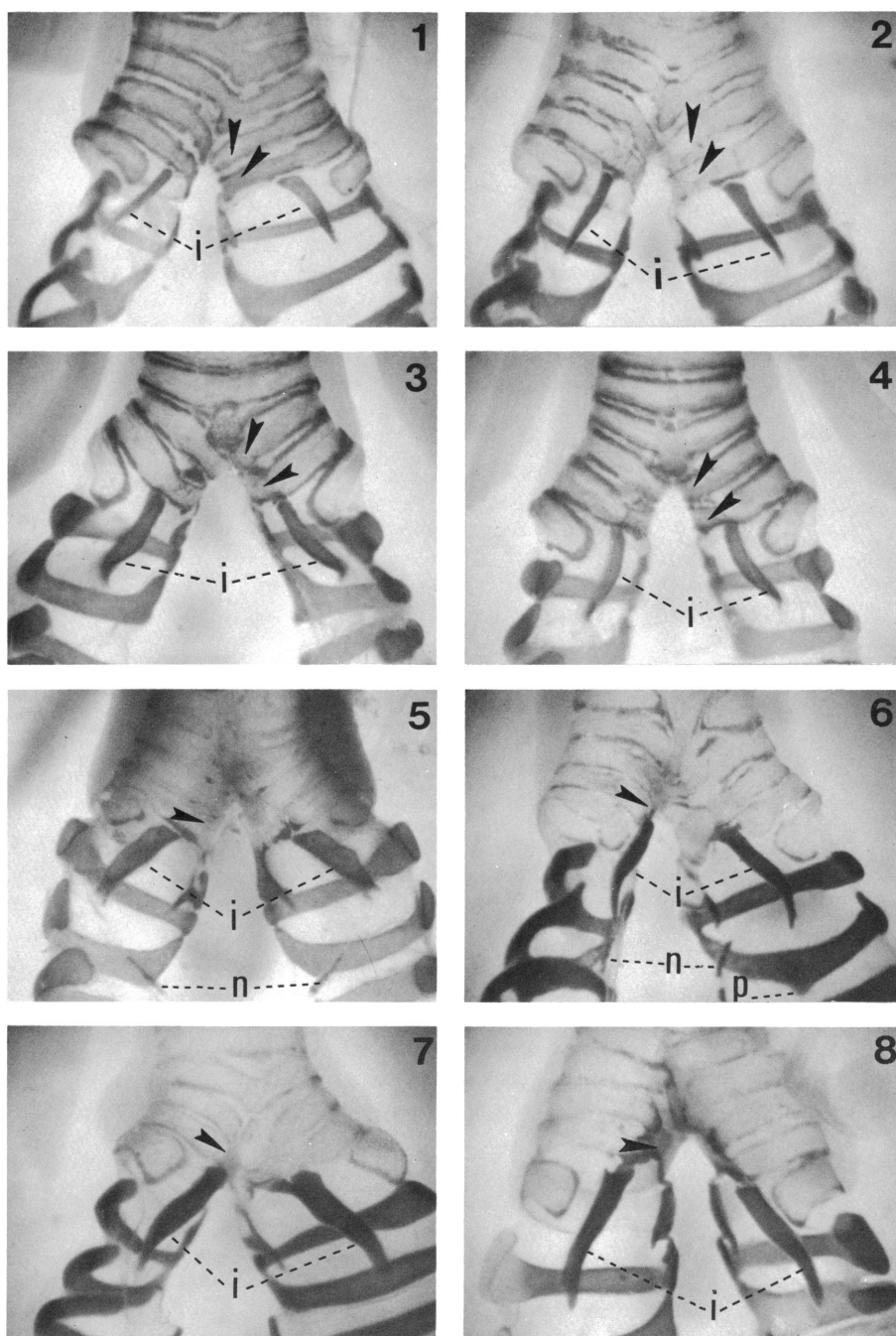


Fig. 4. Syringes of the four genera in the *Myiophobus* group (dorsal aspect; magnification $\times 16$). (1) *Myiobius barbatus*, AMNH 9391; (2) *M. barbatus*, LSU 75470; (3) *Terenotriccus erythrurus*, UK 65481; (4) *Terenotriccus erythrurus*, AMNH 9389; (5) *Hirundinea ferruginea*, USNM 504581; (6) *Pyrrhomyias cinnamomea*, PMNH 2014; (7) *Myiophobus inornatus*, LSU 98045; (8) *Myiophobus fasciatus*, LSU 102584. Arrows indicate calcified A elements that form complete rings around the bronchi; 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.

TABLE 1
Characters Used for Phylogeny of the *Myiophobus* Group in the *Empidonax* Assemblage

	Character, description	Distribution by taxa
1	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	<i>Myiophobus</i> , <i>Pyrrhomyias</i> , and <i>Myiobius</i>
3	Trabecular plate on nasal septum not forked	<i>Pyrrhomyias</i> , <i>Hirundinea</i> , and <i>Myiobius</i>
4	Loss of intrinsic syringeal muscles	As above
5	Narrow strand of cartilage located ventrally within internal tympaniform membrane, between ventral ends of B2 and B3	<i>Pyrrhomyias</i> and <i>Hirundinea</i>
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>Pyrrhomyias</i>
9	Internal cartilages narrow and very slightly J-shaped	<i>Pyrrhomyias</i>
10	Internal cartilages broad and linear	<i>Hirundinea</i>
11	Concealed crown patch lost	<i>Hirundinea</i> (and in <i>Myiobius erythrurus</i>)
12	Two complete and independent calcified rings (A2s and A3s) in support of each bronchus	<i>Myiobius</i>
13	Pendant, globular nest with side entrance	<i>Myiobius</i>
14	Interorbital septum ossified, or nearly so	<i>Myiobius</i>
15	Rictal bristles as long as or longer than broad flat bill	<i>Myiobius</i>

enlarged concept of *Myiobius* as perceived by Sclater and Berlepsch.

EVIDENCE FOR CLOSEST RELATIVES WITHIN 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 each of my tyrant assemblages, and for clustering and defining the limits of genera. Secondary considerations are given to what I interpret as derived characters in nesting behavior and external morphology.

The three primary lineages within the *Empidonax* assemblage are based on differences in the degree to which the A elements provide support for each bronchus (Lanyon, 1986); these variations 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. In only one of these lineages, my *Myiophobus*

group, do any of the A elements form complete and calcified rings around each bronchus (character 1). 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. The calcified pessulus in all specimens of this group is probably a correlate of this greater degree of calcification and completeness of the A elements. I found this basic configuration of the syrinx in three genera: *Myiophobus* (*fasciatus*, *flavicans*, and *inornatus*), *Pyrrhomyias*, and *Hirundinea* (fig. 4). *Myiophobus* and *Pyrrhomyias* have concealed crown patches in their plumage, a derived character that is unique among the 33 genera in the *Empidonax* assemblage and hence useful for providing supporting evidence of the monophyly of this cluster. *Hirundinea* is presumed to have lost this character.

I have examined syringes of all three species of *Myiobius* (10 specimens) and of the monotypic *Terenotriccus* (4 specimens) and find

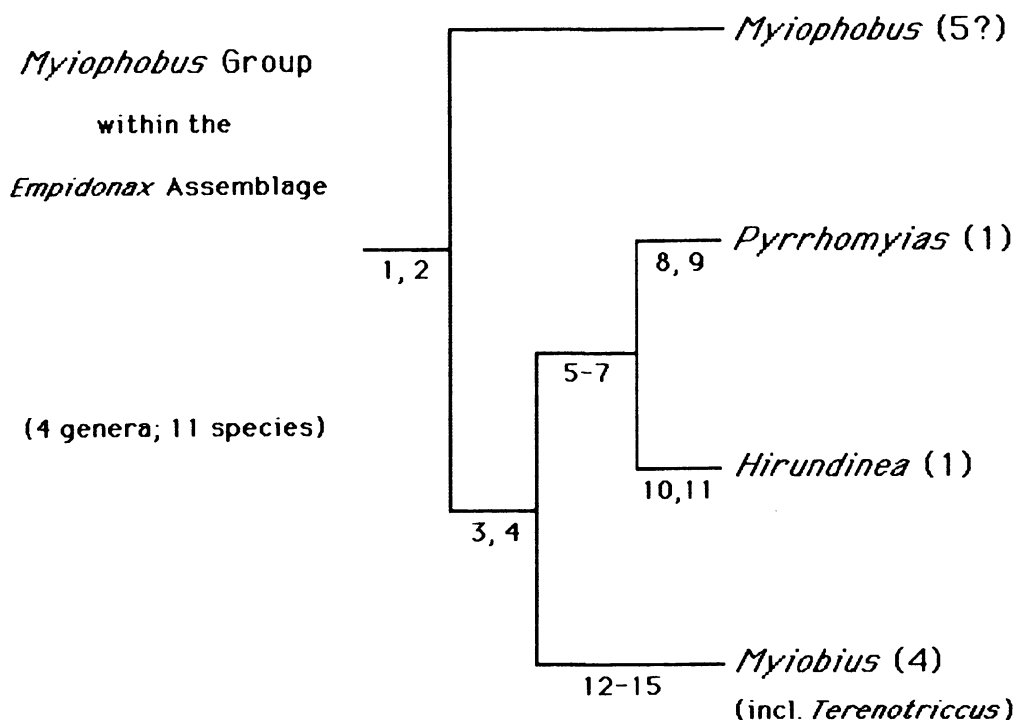


Fig. 5. Phylogenetic relationships within the *Myiophobus* group of the *Empidonax* assemblage. Numbers identify diagnostic character states described in text and in table 1. Numbers in parentheses indicate number of species per genus.

that they too have A elements that form complete calcified rings around the bronchi and a calcified pessulus that is continuous with the A4 elements (character 1; fig. 4). These syringes differ from those of *Myiophobus* and its allies only in that there are normally two complete and independent rings around each bronchus (the A2s and A3s; rarely the A3 is incomplete; character 12). The internal cartilages are basically straight, pointed distally, and attached to the dorsomedial segment of the A2s. The three species of *Myiobius* have concealed crown patches in their plumage (character 2), which strengthens the hypothesis that they have shared a common ancestry with my *Myiophobus* group. This character has presumably been lost in *Terenotriccus*, as it has in *Hirundinea*.

Within this newly enlarged *Myiophobus* group (fig. 5), *Myiobius* and *Terenotriccus* cluster with *Pyrrhomyias* and *Hirundinea* by virtue of their sharing the derived configuration of the trabecular plate described above,

i.e., the lack of posterior forking (character 3), and by the absence of intrinsic syringeal muscles (character 4; unique within the assemblage). Ames (1971), working exclusively with syringeal characters as a basis for defining groups of closely related tyrants, placed four genera in what he called his "*Myiobius* group": *Myiobius*, *Terenotriccus*, *Pyrrhomyias*, and *Onychorhynchus* (Ames did not examine *Hirundinea*). The characters that he used to define this group were the possession of two complete A rings in each bronchus and the absence of intrinsic muscles. *Onychorhynchus*, though it possesses two or three complete and calcified A bands around each bronchus, must have derived this character independently from my *Myiophobus* group, for its nasal capsule is virtually without ossification as are all of the so-called flatbilled flycatchers with which I believe it to be allied. Most of the "flatbills" have one or two of these complete A bands supporting each bronchus. Ames also suggested that the man-

akin genus *Piprites* probably also belongs with his *Myiobius* group. The nasal capsule of *Piprites* has none of the derived character states that define my *Empidonax* assemblage, however, and its syringeal morphology is not like that of *Myiobius* or any of my *Myiophobus* group.

The monotypic *Pyrrhomyias* and *Hirundinea* are considered sister taxa because they share derived characters in the syrinx, plumage, and nesting behavior (characters 5–7, table 1), but deserve generic distinction (characters 8–11, table 1; see Lanyon, 1986, for more detail and an account of the historical treatment of these taxa).

Ridgway (1905) described *Terenotriccus* in recognition of minor differences in the external morphology of *erythrurus* as compared with *Myiobius*. However, the number of derived character states shared by *Myiobius* and *Terenotriccus*, including syringeal morphology and nesting biology, argues for the reunion of these genera. A compelling argument for this merger is the possession of two complete and independent calcified rings (A2s and A3s; character 12) in support of each

bronchus, which is unique within the assemblage. Equally compelling is the fact that they both have a highly derived nesting behavior—the construction of a pendant, globular nest with side entrance (character 13) [Euler, 1900; Ihering, 1904; Carriker, 1910; Huber, 1932; Skutch, 1960 (photos of *erythrurus* and *barbatus* nests); Gross, 1964 (photo of *atricaudus* nest); Wetmore, 1972]. The pendant, globular, or pear-shaped nest has evolved independently in one other genus (*Silvicultrix*) within my *Empidonax* assemblage (Lanyon, 1986), as well as among the tody-tyrant and flatbilled flycatchers (Lanyon, MS) and in one group (*Phylloscartes*, *Mionectes*, and allies) within my *Elaenia* assemblage (Lanyon, 1988). The cup-shaped nests of *Myiophobus*, *Pyrrhomyias*, and *Hirundinea* are presumed to be the primitive behavior pattern (Lanyon, 1986). Additional characters shared by *Myiobius* and *Terenotriccus* are the ossification of the interorbital septum (character 14), a derived character state in the *Empidonax* assemblage, and the heavy rictal bristles that are as long as or longer than the broad flat bills (character 15).

REFERENCES CITED

- Ames, P. L.
1971. The morphology of the syrinx in passerine birds. *Peabody Mus. Nat. Hist. Yale Univ. Bull.*, 37: 1-194.
- Berlepsch, H. G. von
1907. Studien über Tyranniden. *Ornis*, 14: 463-493.
- Carriker, M. A.
1910. An annotated list of the birds of Costa Rica including Cocos Island. *Ann. Carnegie Mus.*, 6: 314-915.
- Darwin, C.
1839. The zoology of the voyage of H. M. S. Beagle, part 3, Birds. London: Smith, Elder and Co.
- Euler, C.
1900. Descrição de ninhos e ovos das aves do Brasil. *Revista do Museu Paulista*, 4: 9-149.
- Gross, A. O.
1964. Nesting of the Black-tailed Flycatcher on Barro Colorado Island. *Wilson Bull.*, 76: 248-256.
- Hellmayr, C. E.
1927. Catalogue of birds of the Americas and the adjacent islands, part 5. *Publ. Field Mus. Nat. Hist., Zool. ser.*, 13: 1-517.
- Huber, W.
1932. Birds collected in northeastern Nicaragua in 1922. *Proc. Acad. Nat. Sci. Philadelphia*, 84: 205-249.
- Hudson, W. H.
1920. Birds of La Plata, vol. 1. New York: E. P. Dutton.
- Ihering, H. von
1904. The biology of the Tyrannidae with respect to their systematic arrangement. *Auk*, 21: 313-322.
- Lanyon, W. E.
MS. A phylogeny of the flatbill and tody-tyrant assemblage of tyrant flycatchers. New York, *Am. Mus. Nat. Hist.*
1984. A phylogeny of the kingbirds and their allies. *Am. Mus. Novitates*, 2797: 28 pp.
1985. A phylogeny of the myiarchine flycatchers. In P. A. Buckley, M. S. Foster, E. S. Morton, R. S. Ridgely, and F. G. Buckley (eds.), *Neotropical ornithology. Ornithol. Monogr.*, 36: 361-380. Amer. Ornithol. Union, Washington, D.C.
1986. A phylogeny of the thirty-three genera in the *Empidonax* assemblage of tyrant flycatchers. *Am. Mus. Novitates*, 2846: 64 pp.
1988. A phylogeny of the thirty-two genera in the *Elaenia* assemblage of tyrant flycatchers. *Am. Mus. Novitates*, 2914: 57 pp.
- Ridgway, R.
1905. Descriptions of some new genera of Tyrannidae, Pipridae, and Cotingidae. *Proc. Biol. Soc. Washington*, 18: 207-210.
- Sclater, P. L.
1888. Catalogue of the birds in the British Museum. London: British Museum (Natural History), 14: 1-494.
- Skutch, A.
1960. Life histories of Central American birds, part II. *Cooper Ornithol. Soc., Pacific Coast Avifauna*, 34: 1-593.
- Traylor, M. A., Jr.
1979. Tyrannidae. In M. A. Traylor, Jr. (ed.), *Peters' check-list of birds of the world*, vol. 8. Cambridge, Mass.: Mus. Comp. Zool.
- Warter, S. L.
1965. The cranial osteology of the New World Tyrannoidea and its taxonomic implications. Ph.D. diss., Louisiana State Univ. Micro-films, Ann Arbor, Michigan, order no. 66-761.
- Wetmore, A.
1972. The birds of the Republic of Panamá, part 3. *Smithson. Misc. Coll.*, 150: 1-631.
- Zimmer, J. T.
MS. Unpublished notes on the Tyrannidae. New York, *Am. Mus. Nat. Hist.*, Dept. Ornithol.

APPENDIX

List of anatomical specimens (64 skulls, 33 syringes) examined for developing a phylogeny of the *Myiophobus* group within the *Empidonax* assemblage of flycatchers. Genera and species are listed alphabetically. Not included here are the species in over 100 other genera of tyrant flycatchers whose skulls and syringes have been examined for outgroup comparison.

	Skulls	Syringes
<i>Hirundinea ferruginea</i>	LSU 118266; UMMZ 200850	LSU 64809; USNM 504581
<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, 9390, 9391; LSU 75470; PMNH 2144, 6680
<i>M. erythrurus</i>	AMNH 5799; FMNH 323296–323298; LSU 42891, 111566, 111570; UMMZ 153244, 153245, 214047, 214048; USNM 347158	AMNH 8261, 9389; LSU 108469; UK 65481
<i>M. villosus</i>	FMNH 323302–323305, 323323, 323325; LSU 99418–99420, 99590, 107298	FMNH 323309; LSU 108473
<i>Myiophobus cryptoxanthus</i>	Lacking	Lacking
<i>M. fasciatus</i>	AMNH 7181; FMNH 290297; LSU 81265, 81266; USNM 318764, 346032, 347155	AMNH 4321; LSU 102584, 113850
<i>M. flavicans</i>	AMNH 14156; FMNH 313437; UMMZ 203823	LSU 107656
<i>M. inornatus</i>	LSU 99424	LSU 98045
" <i>Myiophobus</i> " <i>lintoni</i>	Lacking	Lacking
" <i>M.</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>	ROM 118777	Lacking
" <i>Myiophobus</i> " <i>roraimae</i>	FMNH 319446; LSU 107313	AMNH 816778; LSU 118050; USNM 504572, 504574, 504577
<i>Pyrrhomyias cinnamomea</i>	AMNH 7179; FMNH 291897; LSU 74891, 79825; USNM 428730	LSU 107652; PMNH 2014, 2057
<i>Terenotriccus erythrurus</i> . See <i>Myiobius erythrurus</i>		

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