GENERIC STATUS OF EULER'S FLYCATCHER: A MORPHOLOGICAL AND BIOCHEMICAL STUDY

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ABSTRACT.—A concordance in the distribution of uniquely derived character states of the syrinx and of six protein coding loci confirms that *euleri* should be removed from the genus *Empidonax* and that its nearest relatives are *Cnemotriccus* and *Aphanotriccus*. A hypothesis that *euleri* is the sister taxon of *Aphanotriccus* is based on the sharing of a uniquely derived syringeal structure and two synapomorphic allozymes, and on the comparatively low genetic distance between them. A new genus, ***Lathrotriccus,*** is proposed for *euleri*, which differs from *Aphanotriccus* in its cranial morphology. The reassignment of *euleri* increases the desirability of obtaining anatomical specimens and tissue of *griseipectus*, the only remaining South American endemic in *Empidonax*, and of tissue of *Xenotriccus*, a near relative of *euleri* on the basis of syringeal morphology. *Received 22 July 1985, accepted 5 November 1985.*

IN 1868 Jean Louis Cabanis (1868) described a new species of South American flycatcher that he named for Carl Euler, a Swiss ornithologist with extensive field experience in South America. The widespread *euleri* (occupying much of South America east of the Andes, from Colombia to Argentina) was originally assigned to *Empidochanes*, a name used by most workers for what was to become known as *Cnemotriccus*. *Empidochanes* Sclater 1862 later proved to be a synonym of *Myiophobus* Cabanis and Heine 1859. Various populations of *euleri* were placed in the predominantly North American genus *Empidonax* as early as the late 1800's, with little justification for the transfer, and the species has remained there in one form or another ever since (Hellmayr 1927, Traylor 1979). *Empidonax euleri* is one of only two endemic South American species in the genus as presently constituted (Traylor 1979). The other, *E. griseipectus*, is confined to a comparatively small range west of the Andes in southwest Ecuador and northwest Peru. The first hint of discordance concerning the generic affinity of *euleri* came with an electrophoretic study (Zink and Johnson 1984) of genetic differentiation at protein coding loci within *Empidonax*. These authors discovered that *euleri* differed from 11 other species of *Empidonax* by a genetic distance larger than that separating *Contopus* from *Empidonax*, and they proposed, on "close behavioral, ecological, and morphological similarities," "that *euleri* is inappropriately included in *Empidonax*" and "may be more closely related to *Cnemotriccus*." They did not examine the proteins of *Cnemotriccus*. Zink and Johnson's results prompted us to reexamine the generic relationships of *euleri*, using a combined morphological and biochemical approach.

The genus *Empidonax* is the largest of 33 genera that belong to an assemblage of tyrant flycatchers, the monophyly of which has been established on the basis of cranial morphology; within this assemblage, primary lineages have been defined by virtue of the sharing of the more conservative variants in syringeal morphology (W. Lanyon 1986). One of these lineages, the *Empidonax* group, is dominated numerically by two large genera, *Empidonax* and *Contopus*, and in addition includes *Cnemotriccus*, *Aphanotriccus* (including *Praedo*), *Xenotriccus* (including *Aechmolophus*), *Sayornis*, and *Mitrephanes*. Within the context of this *Empidonax* group, we will discuss the generic affinities of *euleri*. A more complete analysis of relationships between the other genera in this group will be included in a report on the phylogeny of the entire *Empidonax* assemblage (W. Lanyon 1986). We do not address the considerable problems of intraspecific relationships within *euleri* (see Meyer de Schauensee 1966).

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MATERIALS AND METHODS

Syringeal morphology has proven effective for defining generic limits and for clustering genera of tyrant flycatchers (Lanyon 1982, 1984, 1985; Lanyon and Fitzpatrick 1983). The number, shape, and position of the bony and cartilaginous supporting elements in the syrinx were studied by double-staining with alcian blue for cartilage and alizarin red for ossified bone (after Dingerkus and Uhler 1977). The terminology for syringeal morphology is that used by Ames (1971) for the passerine syrinx. Syringes (numbers of individual specimens in parentheses) were examined from the following species: *Aphanotriccus audax* (3), *A. capitalis* (1), *Cnemotriccus fuscatus* (4), *Contopus borealis* (3), *C. caribaeus* (3), *C. cinereus* (2), *C. fumigatus* (3), *C. latirostris* (1), *C. sordidulus* (2), *C. virens* (3), *Empidonax affinis* (1), *E. albigularis* (1), *E. alnorum* (1), *E. atriceps* (2), *E. difficilis* (2), *E. euleri* (4), *E. flavescens* (1), *E. flaviventris* (3), *E. fulvifrons* (2), *E. hammondii* (2), *E. minimus* (3), *E. oberholseri* (2), *E. traillii* (3), *E. virescens* (2), *E. wrightii* (2), *Mitrephanes olivaceus* (1), *M. phaeocercus* (1), *Sayornis nigricans* (4), *S. phoebe* (3), *S. saya* (1), *Xenotriccus callizonus* (1), and *X. mexicanus* (2). The specimens of *euleri* were taken in Peru, Bolivia, and Paraguay. Syringes were removed from specimens in the anatomical collections at the American Museum of Natural History (AMNH), New York, and from specimens borrowed from the Carnegie Museum of Natural History, Pittsburgh; the Field Museum of Natural History, 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 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; and the Royal Ontario Museum (ROM), Toronto, Canada. Specimens cited here are identified to collection by the abbreviations given above.

Tissue homogenates (heart, liver, and skeletal muscle) were prepared from three individuals of each of the following taxa: *Aphanotriccus audax, Cnemotriccus fuscatus, Contopus virens, Empidonax euleri, E. flaviventris,* and *Mitrephanes phaeocercus.* Hereafter, we refer only to these generic names when discussing biochemical results. Tissues from three Bolivian specimens of *euleri* were acquired from the Louisiana State University Museum of Zoology Collection of Frozen Tissues, where they were stored at −70°C. Protein separation was accomplished through horizontal starch-gel electrophoresis using one of three buffer systems, following Selander et al. (1971): Poulik, pH 8.2; Tris-citrate, pH 8.0; and Tris-maleate, modified to pH 6.5. Twenty-eight enzymes were surveyed using enzyme-specific assays (Harris and Hopkinson 1976), thereby ensuring that characters were homologous: acid phosphatase (E.C. 3.1.3.2), adenosine deaminase (E.C. 3.5.4.4), alcohol dehydrogenase (E.C. 1.1.1.1), creatine kinase-1,2 (E.C. 2.7.3.2), esterase "D" (E.C. 3.1.1.1), fumarase (E.C. 4.2.1.2), α-glycerophosphate dehydrogenase (E.C. 1.1.1.8), glutamine deaminase (E.C. 3.5.1.2), glutamic-oxalacetic transaminase-1 (E.C. 2.6.1.1), phosphoglucose isomerase (E.C. 5.3.1.9), isocitrate dehydrogenase-1,2 (E.C. 1.1.1.42), leucyl aminopeptidase (E.C. 3.4.11.1), lactate dehydrogenase-2 (E.C. 1.1.1.27), malic dehydrogenase-1,2 (E.C. 1.1.1.37), malic enzyme (E.C. 1.1.1.40), mannosephosphate isomerase (E.C. 5.3.1.8), nucleoside phosphorylase (E.C. 2.4.2.1), phosphoglucomutase-1 (E.C. 2.7.5.1), peptidase "A," "B," "D" (E.C. 3.4.11), 6-phosphogluconic dehydrogenase (E.C. 1.1.1.44), sorbitol dehydrogenase (E.C. 1.1.1.14), and superoxide dismutase-1,2 (E.C. 1.15.1.1). Allelic frequencies (as estimated for three individuals) were determined for each taxon across the surveyed enzymes, and these data were analyzed using the UPGMA and distance Wagner algorithms contained in the BIOSYS program of Swofford and Selander (1981). To ensure that the consideration of additional ingroup taxa would not alter the construction of phenograms, a jackknife manipulation was performed (S. Lanyon 1985). Jackknifing demonstrates the effect of taxon selection on tree topology. In this study of six taxa, six pseudoreplicate trees were produced, each containing a different set of five taxa. A strict consensus tree was produced from these pseudoreplicate trees to identify those portions of the topology that remain consistent.

RESULTS

Syringeal morphology.—The syringeal evidence for the clustering of the genera in the *Empidonax* group is the unique modifications of the cartilaginous segments of the A2 elements (character 1 in Fig. 1; characters are described in Table 1). These modifications, presumably related to the attachment of the internal cartilages, may take the form of a bulbous enlargement on the caudal surface of the cartilaginous segment of the A2, in which case the latter remains firmly connected to and in a straight line with the calcified segment of the A2 (character 2), or the enlarged cartilaginous segment of the A2 element is modified into a broad, transverse cartilage that is displaced caudally to a point where it lies at an oblique angle to the dorsal end of the calcified A2 and is barely if at all connected to that element (character 3).

Empidonax, Contopus, Mitrephanes, and *Sayornis* cluster together (Fig. 1) by virtue of sharing character 3 (unique among all tyrant flycatch-

TABLE 1. Characters used for phylogeny of the *Empidonax* group.

Character description	Distribution by taxa
Syringeal morphology	
1 Cartilaginous segments of A2s modified for attachment of internal cartilages	All taxa in *Empidonax* group
2 Cartilaginous segments of A2s enlarged caudally but continuous and in a straight line with the calcified A2s	*Cnemotriccus, Aphanotriccus, Xenotriccus,* and *euleri*
3 Cartilaginous segments of A2s modified into broad, transverse cartilages at oblique angle to, and barely if at all connected with, dorsal ends of calcified A2s	*Empidonax, Contopus, Mitrephanes,* and *Sayornis*
4 Presence of calcified nodule on lateral surface of each A1 and A2, with cartilaginous connection between them	*Aphanotriccus* and *euleri*
External morphlogy	
5 Adult plumage with rufous wing bars	*Cnemotriccus, Aphanotriccus,* and *euleri*
6 Prominent pointed crest	*Xenotriccus*
Nesting behavior	
7 Nest located in crevices and cavities in trees	*Cnemotriccus* and *euleri* (*Aphanotriccus*?)
Allozymes	
8–13 Np-*a*, Me-*b*, Gpi-*b*, Sod1-*a*, Gda-*a*, Sdh-*a*	*Cnemotriccus, Aphanotriccus,* and *euleri*
14–15 PepB-*a*, Ada-*a*	*Aphanotriccus* and *euleri*
16 PepD-*b*	*Cnemotriccus* and *Aphanotriccus*

ers). In most specimens, representing all four genera, there is no connection between the dorsal end of the calcified A2 and the transverse cartilage. In this condition the internal cartilages are connected by thin cartilage to both the dorsal end of the calcified segment of the A2 and the dorsocaudal corner of the transverse cartilage. In a few specimens the calcified A2 remains barely attached but always at an oblique angle to the transverse cartilage. The medial, cartilaginous segment of the A3 usually connects with the transverse cartilage, also at an oblique angle, but in a few specimens continues around the medial wall of the bronchus, completing the A3 bronchial ring without connection with the transverse cartilage. The extent of variation in syringeal morphology that we found within our sample of specimens from the genus *Empidonax* (Fig. 2) should be compared with the variation among representative specimens from the other three genera in this cluster (Fig. 3).

The syringes of *Empidonax, Contopus, Mitrephanes,* and *Sayornis* are so similar that identification to genus on the basis of the syrinx alone is not possible. Determination of generic limits and relationships within this cluster and resolution of the polychotomy in Fig. 1 must rely on other than syringeal characters. This is reminiscent of the lack of evolution in syringeal morphology among the kingbirds and their allies, where syringeal characters fail to distinguish between *Tyrannus* and *Empidonomus,* and between *Myiodynastes* and *Conopias* (Lanyon 1984). Likewise, within the assemblage of myiarchine flycatchers, *Myiarchus, Sirystes, Casiornis,* and *Rhytipterna* cannot be identified by syringeal characters alone (W. Lanyon 1985).

Given the conservative evolution of the syrinx within *Empidonax* and its closest allies, we were skeptical initially that syringeal morphology would clarify the generic relationship of *euleri.* Surprisingly, we found that all four of the *euleri* syringes lack the transverse cartilage (character 3) unique to *Empidonax* and its allies. Instead, they have the enlarged cartilaginous segments of the A2s continuous and in a straight line with the calcified segments of those elements (character 2) and, for this reason, cluster with *Cnemotriccus, Aphanotriccus,* and *Xenotriccus,* which also share this character (Fig. 4). Within this cluster, the two species of *Aphanotriccus* appear to be the sister group of *euleri,* for these three species share a syringeal

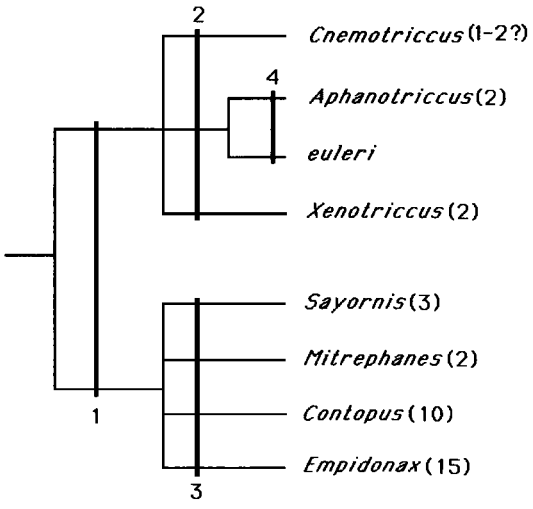

Fig. 1. Phylogenetic relationships within the *Empidonax* group, based on syringeal morphology. Numbers identify diagnostic character states described in text and in Table 1. Number of species per genus in parentheses.

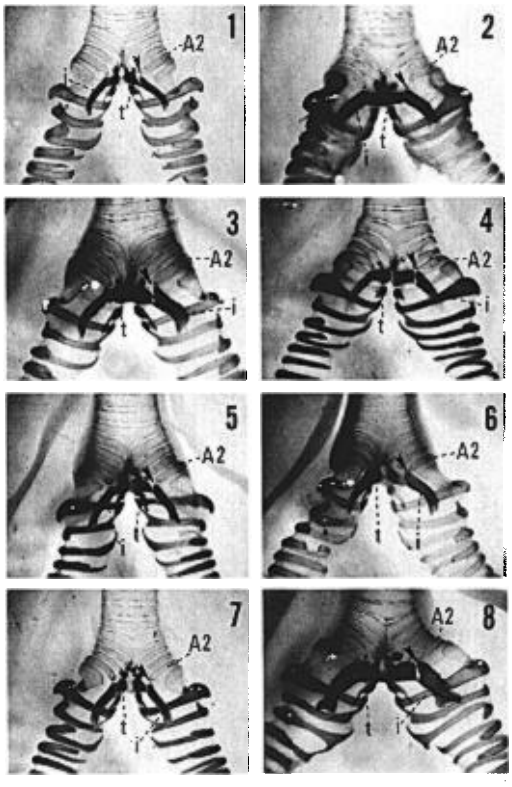

Fig. 2. Intrageneric variation in the syringes of eight species of *Empidonax* (dorsal aspect; magnification = 5×): (1) *E. minimus*, AMNH 8217; (2) *E. alnorum*, AMNH 12873; (3) *E. wrightii*, UK 51239; (4) *E. flaviventris*, AMNH 6770; (5) *E. oberholseri*, UK 51240; (6) *E. affinis*, USNM 506408; (7) *E. hammondii*, MVZ 4139; (8) *E. difficilis*, UK 66993. Calcified A2 elements as labeled; i = internal cartilage, t = transverse cartilage. Arrows indicate oblique angle between transverse cartilage and calcified A2 element.

structure not found in *Cnemotriccus* or *Xenotriccus*, or in any other genus within the entire *Empidonax* assemblage. They have a calcified nodule on the lateral surface of each A1 and A2 element, and a cartilaginous connection between the adjacent nodules (character 4; Fig. 4).

Allelic frequencies and allozyme relationships.— The allelic frequencies (Table 2) verified (Zink and Johnson 1984) that *euleri* was quite distant from *Empidonax flaviventris* and *Contopus virens*. Rogers's *D* for comparisons between *euleri* and these two taxa were equal to 0.422 and 0.385, respectively (Table 3). The comparable values reported by Zink and Johnson were 0.336 and 0.284. This supports the conclusion that *euleri* does not belong to the *Empidonax*/*Contopus* cluster. Theoretically, due to the time-dependent manner in which proteins are thought to evolve (Jukes and Kimura 1984), the distance between *euleri* and any true *Empidonax* or *Contopus* should be the same (at least within a single study). The fact that the distances between *euleri* and these two sister taxa are not identical could indicate that the assumption of rate constancy has been violated. A more reasonable interpretation is that the discrepancy arose from sampling error. Large numbers of loci are required to approximate genetic distances. This can be demonstrated by observing that the frequency estimates for the 26 loci analyzed in both this study and in the study of Zink and Johnson are quite different. In fact, Zink and Johnson, using larger samples, found 14 more alleles across the 26 loci and 3 taxa shared in common by these two studies. This finding not only explains the variability in distance values but also indicates that trees derived from these data must be viewed critically.

A UPGMA phenogram (Fig. 5) illustrates the distant nature of *euleri* from *Empidonax*. A distance Wagner analysis produced the same topology. Jackknifing demonstrated that the hypotheses represented by the UPGMA tree were not affected by changes in the set of taxa used to construct the tree. Furthermore, the allozyme data support the hypothesis based on syringeal morphology that *euleri* is the sister group

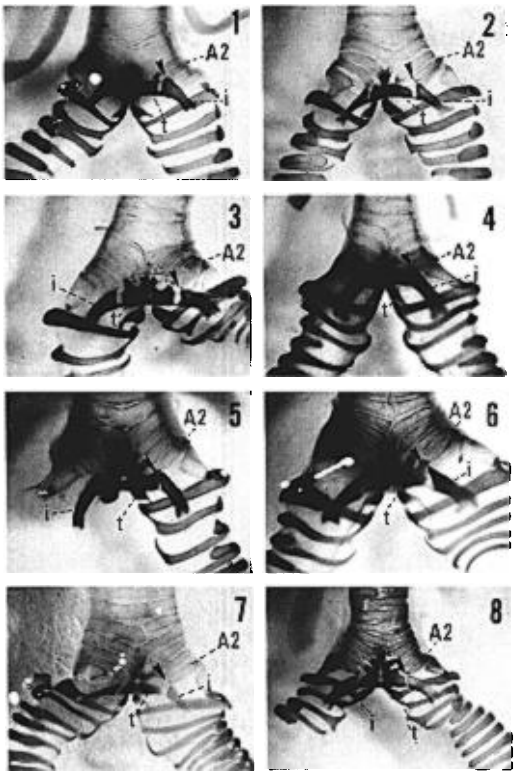

Fig. 3. The syringes of *Sayornis*, *Contopus*, and *Mitrephanes* (dorsal aspect; magnification = 5×): (1) *Sayornis nigricans*, PMNH 4695; (2) *S. phoebe*, AMNH 8199; (3) *Contopus cinereus*, LSU 102566; (4) *C. latirostris*, ROM 111691; (5) *C. virens*, UK 45187; (6) *C. fumigatus*, AMNH 8585; (7) *C. borealis*, LSU 103450; (8) *Mitrephanes olivaceus*, LSU 108479. Labels as in Fig. 2.

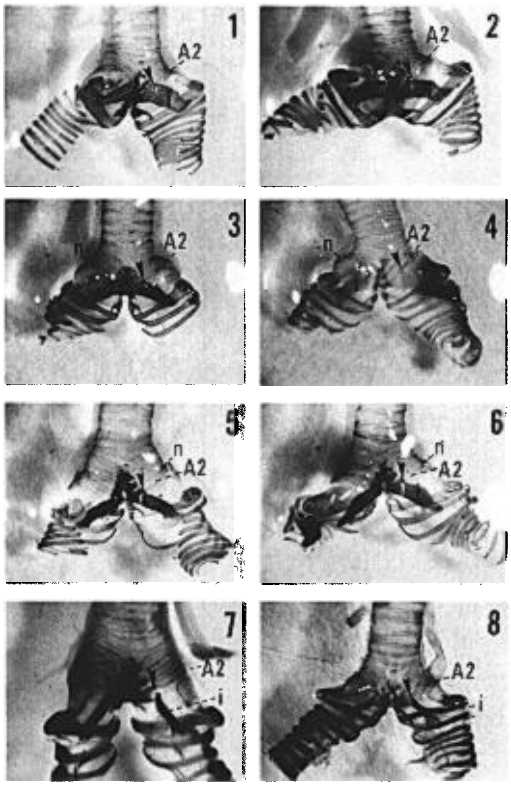

Fig. 4. The syringes of *Cnemotriccus*, *Aphanotriccus*, *Xenotriccus*, and *euleri* (dorsal aspect; magnification = 15×): (1) *Cnemotriccus fuscatus*, LSU 114499; (2) *C. fuscatus*, USNM 505993; (3) *Aphanotriccus audax*, LSU 108499; (4) *A. capitalis*, AMNH 8244; (5) *Lathrotriccus euleri*, LSU 102573; (6) *L. euleri*, LSU 102571; (7) *Xenotriccus mexicanus*, ROM 109631; (8) *X. mexicanus*, AMNH 8789. Calcified A2 elements as labeled; i = internal cartilage, n = nodule on lateral surface of A1. Arrows indicate straight connection between enlarged cartilaginous segment (medial) and calcified segment of A2.

of *Aphanotriccus*, with *Cnemotriccus* as the next closest taxon (no tissue was available for *Xenotriccus*). The distance between *euleri* and *Aphanotriccus* ($D = 0.138$) falls in the upper range of interspecific comparisons for the genus *Empidonax* (Zink and Johnson 1984), suggesting that *euleri* either be assigned a new genus or be placed in *Aphanotriccus*.

The low number of individuals analyzed for each taxon makes a cladistic analysis of reduced value because too few alleles were observed. In a cladistic analysis where all alleles, regardless of their frequency, contribute equally to the analysis, it is important to detect even rare alleles. Recall that Zink and Johnson (1984) found 14 alleles not observed in this study due to their use of larger sample sizes. Nevertheless, using *Empidonax flaviventris*, *Contopus virens*, and *Mitrephanes phaeocercus* as a composite outgroup, nine potential synapomorphic character states were identified. Six such character states (characters 8–13, Table 1) support the clade *Cnemotriccus fuscatus*, *Aphanotriccus audax*, and *euleri*. The remaining three character states (Table 1) conflict; characters 14 and 15 link *A. audax* with *euleri* and character 16 supports a sister-group relationship for *A. audax* and *C. fuscatus*.

Discussion

Differences between the syringeal morphology of *euleri* and that of the genus *Empidonax* (compared with the great similarity among the

TABLE 2. Allelic frequencies for variable loci. Abbreviations for loci follow Harris and Hopkinson (1976). Lower-case letters designate alleles (frequencies in parentheses). The following loci were surveyed and found to be monomorphic and fixed for the same allele in all taxa: Acp, Ck1, Ck2, Fum, ldh2, Lap, Mdh1, Mdh2, Pgm1, and Sod2.

	Species					
Locus	*Empidonax flaviventris*	*Contopus virens*	*Mitrephanes phaeocercus*	*Aphanotriccus audax*	*Cnemotriccus fuscatus*	*euleri*
Ada	b	b	b	a (0.167) b (0.833)	b	a (0.167) b (0.833)
Adh	b	b	b	a (0.167) b (0.833)	b	b
EstD	a (0.167) b (0.833)	b	b	a (0.833) b (0.167)	a (0.167) b (0.833)	a
αGpd	b	a (0.167) b (0.833)	a	a (0.167) b (0.833)	a	a
Gda	b	b	b	a	a (0.667) b (0.333)	a
Got1	a	a	b	a	a	a
Gpi	a	a	a	a (0.333) b (0.667)	b (0.833) c (0.167)	b
Idh1	a	a	a (0.833) b (0.167)	a (0.833) b (0.167)	a	a (0.833) b (0.167)
Ldh2	b	b	a	a	a	a
Me	a	a	a	a (0.333) b (0.667)	a (0.167) b (0.833)	b
Mpi	b	a (0.167) b (0.833)	b	a	a	a (0.750) b (0.250)
Np	b	b	b	a (0.167) b (0.833)	a (0.333) b (0.667)	a (0.500) b (0.500)
PepA	b	c	b (0.167) c (0.833)	c	a	c
PepB	b (0.167) d (0.833)	b (0.333) d (0.667)	b	a (0.500) c (0.333) e (0.167)	d	a
PepD	c	a (0.167) c (0.833)	c (0.333) d (0.667)	b	b (0.833) d (0.167)	c
6Pgd	a (0.333) b (0.667)	a (0.333) b (0.667)	b	b	a	b
Sdh	b	b	b	a	a	a
Sod1	b	b	b	a	a	a

syringes of *Empidonax, Contopus, Mitrephanes,* and *Sayornis*), and the large genetic distance of *euleri* from *Empidonax*, confirm the findings of Zink and Johnson (1984). We concur with these authors that *euleri* should be removed from *Empidonax*. Specifically, *euleri* was found to be most closely related to *Cnemotriccus, Aphanotriccus,* and *Xenotriccus* on the basis of one syringeal character (character 2, Table 1) and to *Cnemotriccus* and *Aphanotriccus* (*Xenotriccus* tissue lacking) on the basis of six electrophoretic characters (characters 8–13, Table 1). However, our data from syringeal morphology and from a UPGMA analysis of electrophoretic data suggest that *Aphanotriccus*, not *Cnemotriccus* as proposed by Zink and Johnson, is the sister group of *euleri.*

During the final stages of the preparation of this manuscript, we discovered relevant information in John Zimmer's unpublished notes (MS, 1931) on *Praedo* (= *Aphanotriccus*) *audax*: "In the bill as in many other features, this form is very similar to *Empidonax lawrenceii* [= *euleri*] as well as to *Aphanotriccus capitalis.* All three forms have the same pattern (band on breast; whitish eye-ring and line over lores; two light wing-bands; buff inner margins of remiges; doubled rounded tail; long rictal bristles; and certainly the same shaped bill; also very small feet and slender legs . . . I should not be sur-

TABLE 3. Matrix of genetic distance coefficients.[a]

Species	1	2	3	4	5	6
1 *Empidonax flaviventris*	—	0.065	0.214	0.390	0.376	0.422
2 *Contopus virens*	0.044	—	0.176	0.343	0.373	0.385
3 *Mitrephanes phaeocercus*	0.205	0.149	—	0.371	0.384	0.371
4 *Aphanotriccus audax*	0.434	0.366	0.418	—	0.213	0.138
5 *Cnemotriccus fuscatus*	0.440	0.411	0.447	0.180	—	0.221
6 *euleri*	0.500	0.431	0.427	0.095	0.205	—

[a] Above diagonal, Rogers's (1972) genetic distance; below diagonal, Nei's distance (Nei 1978).

prised to see both *Aphanotriccus* and *Praedo* reduced to synonyms of *Empidonax* if their monotypic species are not forms of *Empidonax lawrenceii* [= *euleri*], but this requires much further study."

Zimmer's observations of the similarity in the external morphology of *Aphanotriccus* and *euleri* support our contention, based on syringeal morphology and electrophoresis, that these taxa are sister groups. However, there are obvious pitfalls in reliance on external morphology for determining the limits of genera, particularly in this *Empidonax* group of flycatchers.• One might also conclude that *euleri* is closer to *Cnemotriccus* than to *Aphanotriccus*, and, indeed, specimens of the first two forms are often confused in collections (Zink and Johnson 1984). We prefer to base our argument that *euleri* and *Aphanotriccus* are each other's closest relative on the basis of their sharing a uniquely derived syringeal structure (character 4) and a uniquely derived allele for PepB and Ada (characters 14 and 15, Table 1), and on the comparatively low genetic distance between them (Table 3).

We refrain from referring *euleri* to *Aphanotriccus* because of significant differences in cranial morphology that exceed intrageneric variation among tyrant flycatchers. In *euleri* the nasal capsule is virtually completely ossified, including the alinasal walls and turbinals; the nasal capsule of *Aphanotriccus* lacks this degree of ossification and appears like that of *Cnemotriccus* and all other genera in the *Empidonax* group (Fig. 6). We propose a new genus to which *euleri* can be assigned.

Lathrotriccus, new genus

Type species.—*Empidochanes Euleri* Cabanis (1968: 195), Cantagallo, Rio de Janeiro, Brazil; Berlin Museum.

Included species.—The type species only.

Distribution.—Colombia southward, east of the Andes, to Argentina and southern Brazil, and including Trinidad and Grenada; see more detailed range for the species in Traylor (1979).

Etymology.—From a combination of two Greek words, *lathrios*, meaning secret or hidden (alluding in this instance not to the bird's habits but to its obscurity within the genus *Empidonax*), and *triccus*, meaning small bird.

Diagnosis.—Separable from *Empidonax* by having the cartilaginous segments of the A2 syringeal elements continuous and in a straight line with the calcified segments of the A2s (lacking transverse cartilages); separable from *Cnemotriccus* by having calcified nodules on the lateral surfaces of each A1 and A2 syringeal element; and separable from *Empidonax*, *Cnemotriccus*, and *Aphanotriccus* by having the alinasal walls and turbinals of the nasal capsule fully ossified.

The generic relationships of *Lathrotriccus euleri* are further clarified by considering derived plumage patterns and nesting behavior in addition to syringeal morphology (characters 1–4, Table 1) and electrophoresis (characters 8–16, Table 1). We offer a phylogeny (Fig. 7) based on all of these data, as a working hypothesis for subsequent testing as new data become

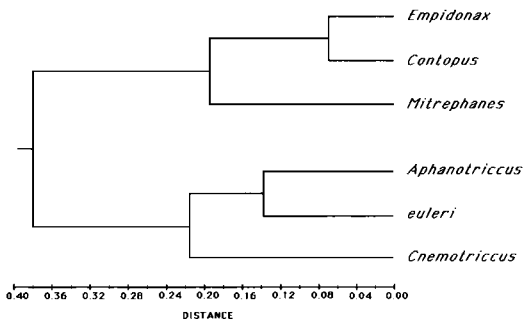

Fig. 5. UPGMA phenogram based on Rogers's *D* values presented in Table 3 (cophenetic correlation coefficient equals 0.988).

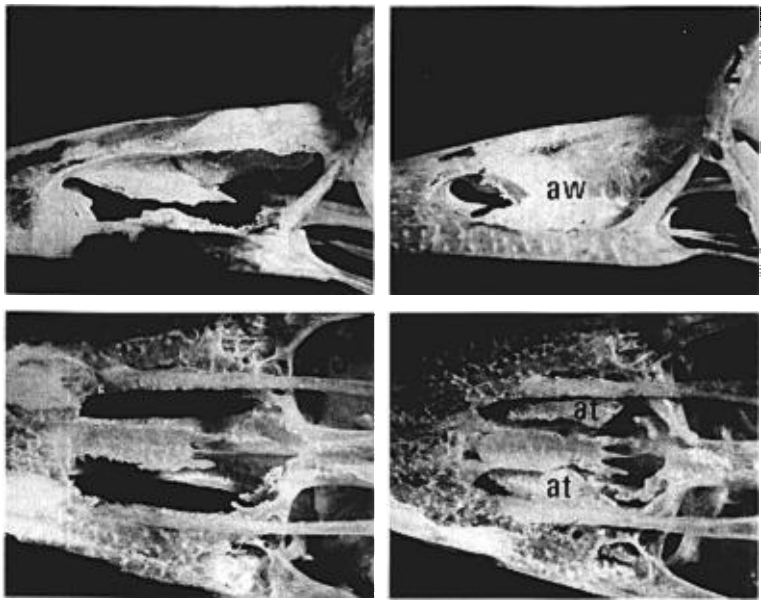

Fig. 6. The nasal capsule in *euleri* is more fully ossified than in any other member of the *Empidonax* group, here represented by *Cnemotriccus* (anterior end of skull to left; magnification = 5×): (1, 3) *Cnemotriccus fuscatus*, AMNH 6685, lateral and ventral views; (2, 4) *Lathrotriccus euleri*, AMNH 6934, lateral and ventral views. aw = alinasal wall, at = alinasal turbinal.

available. *Cnemotriccus*, *Aphanotriccus*, and *Lathrotriccus* possess rufous wing bars (character 5), whereas *Xenotriccus*, and most of the species in the *Empidonax* cluster, have wing bars that are white (i.e. primitive). Although there are conflicting accounts in the literature on the nesting behavior of *Cnemotriccus* and *Lathrotriccus*, an interesting pattern seems to be emerging. Belton (1984) found two kinds of *Cnemotriccus* nests in southern Brazil that, together with differences in vocalizations and responses to playback of sound recordings, led him to believe that there may be two species in this genus (the reason for our uncertainty in Figs. 1 and 7 as to the number of species in *Cnemotriccus*). He found two cup nests of *C. f. fuscatus*, one "essentially in the open," the other "placed between a green bromeliad and the trunk." A nest of *C. f. bimaculatus* was "placed in a rotted hole in the side of a tree about 40 cm above ground." Ned K. Johnson (pers. comm.) informed us that the nests of *Cnemotriccus* and of *euleri* that he found in Argentina "were all nearly identical—located in cavities of rotting stubs of trees."

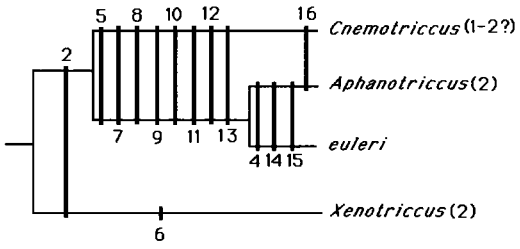

Fig. 7. Generic relationships of *Lathrotriccus euleri* and its closest allies. Numbers identify diagnostic character states described in text and in Table 1. Number of species per genus in parentheses.

Our only information on the nests of *Lathrotriccus euleri* comes from the conflicting accounts of Belcher and Smooker (1937) on Trinidad. Belcher found four nests located in knotholes of trees, while Smooker found two nests in the horizontal fork of a small tree. Edwin O. Willis (pers. comm.) observed nests of *euleri* in Brazil that were "mossy cups in small niches low on the sides of tree trunks."

The nesting habits of *Aphanotriccus* have not been reported. While we need more data on the nesting behavior of all these genera, a working hypothesis is that there has been evolution toward a more obligatory use of tree crevices and cavities (therefore a derived character) in both *Cnemotriccus* and *Lathrotriccus*, and

presumably in *Aphanotriccus* as well (character 7), than has occurred elsewhere within the *Empidonax* group.

The presence of an incubation patch in males could contribute to understanding relationships among these genera. Davis (1945) found a brood patch in a male *euleri* in Brazil, whereas this character is unreported in the well-studied North American species of *Empidonax* and their close relatives and, indeed, is rare within the family Tyrannidae (Davis 1945, Kendeigh 1952, Parkes 1953). It remains to be demonstrated whether this character is shared by the less well-known *Cnemotriccus* and *Aphanotriccus* or is simply autapomorphic for *euleri*.

The recognition of *Xenotriccus* as the sister group of *Cnemotriccus, Aphanotriccus,* and *Lathrotriccus* requires confirmation with electrophoretic data. We know that it has more generalized nesting habits: *X. callizonus* builds its cup-shaped nest into an upright fork or crotch of a low bush (Alvarez del Toro 1965), while *X. mexicanus* constructs a similar cup-shaped nest (Rowley 1962, 1963). *Xenotriccus* differs from the other three genera in possessing a very prominent, pointed crest (character 6).

Our removal of *euleri* from *Empidonax* increases the importance and desirability of obtaining anatomical specimens and tissue of *E. griseipectus,* the only remaining endemic South American member of that genus. That *Empidonax* should have a bona fide resident representative in western South America is not unique or even unusual among the genera in our *Empidonax* cluster (Fig. 1), although these four genera certainly could be characterized generally as being North and Middle American in distribution. The range of *Sayornis nigricans* incudes the Andean region, from northern Venezuela to Argentina, while *Contopus fumigatus, C. cinereus,* and *Mitrephanes phaeocercus* have resident populations west of the Andes. The curious aspect of distributional patterns among the three genera with which we ally *Lathrotriccus euleri* is that, on the one hand, *Cnemotriccus fuscatus* is exclusively South American and widespread east of the Andes (a range virtually identical to that of *euleri*), whereas *Aphanotriccus* and *Xenotriccus* have restricted ranges in southern Mexico and Central America (*A. audax* barely reaches northwestern Colombia). Traylor (1977) suggested that *Aphanotriccus* and *Xenotriccus* "are each composed of two relict species" that "may be remnants of an earlier stock from which the currently successful Central and North American genera *Contopus, Empidonax,* and *Sayornis* were derived." We can conceive of no means to test such a hypothesis.

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