BEHAVIOR, MORPHOLOGY, AND SYSTEMATICS OF THE FLAMMULATED FLYCATCHER OF MÉXICO

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ABSTRACT.—Field and laboratory studies have clarified the generic relationships of the Flammulated Flycatcher (*Deltarhynchus flammulatus*), a monotypic Mexican endemic. A derived character state of the nasal septum argues for the placement of *Deltarhynchus* with the myiarchine flycatchers (*Myiarchus, Rhytipterna, Casiornis,* and *Sirystes*). External morphology and behavior suggest a close relationship with *Myiarchus.* The number, location, and configuration of the syringeal cartilages are sufficiently divergent, however, to suggest that *Deltarhynchus* is not as closely related to *Myiarchus* as are *Rhytipterna* and *Sirystes* and that it should be maintained as a separate genus. *Received 22 October 1981, accepted 18 December 1981.*

THE Flammulated Flycatcher (*Deltarhynchus flammulatus*), known only from a few scattered localities in southwestern and southern México, is a rare bird both in the field and in museum collections. The nest and eggs have not been described, nor has an anatomical specimen been available for study heretofore. Lawrence (1875) originally assigned it to *Myiarchus,* but Ridgway (1893) created the monotypic genus *Deltarhynchus* and cited the relatively shorter and more broadly triangular bill, more rounded wing, and the partly streaked underparts. Subsequent checklists (Hellmayr 1927, Miller et al. 1957, Traylor 1977) have followed Ridgway but acknowledge the close relationship with *Myiarchus* by having *Deltarhynchus* placed immediately after that successful and wide-spread genus. Traylor (op. cit.) commented that *Deltarhynchus* "is pure *Myiarchus* in plumage . . . . Unfortunately nothing has been published on the anatomy or behavior of *flammulatus.* If it is found to be a hole nester, using a few scraps of snake skin for decoration, it should certainly be merged in *Myiarchus.*"

I visited México in 1979 to acquire field experience with the Flammulated Flycatcher, record its vocal repertoire, find the nest and eggs, and obtain anatomical specimens that might shed light on its relationships and generic status. This is a report of the results of that fieldwork and of my subsequent anatomical studies.

DISTRIBUTION AND HABITAT

The Flammulated Flycatcher has a discontinuous distribution in dry deciduous woodlands along the Pacific coast of México, from southern Sinaloa to Chiapas (Miller et al. 1957). Many of the localities where the species has been observed or collected may be characterized as open, thorn woodland, dominated by mesquite (*Prosopis* spp.) and acacia (*Acacia* spp.), but this flycatcher strangely is not common in nor invariably associated with this typical, widely occurring Pacific coastal habitat. Population densities at most sites of occurrence are reportedly low.

The locality at which I concentrated my field studies was in Chiapas, along the road that leads from Tuxtla Gutiérrez to El Sumidero. Curiously, this and the other known localities in the Cuenca Central of Chiapas are within the Atlantic drainage, unlike all other known localities for the species. Almost certainly, the birds of the Cuenca Central are isolated ecologically from the nearest populations in the Pacific lowlands. Miguel Alvarez del Toro, Ernest P. Edwards, and others have observed it here, and it was at this locality that L. Irby Davis made a tape recording on 26 May 1953, almost surely the only previous recording of the species. It was a copy of Davis' recording, obtained from the Laboratory of Ornithology at Cornell University, that facilitated the location of my first Flammulated Flycatcher—always difficult in a population of low density, but more so when one lacks knowledge of the diagnostic vocalizations.

Though I found this species initially at 1,290 m, my ultimate study area was somewhat lower on the El Sumidero road, at an elevation of 1,030–1,120 m and 10 km north of Tuxtla (Fig. 1). The deciduous woodlands on these slopes

Fig. 1. Field study of the Flammulated Flycatcher was concentrated in the deciduous woodlands on the slopes above Tuxtla Gutiérrez, in Chipas, México, elevation 1,050 m.

above Tuxtla renew their foliage in April and May (Alvarez del Toro pers. comm.). Here, I recorded and observed four territorial pairs of Flammulated Flycatchers within an area of about 6 ha. Some of the avian associates at this study area were the Thicket Tinamou (*Crypturellus cinnamomeus*), White-fronted Dove (*Leptotila verreauxi*), Russet-crowned Motmot (*Momotus mexicanus*), White-throated Magpie-Jay (*Calocitta formosa*), Banded Wren (*Thryothorus pleurostictus*), White-lored Gnatcatcher (*Polioptila albiloris*), Fan-tailed Warbler (*Euthlypis lachrymosa*), Red-breasted Chat (*Granatellus venustus*), Yellow Grosbeak (*Pheucticus chrysopeplus*), Blue Bunting (*Cyanocompsa parellina*), and Olive Sparrow (*Arremonops rufivirgatus*).

Two species of *Myiarchus*, Nutting's Flycatcher (*M. nuttingi*) and the Dusky-capped Flycatcher (*M. tuberculifer*), foraged in my study area but were not giving dawn songs locally and hence were not breeding. At another locality near Tuxtla, however, I found the Dusky-capped Flycatcher and the Flammulated Flycatcher to have broadly overlapping breeding territories, with the males delivering dawn songs from the same trees. Elsewhere within its range in México, *Deltarhynchus* is sympatric with breeding populations of a third species of *Myiarchus*, the Brown-crested Flycatcher (*M. tyrannulus*). At no time did I observe interactions between these *Myiarchus* flycatchers and *Deltarhynchus*.

FORAGING BEHAVIOR

Fitzpatrick (1978) has noted that *Myiarchus* and related tyrannids capture their prey principally by picking it off some substrate during a flight away from a perch. His term for this is the Sally-Glean, as differentiated from other primary techniques of prey capture such as Aerial Hawk, Perch-to-Ground, and Perch-Glean. A distinct type of Sally-Glean and the one used by *Myiarchus* most of the time, according to Fitzpatrick, is the Outward Hover-Glean: "The bird searches for prey from an exposed, usually well-lighted site, looking primarily outward or downward. The approach flight is rapid and direct, and prey is snatched from an exposed substrate (upper surface of a leaf, or a twig) during a short hover in which the bird may still be moving forward . . . . The follow-up flight is a continuation of the sally, and almost invariably carries the bird well away from its former perch." This description of foraging behavior applies to the Flammulated Flycatcher as well. Though I have no quan-

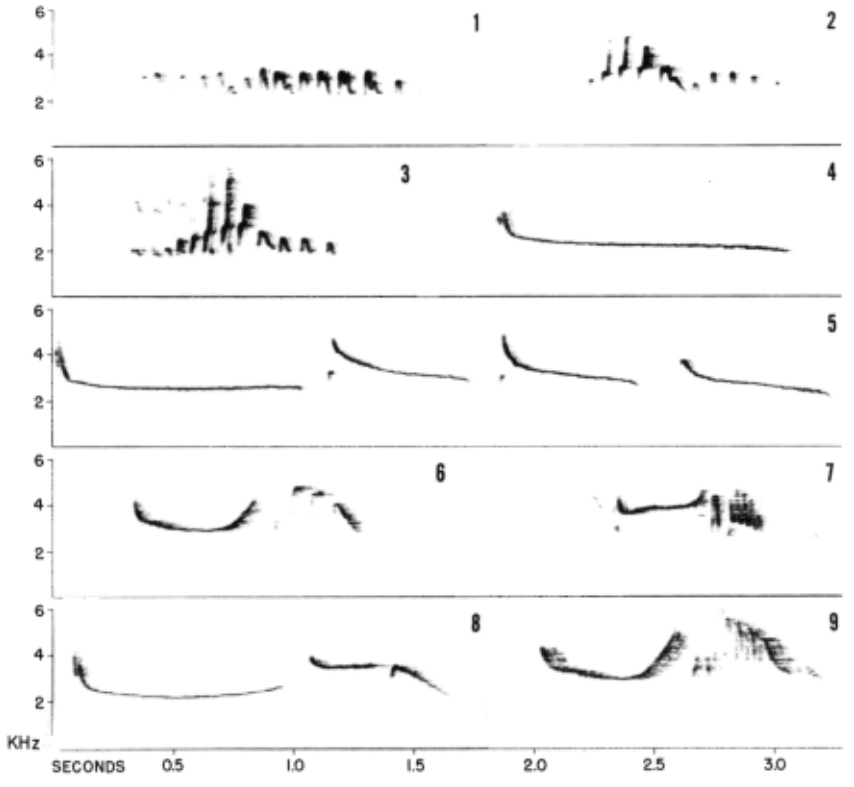

Fig. 2. Sound spectrograms of calls of the Flammulated Flycatcher.

titative data, my general observations suggest no significant differences in method of prey capture between *Deltarhynchus* and *Myiarchus*.

When excited, as in either agonistic or epigamic encounters, Flammulated Flycatchers will elevate the feathers of the crown as do *Myiarchus* (and many other tyrannids), thus giving the impression of a "crest." I have no observations, however, of the serpentine movements of the head that are so typical of *Myiarchus*, in which the bird extends the neck fully and bobs the head, often in response to the sight of an item of prey or of an observer.

VOCALIZATIONS

Sound recordings were made with a Sony TC150 cassette tape recorder, operated at a tape speed of 1⅞ ips and a Dan Gibson electronic EPM parabolic microphone. Whenever a new recording was made in the field, the tone of a pitch pipe (middle "A," 440 Hz) was recorded as a permanent check on the speed of the recorder and on possible distortion. A subsequent analysis was made of 1.5 h of recordings of the vocalizations of seven pairs of *Deltarhynchus*. Representative vocal characters were selected for analysis with a Sona-Graph, model 6061B, using the narrow-band (45 Hz) filter. To illustrate the extent of variation in these vocal characters, I photographed sound spectrograms (graphically portraying frequency against time) and reproduced them here as halftone illustrations, thus retaining the maximum detail possible. See Lanyon (1978) for a discussion of terminology as applied to myiarchine vocal characters.

The vocal characters of *Deltahynchus* can be categorized conveniently as either calls or dawn song, as defined below. The carrier frequency of these vocal characters is restricted to the 2.0–6.0 kHz range.

Calls.—Both sexes share the same repertoire of calls given during the daylight hours. These calls are ritualized sound signals used to communicate such information as location, specific identity, territorial limits, alarm, and other reproductive and social functions. As in my

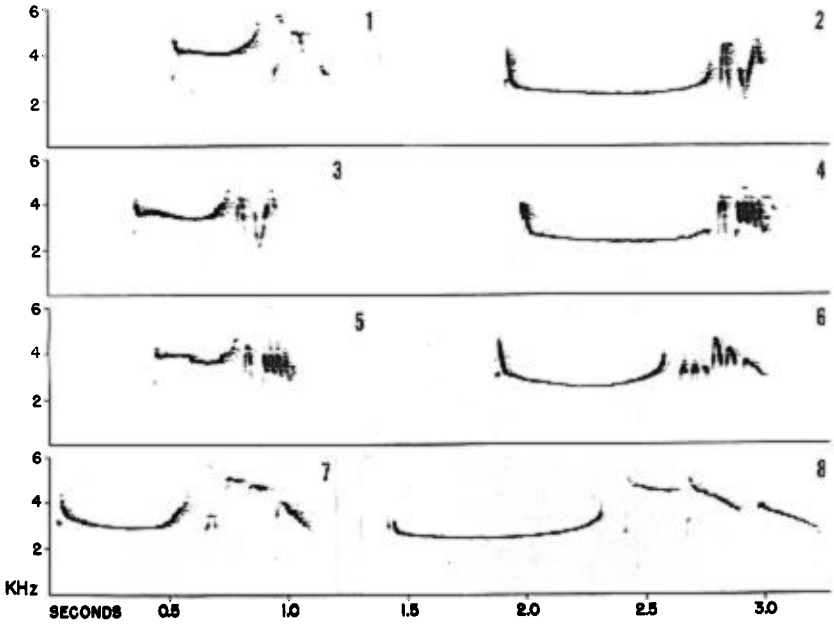

Fig. 3. Sound spectrograms of phrases in the dawn song of the Flammulated Flycatcher.

studies of *Myiarchus*, I gave special attention to those calls given in response to the playback of a recording of the species' vocal repertoire or in natural encounters with intruding conspecifics. This procedure maximizes the comparability of vocal characters in interspecific comparisons.

In response to playback, or when excited by intruding conspecifics, *Deltarhynchus* vocalizes with a variety of pulsed notes, with sustained whistled notes, and with various combinations of these two categories. The roll (Fig. 2: 1–3) is a multi-syllabled call that results from a rapidly delivered series of pulsed renditions of the carrier frequency. The traces of these pulsed elements are typically chevron-like. An increase in frequency excursion and in intensity may accompany an increase in the level of motivation. The carrier frequency may be modulated at a frequency up to 30 Hz, in which case the sound energy is continuous (not pulsed) and a tremulous note or vibrato results (Fig. 2: 7). Whistles (Fig. 2: 4–9) are sustained renditions of the carrier frequency with little or no modulation (steady state, "pure tone"). Given as an isolated call, a whistle may last up to 1.3 s and sound extremely melancholic to the human ear (Fig. 2: 4). Phonetically, this prolonged whistle may be represented as "churr-r-r-r," in which the "ch" suggests the rather noisy, explosive introductory segment. In the excitement of a territorial encounter, a rapid series of as many as four of these whistles may be given, each slightly lower in frequency than the preceding—"churr-bee be," or "churr-r-r, bee bee beer" (Fig. 2: 5). With an increase in excitement, the initial whistle may be followed by chevron-like notes (Fig. 2: 6), a vibrato (fig. 2: 7), or much shortened whistled notes (Fig. 2: 8). When the introductory whistle is short in duration, it is typically at a higher frequency than the longer whistles, exhibits a prominent glissando (rapid change in frequency), and has a sharper, more piercing quality. Phonetically, these calls may be represented as "chee-bee beet"; they end very abruptly compared with those calls consisting exclusively of whistled notes.

Foraging birds not excited by playback or intruding conspecifics will deliver isolated, melancholic whistles (Fig. 2: 4) at intervals from several seconds to several minutes in length. Presumably, these calls serve as location notes in the communication between paired birds, for often they are given by an individual after the removal of its mate by collecting and also in response to the termination of playback (1 or 2 min after the cessation of

Fig. 4. Natural cavity used for nesting by the Flammulated Flycatcher. See Fig. 5 for a photograph of the contents of the cavity.

the tape recording). Interspersed between these melancholic whistles are occasional renditions of low intensity rolls (Fig. 2: 1), particularly at times of shift from one foraging perch to another.

I have no evidence that isolated chevron-like notes are an important part of the vocal repertoire of *Deltarhynchus*, as they are in many species of *Myiarchus* (the "huit" note). Likewise, the *rasp* and *rasping whistle*, so characteristic of many *Myiarchus*, are absent from my sample of *Deltarhynchus* recordings.

Dawn song.—The males of most species of tyrannid flycatchers give a stereotyped, species-specific pattern of vocalizations just before and at dawn, beginning at the onset of territorial defense and extending for varying lengths of time through the breeding season. This has become known in the literature as the "dawn" song, though it may be heard at other times of day but much less frequently and predictably. The unique features of dawn song are not the vocal components per se, for these are the vocalizations used by both sexes during the daylight hours, but rather the arrangements of these components into predictable patterns, often having consistent temporal characteristics.

The dawn song of the male of *Deltarhynchus* consists of a variety of phrases, each typically about 1.0 s in length, rendered at intervals of about 3.0 s (Fig. 3). The only constant feature among these phrases is that each is introduced by one of the daytime whistles, sometimes of the sharper, piercing variety (Fig. 3: 1, 3, 5), and sometimes of the longer, more melancholic variety (Fig. 3: 2, 4, 6, 8). Typically the two types of whistles are alternated in consecutive phrases. Following the introductory whistle, each phrase is terminated with a short rolling note, a vibrato, or a series of short whistled notes, all of which are represented in the daytime repertoire. Typical dawn-song phrases might be represented phonetically as "chee-bee beet" and "churr-r-r-bee bee."

BREEDING BIOLOGY

Male Flammulated Flycatchers were giving their dawn songs during the first morning that I worked in my study area, on 4 June. Males were mist-netted and marked in order to insure identification and to facilitate observation of the females. On the 4th and again on the 11th of June, I noted that one of the females was carrying nesting material and consistently flying off in the same direction. On 16 June the male of this pair attempted copulation, suggesting that the female was probably in the laying phase of her cycle. My wife and I had the female under observation for 45 min on 17 June, and I concluded that the female was still laying. On 18 June we followed the female from 0955 to 1035, at which time she entered a natural cavity in a stump; the cavity entrance, 6 cm in width, was only 90 cm off the ground (Fig. 4). I delayed inspection of the cavity until I was convinced that the female was actually incubating. When I later approached the stump, I was impressed with the shallowness of the cavity and the fact that I could see the female. Clearly, the female could see me as well, for she made a hasty departure when I was still a half meter from the stump. There

were three eggs, and these were identical to the eggs of all *Myiarchus* with respect to ground color and markings (Fig. 5). The lining of the cup-shaped nest consisted solely of fine vegetable fibers and small fragments of dried leaves and shredded bark. I could find no evidence of either fur or feathers, and there were no pieces of shed reptilian skin, plastic, or paper. I found no other nests of this species.

Fig. 5. Cup-shaped nest and complete clutch of three eggs of the Flammulated Flycatcher can be seen easily through the entrance to the shallow nest cavity.

MORPHOLOGY

EXTERNAL

The overall appearance of the Flammulated Flycatcher in the field is that of a small *Myiarchus*. Undoubtedly, it has been confused on occasion with wintering or resident *Myiarchus tuberculifer*, with which it often occurs. Not only are these species similar in size and general coloration, even to having the remiges and rectrices fringed with Antique Brown (color terminology follows Smithe 1975), there are great similarities in their melancholic whistles as well, which might contribute to mistaken identities in the field. The flammulations of the breast, though conspicuous when the bird is in the hand, are not useful in the field except under the most favorable circumstances. Like *M. tuberculifer*, *Deltarhynchus* has black tarsi, feet, and bill (except for slight paling at the base of the lower mandible) and an orange lining of the mouth. The most dependable field character is one called to my attention by Ernest P. Edwards (pers. comm.) before I went to México: grayish-white lores and orbital ring. I have since noted that Ridgway (1907) and Blake (1953) acknowledge this character. Peterson failed to portray this in his Méxican field guide (1973), probably because of the "make" of the two specimens available to him at the American Museum of Natural History, neither of which was prepared to reveal this character.

The "relatively shorter and broadly triangular bill" (compared with that of *Myiarchus*) was the principal basis for Ridgway's (1893) *Deltarhynchus*. It is certainly true that the ratio of bill width to bill length in *Deltarhynchus* averages greater than in any species of *Myiarchus*, but, because there is overlap with some individuals of *M. barbirostris* on Jamaica, it would be imprudent to base generic distinction on this character alone.

The rectrices of the juvenal plumage are broadly edged (not merely fringed, as in adult *Deltarhynchus*) with Antique Brown, as they are in all species of *Myiarchus* and in most juvenal-plumaged flycatchers of the subfamily Tyranninae (*sensu* Traylor 1977).

INTERNAL

There are two complexes of internal morphological characters that are extremely useful in diagnosing *Myiarchus* flycatchers and close relatives: (1) the nasal septum, specifically the degree to which there is ossification and buttressing with internal supporting structures (Warter 1965, Traylor 1977), and (2) the syrinx, most notably the number, shape, and position of the internal cartilages (Ames 1971). It was the convincing anatomical findings of Warter and Ames that provided the basis for the subsequent shift of several genera, heretofore considered cotingids, to a position close to *Myiarchus* among the Tyrannidae (Snow 1973, Traylor 1977). Because of the value of these two character complexes in diagnosing *Myiarchus* and close relatives (Lanyon in prep.), I was eager to examine the skull and syrinx of *Deltarhynchus*, heretofore unavailable for study.

Nasal septum.—The primitive state of the nasal septum among suboscines (and all passerines) is one of little or no ossification (Warter 1965, Lanyon MS). Among the derived characters that distinguish the Tyrannoidea (cotingas, manakins, plantcutters, sharpbills, and tyrant flycatchers) from other suboscines is the greater degree of ossification of the septum,

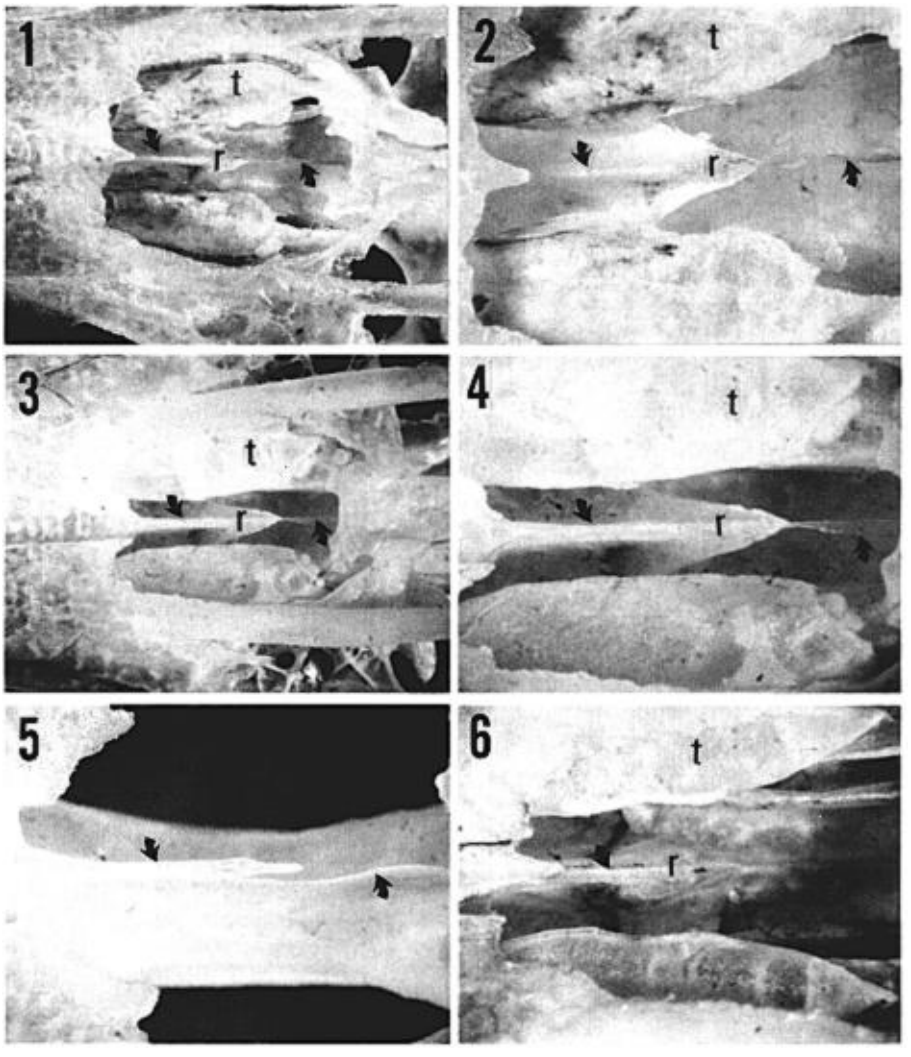

Fig. 6. Photographs, taken through a dissecting microscope, of the ventral aspect of the nasal region of the skulls of some tyrannine flycatchers (anterior end of the skull to the left): 1, 2—*Deltarhynchus flammulatus* (AMNH 11391, 10× and 20×); 3, 4—*Myiarchus swainsoni* (AMNH 9253, 10× and 20×); 5—*Tyrannus tyrannus* (AMNH 5958, 20×); and 6—*Rhytipterna simplex* (AMNH 11597, 20×). Arrows indicate ventral edge of nasal septum, which lacks a trabecular plate; r—internal supporting rod; t—alinasal turbinals, left side.

including the presence of internal supporting rods and trabecular plates in some groups. Among the tyrant flycatchers, the subfamily Tyranninae (as defined by Traylor 1977, but omitting *Laniocera*) appears to be a monophyletic group, characterized by having a well-ossified nasal septum that lacks a transverse trabecular plate. Warter noted [Fig. 2 and Table 2 in Warter (1965) and reproduced in Traylor (1977)] that within this assemblage there are a few genera in which the nasal septum, though lacking the trabecular plate, has a conspicuous internal supporting rod ("r" in Fig. 6); he reported this character state in *Myiarchus* (11 of 22 species), *Rhytipterna* (2 of 3 species), and *Sirystes*. I have now confirmed this derived condition in 20 of the 22 species of *Myiarchus* (2 still unavailable), in all 3 species of *Rhytipterna*, and in *Sirystes*, *Casiornis rufa*, and *Deltarhynchus*. All of the remaining genera placed in the Tyranninae by Traylor (1977) lack this conspicuous internal supporting rod, as illus-

trated by the septum of *Tyrannus tyrannus* in Fig. 6.

The nasal capsule of *Deltarhynchus* (1 and 2 in Fig. 6) is typically tyrannine, in that the nasal septum is well-developed (ossified) but lacks a trabecular plate along the ventral edge. It is typically myiarchine (as exemplified by the skulls of *Myiarchus swainsoni* and *Rhytipterna simplex* in Fig. 6) in the degree to which the capsule has become ossified (note presence of alinasal turbinals, "t") and especially with respect to the well-developed internal supporting rod ("r").

Syringeal cartilages.—The syrinx offers greater potential than does the nasal septum for determining relationships within the Tyranninae, for there is more variation in its morphology within that subfamily of flycatchers. I have now examined syringes from at least one species in each of the tyrannine genera. All syringes were stained for cartilage and bone, using alcian blue and alizarin red (after Dingerkus and Uhler 1977). I follow Ames (1971) in the method of dissection and in terminology.

Myiarchus (12 species examined), *Rhytipterna* (all 3 species), *Casiornis* (1 species examined), and *Sirystes* share a suite of syringeal characters that sets them apart from all other tyrannines. In these four genera there are two pairs of cartilages that lie within the internal tympaniform membranes: (1) a large, dorsal pair, which are J- or L-shaped and are connected anteriorly to the ventral segment of the tracheo-bronchial junction (with no connection to the dorsal ends of the A-2 supporting elements), and (2) a much smaller, ventral pair of variable shape and located within the membranous connections that extend between the posterior ends of the large cartilages and the ventral ends of the B-2 bronchial semirings (Fig. 7).

The syrinx of *Deltarhynchus* is myiarchine with respect to several derived characters, including the shape of and connection between the B-1 and B-2 bronchial semirings, but it differs markedly from that of *Myiarchus, Rhytipterna, Casiornis,* and *Sirystes* in having only a *single pair of internal cartilages.* The latter are located dorsally within the internal tympaniform membrane and are large and straight but somewhat expanded at their posterior ends (*"club-shaped"*). These cartilages connect anteriorly to the *dorsal ends of the A-2 supporting elements* and to the dorsal segment of the tracheo-bronchial junction (Fig. 7).

SYSTEMATICS

The affinity of *Deltarhynchus* with *Myiarchus,* as suggested by external morphology, has never been seriously challenged. John T. Zimmer, in unpublished notes dated 2 August 1951, casually remarked on similarities of the plumage and bill with *Nuttallornis* and *Contopus* but it is not clear whether he intended to pursue this reasoning further. Possession of a derived character state of the nasal septum, i.e. the presence of a conspicuous internal supporting rod in a well-ossified septum that lacks a trabecular plate, argues for the placement of *Deltarhynchus* with the myiarchine flycatchers (*Myiarchus, Rhytipterna, Casiornis,* and *Sirystes*). Indeed, considering the degree of variation that one finds among the species of *Myiarchus* (Lanyon 1967, 1975, 1978), there is nothing in the external morphology, foraging behavior, vocalizations, coloration of the eggs, or the use of a cavity for nesting that would justify generic separation of *Deltarhynchus.* The burden of proof would seem to rest with those who argue for continued generic status of this Méxican endemic.

It was some of the details of the nesting behavior of *Deltarhynchus* that first alerted me to the possibility that it should *not* be merged with *Myiarchus.* I have nesting data on 20 of the 22 species of *Myiarchus* (in prep.), and the pattern of behavior emerging from these data is unique among tyrannid flycatchers and therefore of great value in diagnosing the genus. *Myiarchus* nests are located within cavities in trees (or suitable man-made substitutes), and these cavities are of a depth sufficient to hide the incubating females completely. The lining of these nests is soft; in addition to vegetable fibers, invariably there are quantities of fur and feathers and frequently fragments of shed reptilian skin or plastic and paper substitutes. The *Deltarhynchus* nest discovered in this study was unlike any *Myiarchus* nest known to me in being located in a comparatively shallow cavity and in lacking fur, feathers, and shed reptilian skin or substitutes in its construction. Impressive as these differences may be, one is reluctant to suggest separate generic status solely on the basis of the architecture of a single nest.

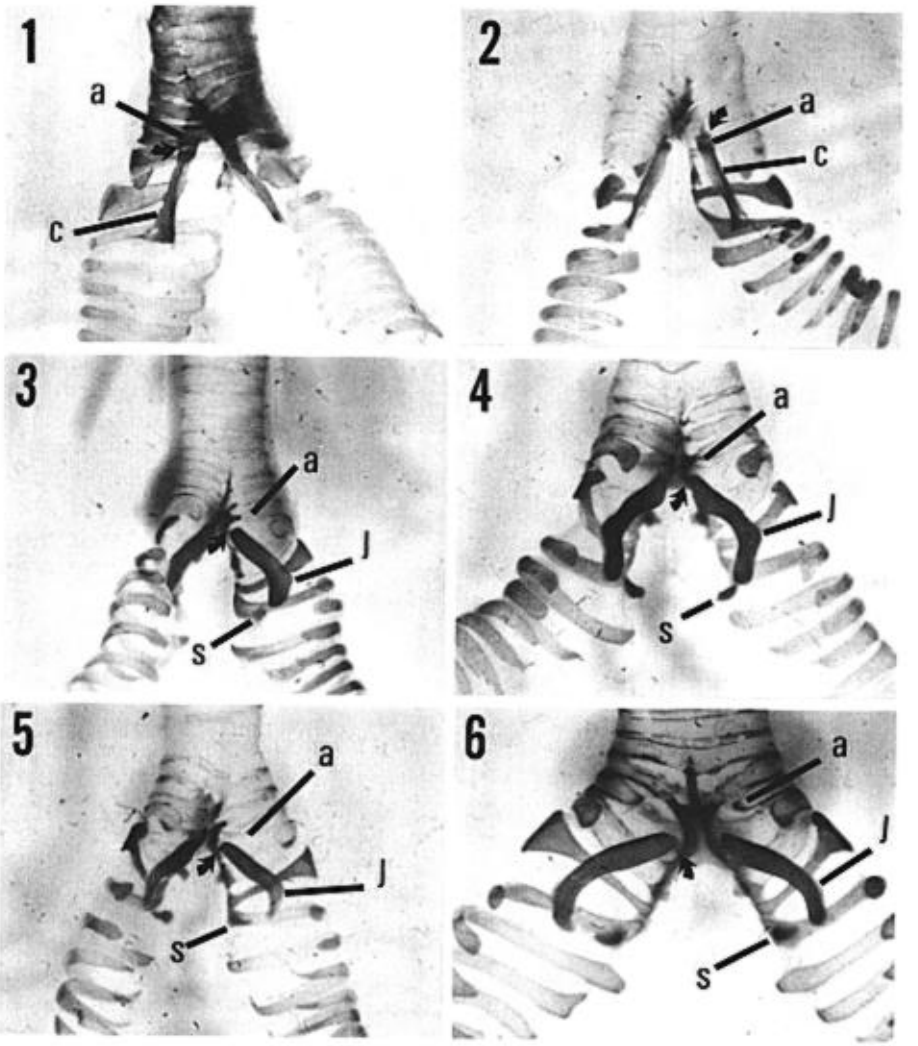

Fig. 7. Photographs, taken through a dissecting microscope, of the dorsal aspect of the syringes of some tyrannine flycatchers: 1, 2—*Deltarhynchus flammulatus* (AMNH 8128, AMNH 7761); 3—*Myiarchus cinerascens* (AMNH 6675); 4—*Myiarchus swainsoni* (AMNH 7991); 5—*Myiarchus semirufus* (AMNH 4503); and 6—*Rhytipterna simplex* (AMNH 8129). Arrows indicate connections of large dorsal cartilages to the dorsal ends of the A-2 supporting elements (in *Deltarhynchus* 1 and 2) or to the ventral segment of the tracheo-bronchial junction (in *Myiarchus* and *Rhytipterna*, 3–6); a—dorsal ends of the A-2 supporting elements; c—club-shaped dorsal cartilages in *Deltarhynchus*; j—J- or L-shaped dorsal cartilages in *Myiarchus* and *Rhytipterna*; s—small ventral cartilages in *Myiarchus* and *Rhytipterna*. All specimens magnified 14×.

The number, location, and configuration of the syringeal cartilages is strong argument, however, for the maintenance of *Deltarhynchus* as a separate genus within the myiarchine complex, as characterized by the skull. Surprisingly, syringeal anatomy suggests that *Deltarhynchus* is not as closely related to *Myiarchus* as are *Rhytipterna*, *Casiornis*, and *Sirystes*.

A more complete phylogeny of the myiarchine flycatchers must await the results of continuing studies of the morphology and nesting behavior of *Rhytipterna*, *Casiornis*, and *Sirystes*. Preliminary data presented here suggest that *Deltarhynchus* should be considered a close relative of that assemblage of tyrant flycatchers but merits separate generic status.

ACKNOWLEDGMENTS

I am grateful to the Dirección General de la Fauna Silvestre, México, for permission to collect the specimens needed for this study. Laurence C. Binford, Ernest P. Edwards, and Allan R. Phillips shared with me their field experiences with *Deltarhynchus*. Lloyd F. Kiff provided me with helpful data from specimens in the collection of the Western Foundation of Vertebrate Zoology, and Raymond A. Paynter gave me access to the collection at the Museum of Comparative Zoology at Harvard. Peter L. Ames sent me several syringes that were critical to this study. James L. Gulledge provided me with a recording of *Deltarhynchus* from the Library of Natural Sounds, Laboratory of Ornithology, at Cornell University. I am especially indebted to Miguel Alvarez del Toro, of Tuxtla Gutiérrez, for information pertaining to my study area and to my wife, Vicky, for her companionship and assistance in the field and for the preparation of the sound spectrograms. Guido Dingerkus and Charles W. Myers, of the American Museum of Natural History, gave me valuable advice for staining and photographing the anatomical material, respectively. Financial support was provided by the Leonard C. Sanford Fund of the American Museum of Natural History.

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APPENDIX. Data on sound recordings used for the spectrograms.

All recordings were made near Tuxtla Gutiérrez, in Chiapas, México in June 1979. Catalog numbers (in the collection of W. E. Lanyon) for the recordings used for the spectrograms illustrated here are as follows. Figs. 2, calls: 1, 201B-007; 2, 201A-465; 3, 201B-230; 4, 201B-495; 5, 201B-067; 6, 201A-298; 7, 201B-324; 8, 202A-137; 9, 202A-030. Fig. 3, dawn song phrases: 1, 201A-321; 2, 201B-408; 3, 201B-284; 4, 201B-286; 5, 201B-291; 6, 202A-667; 7, 201A-338; 8, 201A-436.