

# THE SYRINX IN CERTAIN TYRANT FLYCATCHERS

MILDRED MISKIMEN

## INTRODUCTION

VIBRATING membranes at the junction of the bronchi with the trachea are responsible for bird vocalization. In general, the non-passerine syrinx consists of vibrating membranes of the trachea, bronchi, or both, controlled by two pairs of muscles: the *tracheo-lateralis* extending from the larynx to the side of the syrinx, and the *sterno-trachealis*, from the sternum to the syrinx or lower trachea. According to Romanoff (1960) these muscles arise in the chick embryo from muscles originally extending from the larynx to the sternum. The typical passerine syrinx is centered around the drum, a bone or cartilage ring at the base of the trachea. A narrow strip of bone, the pessulus, divides the end of the drum into right and left halves and marks the junction of the two bronchi with the trachea. Between the proximal bronchial cartilages and the drum lie three or more thicker cartilages known as intermediary bars, or bronchial bars. Typically five pairs of short muscles attach to the drum and bronchial bars, controlling fine adjustments of the vibrating membranes of the bronchial walls.

While studying the passerine syrinx in 1949, I obtained a few specimens of the family Tyrannidae. In the paper published on that work (Miskimen, 1951: 503) I noted that the syringeal muscles of the Eastern Wood Pewee, *Contopus virens*, and the Traill's Flycatcher, *Empidonax traillii*, were unlike muscles of other passerines studied. Since that time I have studied the syringeal structures of specimens from six genera of tyrannids in an attempt to determine (1) what features are peculiar to members of the family Tyrannidae, and (2) the extent of uniformity within the group.

## MATERIALS AND METHODS

One difficulty encountered in this study was that in the family Tyrannidae only the genus *Empidonax* is represented by more than one species in northeastern United States. Some collectors of *Empidonax* hesitate to identify species unless they hear the song or identify a nest. I have secured several specimens positively identified as *E. traillii* and one specimen identified only as *Empidonax*. These and the other specimens upon which this study is based are listed below. The specimen of *Muscivora tyrannus* is from the spirit collection of The American Museum of Natural History in New York. The *Myiarchus* specimens, with the exception of *M. crinitus*, were contributed by Dr. Wesley E. Lanyon of The American Museum of Natural History, and were collected in connection with his 1960 expedition to Central America and the Caribbean Islands. The other specimens are from Ohio, Indiana, and New Jersey.

*List of species and specimens.*—*Tyrannus tyrannus*, 3; *Muscivora tyrannus*, 1; *Myiarchus crinitus*, 2; *M. cinerascens*, 5; *M. nuttingi*, 6; *M. berlepschii*, 1; *M. validus*, 1; *M. sclateri*, 2; *M. barbirostris*, 1; *M. stolidus*, 2; *Sayornis phoebe*, 2; *Empidonax traillii*, 2; *E. sp.*, probably not *traillii*, 1; *Contopus virens*, 4.

My study has been handicapped for want of further material, and I would like to correspond with anyone who could give me information about possible sources of specimens. I could cooperate with collectors of skins, for I can use preserved, labeled specimens from which skins have been removed. While I am particularly interested in the family Tyrannidae, because of its phylogenetic position, I would appreciate receiving material representing other families, particularly if consisting of several genera and species.

Preparatory to study of the tyrannid syrinx I removed the entire trachea and bronchi from the specimens and placed them in individual vials in a preservative mixture of ethyl alcohol, glycerol, and water in the ratio 3:1:1. The glycerol prevents excess drying of the specimens during prolonged examination. In order to correct for dilution by tissue fluids I renewed the preservative in each vial after three days, and again after three or four months. Specimens transferred to this mixture from other preservatives showed no damage. After recording the muscle positions and attachments I stained the cartilages, using the Alizarin Red method prescribed by Guyer (1947: 157) for embryos, but modified the timing according to the sizes of the specimens. I liked this stain better than Methylene Blue, for the cartilages become bright pink, with thicker portions showing deeper color, while connective tissues and muscles remain transparent, the muscles showing as faint shadows. Pure glycerol is the best material for storing the stained specimens, since it does not destain as rapidly as alcohol and water do, and the clearness of glycerol facilitates observing cartilages.

The syringeal skeletal elements appeared to be cartilaginous, not bony as in other birds. This I confirmed by using Methylene Blue counterstained with Alizarin Red, as described by Moog (1949: 80). No evidence of ossification appeared.

#### MUSCLE DESCRIPTIONS

There are one or two intrinsic syringeal muscles in the tyrannid syrinx. I have given them names because I have not found them named or described in the literature (Figure 1, A-C).

1. *M. Syringeo-ventralis*, a thick, short muscle extending transversely across the ventral syrinx.

ORIGIN: the longitudinal, mid-ventral line of the drum, and also, in some, along the cephalic edge of the drum (compare Figure 1, A and 1, B).

INSERTION: on one or more bronchial bars.

ACTION: probably changes the shape of the syrinx by bending the bronchial bars.

2. *M. Syringeo-lateralis* (present in *Myiarchus*), longitudinal on the lateral part of the drum (Figure 1, C).

ORIGIN: the lateral, cephalic edge of the drum.

INSERTION: on one or more of the bronchial bars.

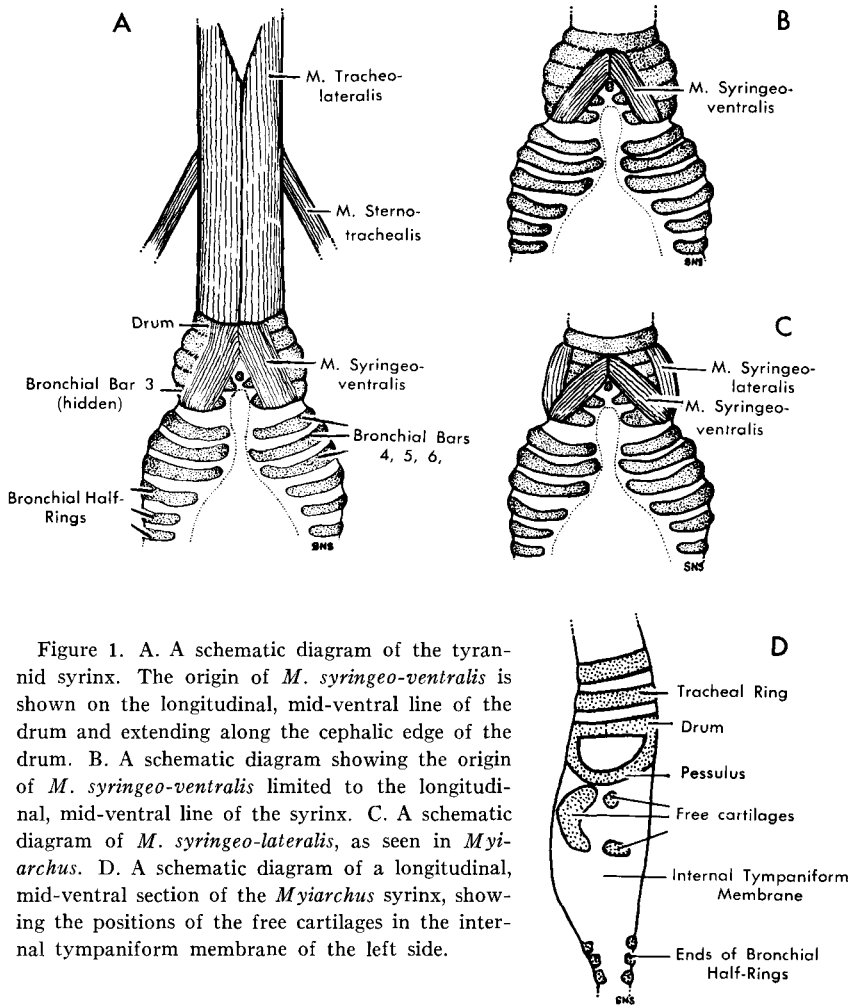


Figure 1. A. A schematic diagram of the tyrannid syrinx. The origin of *M. syringeo-ventralis* is shown on the longitudinal, mid-ventral line of the drum and extending along the cephalic edge of the drum. B. A schematic diagram showing the origin of *M. syringeo-ventralis* limited to the longitudinal, mid-ventral line of the syrinx. C. A schematic diagram of *M. syringeo-lateralis*, as seen in *Myiarchus*. D. A schematic diagram of a longitudinal, mid-ventral section of the *Myiarchus* syrinx, showing the positions of the free cartilages in the internal tympaniform membrane of the left side.

**ACTION:** probably draws the bronchial bars cephalad, altering tension of the tympaniform membranes.

The following descriptions show similarities and differences among genera. In the genus *Myiarchus*, although specimens of several species have been studied, I have here described only *M. crinitus*, and have mentioned only features that are distinctive of the genus. There are differences among the various species of *Myiarchus* that I am not prepared to analyze now, because of variations among individuals of a species.

TYRANNUS TYRANNUS. EASTERN KINGBIRD

*Muscles*

*M. Tracheo-lateralis*, on the lateral surface of the trachea, and the ventral surface from ring 6 to the drum; longitudinal.

ORIGIN: on the cricoid cartilage of the larynx.

INSERTION:

(a) dorsal insertion on bronchial bar 2, dorsal end;

(b) ventral insertion along the ventral, cephalic edge of the drum to the mid-line.

ACTION: draws the syrinx cephalad.

*M. Sterno-trachealis*, from the sternum to the trachea, diagonal.

ORIGIN: on the anterolateral portion of the sternum.

INSERTION: on *M. tracheo-lateralis* and tracheal ring 6.

ACTION: draws the syrinx caudad.

*M. Syringeo-ventralis*, on the ventral syrinx, transverse.

ORIGIN: on the longitudinal, mid-ventral line of the syrinx and extending along the cephalic edge of the drum.

INSERTION: on bronchial bars 3 and 4, at the dorsal ends.

ACTION: not clear.

*M. Syringeo-lateralis*, not observed.

*Cartilages*

*Drum*, one complete ring, not distinguishable from other tracheal rings, and without a pessulus.

*Bronchial bars* 1 and 2 attach ventrally, by connective tissue, to each other and to the drum, sharing with the drum the origin of *M. syringeo-ventralis*. The dorsal ends are free of muscle attachments.

A *cartilage ring* next surrounds each bronchus, dividing the internal tympaniform membrane into two parts. Connective tissue attaches the ring to the ventral end of bar 2, but there is no muscle attachment.

*Bronchial bars* 3 and 4 are posterior to the bronchial ring. They are extremely thin, and they bear the insertion of *M. syringeo-ventralis* at the dorsal ends.

There is no large external tympaniform membrane in this species but the internal tympaniform membrane is very extensive. As there is no pessulus the internal membrane is supported only by the cartilaginous bronchial rings.

MUSCIVORA TYRANNUS. FORKED-TAILED FLYCATCHER

*Muscles*

*M. Tracheo-lateralis*, on the lateral surface of the trachea, and on the ventral surface from ring 5 to the drum.

ORIGIN: on the cricoid cartilage of the larynx.

INSERTION: on the cephalic edge of the drum, lateral and ventral.

ACTION: draws the syrinx cephalad.

*M. Sterno-trachealis*, from the sternum to the trachea, diagonal.

ORIGIN: on the anterolateral portion of the sternum.

INSERTION: on *M. tracheo-lateralis* at the level of tracheal ring 5, some fibers continuous with that muscle.

ACTION: draws the syrinx caudad.

*M. Syringeo-ventralis*, on the ventral portion of the syrinx, transverse.

ORIGIN: on the longitudinal, mid-ventral line of the syrinx.

INSERTION: on bronchial bar 2, at the dorsal end.

ACTION: probably reduces the curvature of bar 2.

*M. Syringeo-lateralis*, not observed.

#### Cartilages

*Drum*, wider than the tracheal rings, probably represents two or three fused rings.

No pessulus observed.

*Syringeo-bronchial rings*, two pairs, located posterior to the drum and attached to the drum at the mid-ventral point. The internal portions are extremely thin.

*Bronchial bars*, two pairs, with muscle attachments.

### MYIARCHUS CRINITUS. GREAT CRESTED FLYCATCHER

#### Muscles

*M. Tracheo-lateralis*, on the lateral surface of the trachea, and the ventral surface from tracheal ring 8 to the drum; longitudinal.

ORIGIN: on the cricoid cartilage of the larynx.

INSERTION: on the cephalic edge of the drum, lateral and ventral.

ACTION: draws the syrinx cephalad.

*M. Sterno-trachealis*, from the sternum to the trachea, diagonal.

ORIGIN: on the anterolateral portion of the sternum.

INSERTION: on *M. tracheo-lateralis* at tracheal ring 6, some fibers continuous with that muscle.

ACTION: draws the syrinx caudad.

*M. Syringeo-ventralis*, on the ventral portion of the syrinx, transverse.

ORIGIN: on the longitudinal, mid-ventral line of the syrinx and extending along the cephalic edge of the drum.

INSERTION: on bronchial bar 3, the median portion.

ACTION: not clear.

*M. Syringeo-lateralis*, on the lateral portion of the syrinx, longitudinal.

ORIGIN: on the lateral, cephalic edge of the drum.

INSERTION: on bronchial bar 3, immediately dorsal to the insertion of *M. syringeo-ventralis*.

ACTION: probably draws bars 2 and 3 cephalad.

#### Cartilages

*Drum*, of two rings partly fused, with a pessulus.

*Bronchial bars*, four, with muscle attachments on bar 3. Bar 4 is large, not attached to muscles, and is club-shaped at the dorsal end.

*Internal cartilages*, three; round, elongate, and angular (see Figure 1, D).

### SAYORNIS PHOEBE. EASTERN PHOEBE

#### Muscles

*M. Tracheo-lateralis*, on the lateral surface of the trachea, and the ventral surface from tracheal ring 8 to the drum; longitudinal.

ORIGIN: on the cricoid cartilage of the larynx.

INSERTION: on the lateral and ventral portions of the drum and the dorsal portions of bronchial bars 1, 2, and 3.

ACTION: draws the syrinx cephalad.

*M. Sterno-trachealis*, from the sternum to the trachea, diagonal.

ORIGIN: on the anterolateral portion of the sternum.

INSERTION: on *M. tracheo-lateralis*, at tracheal ring 5.

ACTION: draws the syrinx caudad.

*M. Syringeo-ventralis*, on the ventral portion of the syrinx, transverse.

ORIGIN: on the longitudinal, mid-ventral line of the syrinx.

INSERTION: on bronchial bars 1, 2, and 3, at the dorsal ends.

ACTION: not clear.

*M. Syringeo-lateralis*, not observed.

#### *Cartilages*

*Drum*, of three rings, fused ventrally only, with a pessulus.

*Bronchial bars*, three, with muscles attached; bar 3 with the dorsal end enlarged and club-shaped, similar to bar 4 in *Myiarchus*.

*Internal cartilage*, one, round, near the pessulus, the opposite members of the pair attached by strong connective tissue. (The specimen was badly damaged by shot; other cartilages may have been destroyed.)

#### EMPIDONAX TRAILLII. TRAILL'S FLYCATCHER

##### *Muscles*

*M. Tracheo-lateralis*, on the lateral surface of the trachea and the ventral surface below ring 20; longitudinal. (The ventral part of the muscle is much larger than the lateral part.)

ORIGIN: on the cricoid cartilage of the larynx.

INSERTION: on the ventral, cephalic edge of the drum, with a lateral extension to the subterminal, dorsal portion of bronchial bar 3.

ACTION: draws the syrinx cephalad.

*M. Sterno-trachealis*, from the sternum to the trachea, diagonal.

ORIGIN: on the anterolateral surface of the sternum.

INSERTION: on *M. tracheo-lateralis* at tracheal rings 6 and 7. The insertion extends ventrally to the mid-line of the trachea, and extends dorsally slightly beyond *M. tracheo-lateralis*, onto the tracheal cartilages.

ACTION: draws the syrinx caudad.

*M. Syringeo-ventralis*, on the ventral portion of the syrinx, transverse.

ORIGIN: on the longitudinal, mid-ventral line of the syrinx.

INSERTION: on bronchial bar 3, medial portion.

ACTION: not clear.

*M. Syringeo-lateralis*, not observed.

##### *Cartilages*

*Drum*, of two incompletely fused rings, with a pessulus.

*Bronchial bars*, four; muscles attach to bar 3, and bar 4 is large and club-shaped at the dorsal end, much as in *Myiarchus*.

*Internal cartilage*, one, elongate, at right angles to the bronchial bars, and near their dorsal ends.

#### CONTOPUS VIRENS. EASTERN WOOD PEWEE

##### *Muscles*

*M. Tracheo-lateralis*, on the lateral surface of the trachea, and the ventral surface from ring 12; longitudinal.

ORIGIN: on the cricoid cartilage of the larynx.

INSERTION: on the cephalic edge of the drum, and lateral extensions to the four bronchial bars.

ACTION: draws the syrinx cephalad.

*M. Sterno-trachealis*, from the sternum to the trachea, diagonal.

ORIGIN: on the anterolateral surface of the sternum.

INSERTION: on *M. tracheo-lateralis* at tracheal rings 2 and 3. The insertion extends ventrally to the tracheal mid-line, but does not extend dorsally beyond *M. tracheo-lateralis*.

ACTION: draws the syrinx caudad.

*M. Syringeo-ventralis*, on the ventral portion of the syrinx, transverse.

ORIGIN: on the longitudinal, mid-ventral line of the syrinx.

INSERTION: on bronchial bar 4, medial.

ACTION: probably rotates bronchial bar 4 on its long axis while drawing it cephalad.

*M. Syringeo-lateralis*, not observed.

#### Cartilages

*Drum*, of three incompletely fused rings, with a pessulus.

*Bronchial bars*, four, the fourth bar with the dorsal end club-shaped, much as in *Myiarchus*.

*Internal cartilage*, one, elongate, extending from near the pessulus across the central part of the internal tympaniform membrane. This internal cartilage is relatively wider and thicker than corresponding cartilages in the other tyrannids.

#### DISCUSSION AND CONCLUSIONS

Several muscular and skeletal structures of the tyrannid syrinx are conspicuously different from corresponding structures in other bird families. Conditions listed below were found in all tyrannids I have studied.

1. Widening of *M. tracheo-lateralis* near the syrinx, covering the ventral trachea at the lower end (Figure 1, A).

The *Mm. tracheo-laterales* spread out fan-like across the lower end of the trachea, covering the whole area with a thin layer of muscle, and inserting along the entire ventral edge of the drum. In most other birds these muscles form a long, slender pair confined to the sides of the trachea. When I first examined tyrannid specimens I thought *M. tracheo-lateralis* was absent and that a single muscle covered the ventral portion of the syrinx (Miskimen, 1951: 503), but subsequent careful examination of both fresh and preserved material showed the ventral musculature to consist of right and left parts. The fibers on each side of the mid-line are continuous with the more anterior parts of the *Mm. tracheo-laterales*; they do not form separate muscles as I first thought.

2. High insertion of *M. sterno-trachealis*.

In tyrannids, as in non-passerines, this muscle inserts on the trachea, well anterior to the syrinx; in higher passerines it inserts on the syrinx.

3. The presence of a ventral, transverse, intrinsic syringeal muscle, *M. syringeo-ventralis*.

Functionally this muscle appears to replace the group of longitudinal intrinsic syringeal muscles of higher passerines. *M. syringeo-lateralis* cannot at present be considered as typical of the family, because I have observed it only in *Myiarchus*.

4. A cartilaginous syringeal skeleton.

None of the skeletons shows any ossification, by manipulation, staining, or microscopic examination. In most other birds some or all of the syringeal elements are ossified.

5. A narrow drum of incompletely fused tracheal elements.

The tyrannid drum is narrower than other passerine drums, and it consists of two or three parts, each about the size of a tracheal ring, incompletely fused into one structure. The drums of the *Tyrannus* and *Muscivora* specimens had no pessulus.

6. External bronchio-syringeal cartilages movable by muscles at the dorsal ends only, or in some cases free of muscle attachments.

The bronchio-syringeal cartilages of higher passerines are free at both ends, and either or both ends may be moved by attached muscles, or the entire bar may rotate on its long axis. In tyrannids only the dorsal ends of the bars are capable of independent motion, the ventral ends are closely bound to each other and to the drum by connective tissue. In some species the fourth bar bears no muscle attachments.

7. The presence of internal bronchio-syringeal cartilages (Figure 1, D).

In *Tyrannus* and *Muscivora* complete rings of cartilage surround the bronchial parts of the syrinx. In *Myiarchus*, *Sayornis*, *Empidonax*, and *Contopus* small cartilages free of any muscle attachment lie in the internal tympaniform membranes, between the two bronchi near the apex. These cartilages vary in number from one to three on each side; they vary in thickness; and they are round, elongate, or angular in shape. Thus we find cartilaginous elements in the internal tympaniform membranes of all tyrannids so far examined. In all other birds I have examined or seen described, the internal tympaniform membranes are free of cartilage.

These seven conditions of muscle and skeleton seem to be characteristic of the family Tyrannidae. Study of more species and genera, however, may result in changes in this conclusion.

In addition to the uniform features just mentioned there are several structures that vary according to genus and that are probably uniform within a genus:

1. The origin of *M. syringeo-ventralis*.

In *Sayornis*, *Empidonax*, and *Contopus* the origin is on the ventral mid-line of the syrinx, but in *Tyrannus* and *Myiarchus* the attachment continues across the cephalic edge of the drum. Examining eight species



of *Myiarchus* and two species of *Empidonax* I found all the species of each genus uniform in this respect.

2. The presence or absence of *M. syringeo-lateralis*.

This muscle was present in all species of *Myiarchus* but not in any other genus studied.

3. The presence or absence of a pessulus.

The syringes of *Tyrannus* and *Muscivora* lack the pessulus; with the exception of the Turkey Vulture, *Cathartes aura* (Miskimen, 1957), I know of no other bird without a pessulus.

4. The numbers and forms of cartilages in the internal tympaniform membranes.

In *Tyrannus* and *Muscivora* cartilage rings surround the bronchial parts of the syrinx, crossing the membranes. The cartilages of the other genera appear to be different from each other, and within *Myiarchus* and *Empidonax*, each represented by more than one species, the species of each genus have internal cartilages alike.

Without more specimens from other species and genera of Tyrannidae I cannot form firm conclusions about differences between genera. Present findings, however, indicate that the position of origin of *M. syringeo-ventralis*, the presence or absence of *M. syringeo-lateralis*, the presence or absence of a pessulus, and the number and shape of cartilages in the internal tympaniform membranes may prove to be diagnostic features of the genera of Tyrannidae.

Many recent studies have demonstrated an increasing appreciation of the role of vocalization in bird behavior. Lanyon (1960) and Marler (1960) have given extensive references on the topic. Much less work has been done on the vocal mechanism, as shown by Thorpe (1959). At present we do not really know to what extent the syringes of related birds resemble each other, or the amount of individual variation within species. Neither do we know the relation between differences in structure and modifications in voice, nor in what ways the syrinx has evolved in different groups. Further studies should include descriptions of the syrinx of many species and groups of species, and the embryological development of representative forms. Although my work has been largely exploratory, the results indicate that further knowledge along these lines might be useful to students of both behavior and taxonomy, as a supplement to other kinds of information. I have studied neither neuro-muscular connections nor resonance effects of air sacs, both of which are involved in a complete understanding of the avian vocal mechanism.

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#### SUMMARY

Preliminary study based on a limited number of specimens of the family Tyrannidae resulted in tentative conclusions with regard to familial and generic characteristics of the syrinx of this group.

The tyrannid syrinx is characterized by: (1) widening of *M. tracheo-lateralis* near the syrinx, covering the ventral trachea at the lower end; (2) high insertion of *M. sterno-trachealis*; (3) presence of a ventral, transverse intrinsic syringeal muscle, *M. syringeo-ventralis*; (4) a cartilaginous syringeal skeleton; (5) a narrow drum of incompletely fused tracheal elements; (6) external bronchial cartilages movable at the dorsal ends only, or free of muscle attachments; and (7) some form of cartilage support of the large, internal tympaniform membranes.

The following structures vary according to genus: (1) the origin of *M. syringeo-ventralis*; (2) the presence or absence of *M. syringeo-lateralis*; (3) the presence or absence of a pessulus; and (4) the numbers and forms of cartilages in the internal tympaniform membranes.

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