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UNIVERSITY OF KANSAS
LAWRENCE
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Jaw Musculature Of the Mourning and White-winged Doves

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For some time many investigators have thought that the genus *Zenaida*, which includes the White-winged and Zenaida doves, and the genus *Zenaidura*, which includes the Mourning, Eared, and Socorro doves (Peters, 1937:83-88), are closely related, perhaps more closely than is indicated by separating the several species into two genera. It is the purpose of this paper to report investigations on the musculature of the jaw of doves with the hope that, together with the results of other studies, the relationships of the genera *Zenaida* and *Zenaidura* can be elucidated.

METHODS AND MATERIALS

In order to determine in each species the normal pattern of musculature of the jaws, heads of 13 specimens of doves were dissected (all material is in the Museum of Natural History of The University of Kansas): White-winged Doves (*Zenaida asiatica*), 40323, 40324, 40328, 40392, 40393; Zenaida Doves (*Z. aurita*), 40399, 40400; Mourning Doves (*Zenaidura macroura*), 40326, 40394, 40395, 40396, 40397, 40398.

Thirty-seven skulls from the collection of the Museum of Natural History of The University of Kansas and two skulls from the United States National Museum were measured. The measurements are on file in the Library of The University of Kansas in a dissertation deposited there by me in 1963 in partial fulfillment of requirements for the degree of Master of Arts in Zoology. Specimens used were: White-winged Doves, KU 19141, 19142, 19143, 19144, 19145, 19146, 19147, 23138, 23139, 24337, 24339, 24341, 23592, 23593, 24340, 31025, 31276; Mourning Doves, KU 14018, 14781, 15347, 15533, 15547, 15550, 15662, 15778, 15872, 16466, 17782, 17786, 17788, 17795, 19153, 19242, 20321, 21669, 22394, 22715; Eared Doves (*Zenaidura auriculata*), USNM 227496, 318381. Additionally, the skulls of the Zenaida Doves mentioned above were measured. All measurements were made with a dial caliper and read to tenths of a millimeter.

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MYOLOGY

The jaw musculature of doves is not an imposing system. The eating habits impose no considerable stress on the muscles; the mandibles are not used for crushing seeds, spearing, drilling, gaping, or probing as are the mandibles of many other kinds of birds. Doves use their mandibles to procure loose seeds and grains, which constitute the major part of their diet (Leopold, 1943; Kiel and Harris, 1956: 377; Knappen, 1938; Jackson, 1941), and to gather twigs for construction of nests. Both activities require but limited gripping action of mandibles. The crushing habit of a bird such as the Hawfinch (*Coccothraustes coccothraustes*), on the other hand, involves extremely powerful gripping (see, for example, Sims, 1955); the contrast is apparent in the development of the jaw musculature in the two types. Consequently, it is not surprising to find a relatively weak muscle mass in the jaw of doves, and because the musculature is weak there are few pronounced osseous fossae, cristae and tubercles. As a result, the bones, in addition to being small in absolute size, are relatively weaker when compared to skulls of birds having more distinctive feeding habits which require more powerful musculature.

The jaw muscles of the species dissected for this study are, in gross form, nearly identical from one species to another. Thus, a description of the pertinent myology of each species is unnecessary; one basic description is hereby furnished, with remarks on the variability observed

between the species.

The terminology adopted by me for the jaw musculature is in boldfaced italic type. Synonyms are in italic type and are the names most often used by several other writers.

M. pterygoideus ventralis: part of *Mm. pterygoidei*, Gadow, 1891:323-325, table 26, figs. 1, 2, 3 and 4, and table 27, fig. 3—part of *M. pterygoideus internus*, Shufeldt, 1890:20, figs. 3, 5, 6, 7 and 11—part of *M. adductor mandibulae internus*, Edgeworth, 1935:58, figs. 605c and 607—part of *M. pterygoideus anterior*, Adams, 1919:101, pl. 8, figs. 2 and 3.

M. pterygoideus dorsalis: part of *Mm. pterygoidei*, Gadow, 1891:323-325, table 26, fig. 7 and table 27, figs. 1 and 3—part of *M. pterygoideus internus*, Shufeldt, 1890:20—part of *M. adductor mandibulae internus*, Edgeworth, 1935:58, fig. 605c—? part of *M. pterygoideus anterior*, Adams, 1919:101, pl. 8, figs. 2 and 3.

M. adductor mandibulae externus: a) ***pars superficialis***: parts 1 and 2 of *M. temporalis*, Gadow, 1891:320-321—part of *M. temporal*, Shufeldt, 1890:16, figs. 5 and 7—part of *M. adductor mandibulae externus*, Edgeworth, 1935:58-60—*M. capiti-mandibularis medius* and *profundus*, Adams, 1919:101, pl. 8, fig. 1.

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b) ***pars medialis***: ? parts 1, 2 and 3 of *M. temporalis*, Gadow, 1891:320-322—part of *M. masseter* and ? part of *M. temporal*, Shufeldt, 1890:16-18, figs. 5, 6, 7 and 11—part of *M. adductor mandibulae externus*, Edgeworth, 1935:58-60—*M. capiti-mandibularis superficialis*, first part, Adams, 1919:100-101, pl. 8, fig. 1.

c) ***pars profundus***: part 2 of *M. temporalis*, Gadow, 1891:321, table 27, fig. 2—part of *M. temporal* and ? part of *M. masseter*, Shufeldt, 1890:16-18—part of *M. adductor mandibulae externus*, Edgeworth, 1935:58-60—? part of *M. capiti-mandibularis medius* and all of *pars superficialis*, second part, Adams, 1919:100-101.

M. pseudotemporalis profundus: *M. quadrato-maxillaris*, Gadow, 1891:322-323—*M. pterygoideus externus*, Shufeldt, 1890:20-21, figs. 3, 5 and 11—part of *M. adductor mandibulae medius*, Edgeworth, 1935:58-59—? part of *M. pterygoideus posterior*, Adams, 1919:101, pl. 8, figs. 2 and 3.

M. protractor pterygoidei: part 4b of *M. temporalis*, Gadow, 1891: 322-323, table 27, fig. 4—part of *M. entotympanicus*, Shufeldt, 1890:19-20, figs. 3 and 11—part of *M. spheno-ptyergo-quadratus*, Edgeworth, 1935:57.

M. depressor mandibulae: *M. digastricus s. depressor mandibulae*, Gadow, 1891:318-319—*M. biventer maxillae*, Shufeldt, 1890:18-19, figs. 3, 4, 5, 6, 7 and 11.

M. pseudotemporalis superficialis: *M. spheno-maxillaris*, Gadow, 1891:323—part of *M. temporal*, Shufeldt, 1890:16—part of *M. pseudotemporalis*, Hofer, 1950:468-477—part of *M. adductor mandibulae medius*, Edgeworth, 1935:277.

M. adductor mandibulae posterior: ? part of *M. temporal*, Shufeldt, 1890:16—part of *M. adductor mandibulae medius*, Edgeworth, 1935:58-59—? part of *M. pterygoideus posterior*, Adams, 1919:101, pl. 8, figs. 2 and 3.

M. protractor quadrati: part 4a of *M. temporalis*, Gadow, 1891:322-323, table 27, fig. 4—part of *M. entotympanicus*, Shufeldt, 1890:19-20, figs. 3 and 11—part of *M. spheno-ptyergo-quadratus*, Edgeworth, 1935:57.

The terminology adopted by me is that of Lakjar (1926) except that the divisions of *M. depressor mandibulae* are designated by the Latinized equivalents of the names used by Rooth (1953:261-262).

M. pterygoideus ventralis lateralis.—The origin is fleshy and by aponeurosis on the ventral side of the palatine anterior to the palatine fossa. The insertion is fleshy on the ventromedial surface of the lower mandible and continues along the anteromedial surface of the internal angular process to its distal tip. A few fibers leave *pars lateralis* and insert on an aponeurosis which receives also all the fibers of *M. pterygoideus dorsalis lateralis*. The latter fact may have prompted Rooth (1953:257) to make the statement that the fibers originating on the dorsal part of the palatine inserted more laterally than those originating on the ventral side. Rooth worked with *Columba palumbus*, the Woodpigeon, and his description concerned *M. adductor mandibulae internus pterygoideus*, which is composed of *Mm. pterygoideus ventralis et dorsalis* of Lakjar (1926). His assertion that ventral fibers, that is to say, fibers arising on the ventral surface of the palatine, insert medially does not appear to be completely true for doves.

Aponeuroses cover most of the lower surface of the muscle and one or two nerves extend into the substance of the muscle. The nerves run from the anterior edge of *M. pterygoideus dorsalis medialis* and farther posteriorly from a separation in the muscle.

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M. pterygoideus ventralis medialis.—The origin is by aponeurosis from the ventral surface of the palatine and fleshy from the palatine fossa. The aponeurosis is the same that gives origin to the fibers of *pars lateralis*. Part of the aponeurosis becomes tendonlike in the middle of *M.*

pterygoideus ventralis and separates its two divisions. The insertion is fleshy on the lower one-third of the anterior surface of the internal angular process of the lower mandible, and by two tendons on the distal tip of that process. Many of the fibers of *pars medialis* insert on the tendons. The fibers at their insertion are not distinctly separate from those of *pars lateralis* and there is considerable mingling of the fibers. Consequently, the medial part of *M. pterygoideus ventralis* cannot be removed as a part distinct from the lateral part (figs. 1, 4, 10, 21 and 22).

Ordinarily *M. pterygoideus ventralis* does not cross the ventral edge of the lower mandible, but in one white-wing the muscle was slightly expanded on the right side and it could be seen in lateral view. The homologous muscle in *Columba palumbus* apparently is consistently visible in lateral view. (See Rooth, 1953, fig. 6.)

M. pterygoideus dorsalis medialis.—The origin is fleshy on the dorsolateral surface of the palatine immediately anterior to the pterygoid and also on the anterior, dorsolateral, posterior and ventromedial surfaces of the pterygoid. The insertion is fleshy on the ventromedial surface of the lower mandible and the anterior surface of the internal angular process immediately dorsal to the insertion of *M. pterygoideus ventralis lateralis*.

M. pterygoideus dorsalis lateralis.—The origin is fleshy from the dorsolateral surface of the palatine, anterior to the origin of *pars medialis* and the insertion is by means of an aponeurosis on the medial surface of the lower mandible, lateral to the insertion of *M. pterygoideus ventralis lateralis*. The aponeurosis crosses the medial side of the insertion of *M. pterygoideus dorsalis medialis*. The fibers run in a posteroventrolateral direction and insert on the ventromedial side of the aponeurosis (figs. 1, 6, 8, 9, 13-22).

In one individual, a Mourning Dove, the origin of *pars lateralis* of *M. pterygoideus dorsalis* extended to the pterygoid. With this one exception the muscle was uniform throughout the several species.

M. adductor mandibulae externus.—This is the most complex muscle in the jaw owing to its system of tendons and aponeuroses. Three divisions of this muscle were described by Lakjar (1926:45-46) and the divisions appear to be distinguishable in the doves, but there is no clear line of demarcation for any of the parts and the following description is based upon my own attempts to delineate the muscle.

M. adductor mandibulae externus superficialis.—The origin is fleshy from the most lateral area of the temporal fossa. Dorsally the origin is bounded by the base of the postorbital process and ventrally by the temporal process. The fibers converge upon a tendon that passes beneath the postorbital ligament and runs anteriorly among the fibers of *pars profundus*. The insertion is tendinous on the dorsal surface of the lower mandible in common with the dorsal aponeurosis of *pars profundus*. The insertion is immediately anterior to the ventral aponeurosis of *pars profundus* near the medial edge of the dorsal surface on a tubercle at the posterior end of the dorsal ridge of the lower mandible.

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M. adductor mandibulae externus medialis.—The origin is by a flat, heavy tendon from the temporal process. The tendon is attached almost vertically on the temporal process. It twists approximately 130° as it runs anteriorly, and becomes a thin aponeurosis, which gives rise on its dorsal and ventral surfaces to many fibers that insert in a fan-shaped area on the mandibular fossa. Fibers from the dorsal and dorsomedial sides of the heavy tendon run rostrad and insert on the ventral surface of the dorsal aponeurosis of *pars profundus*. From the ventral surface the most posterior fibers converge on an aponeurosis that inserts on a transverse crista on the dorsal surface of the mandible immediately lateral to the ventral aponeurosis of *pars profundus* and dorsal to the insertion of ***M. adductor mandibulae posterior***. The more anterior fibers insert fleshily on the mandibular fossa. The tendon of origin is actually one with the ventral aponeurosis of *pars profundus*, which is situated in a horizontal plane. The insertion is primarily a fleshy attachment on the mandibular fossa. Some of the fibers that arise on the dorsomedial and lateral surfaces of the tendon of origin attach to another tendon, which inserts in the midline of the mandibular fossa on a small tubercle near the anterior end. Also, there is insertion by an aponeurosis anterior to *M. adductor mandibular posterior* as stated above. Fibers attach to the dorsal and ventral side of the aponeurosis.

M. adductor mandibulae externus profundus.—The origin is fleshy from the medial surface of the temporal fossa, the posterior wall of the orbit and the otic process of the quadrate. The origin is bounded laterally by the origin of *pars superficialis* and medially by the origin of *M. pseudotemporalis superficialis*. Ventrally the muscle lies against its own ventral aponeurosis, which originates on the posterior wall of the orbit immediately above the articulation of the otic process of the quadrate, and which also receives many fibers from the surface of the quadrate. The insertion is primarily by means of two aponeuroses. The most dorsal aponeurosis inserts on a tubercle at the posterior tip of the dorsal edge of the mandible. The lateral tendon of *M. pseudotemporalis superficialis* converges with the aponeurosis. It is superficial and there are no fibers on its dorsal surface. The ventral aponeurosis inserts on a crista immediately below the insertion of the dorsal aponeurosis. It receives fibers on its ventral surface from the otic process of the quadrate, and on its dorsal surface gives rise to fibers that insert on the dorsal aponeurosis (figs. 2, 3, 5, 9, 10, 11, 13-18).

The tendon of insertion of *pars medialis* of *M. adductor mandibulae externus* does not become a superficial aponeurosis posteriorly in the Zenaida Dove as it does in the Mourning and White-winged doves.

M. pseudotemporalis profundus.—The origin is fleshy from the medial and partially from the dorsal surface of the lower mandible. The origin is almost completely anterior to and partly dorsal and ventral to the medial (most anterior) insertion of *M. pseudotemporalis superficialis*. The anterior margin of the origin is at the point where the mandibular ramus of the trigeminal nerve enters the mandible. Posteriorly the origin is bounded by the insertion of *M. adductor mandibulae posterior*, and ventrally by a ridge that is situated about halfway down the medial side of the mandible. The insertion is by aponeurosis on the tip of the orbital process of the quadrate and fleshily on the anterior surface of the same process. The aponeurosis extends about three-fifths of the distance along the muscle and it is dorsal or superficial to all of the fibers. Many fibers insert on the ventral side of the aponeurosis (figs. [1](#), [5](#), [13](#), [14](#), [15](#), [16](#), [21](#) and [22](#)).

This muscle is the most variable of all the jaw muscles. In the Mourning Dove the muscle appears rather slender in dorsal view and in the White-winged Dove has an enlarged lateral belly that gives the appearance of a thicker muscle. In the Zenaida Dove *M. pseudotemporalis profundus* is intermediate in shape between those of the other two species. This muscle will be discussed in detail later.

M. protractor pterygoidei.—The origin is fleshy from the junction of the sphenoidal rostrum and the interorbital septum. Fibers converge on the pterygoid in anteroventrolateral and posteroventrolateral directions. The posterior edge of the muscle is in contact with *M. protractor quadrati* with which its fibers mingle. The insertion is fleshy on the posterior surface of the lateral half of the pterygoid to its articulation with the body of the quadrate (figs. [6](#), [8](#), [9](#), [11](#), [13](#)-[20](#)).

M. depressor mandibulae superficialis medialis.—The origin is fleshy from the lateral edge of the basioccipital where the muscle is attached to *Ligamentum depressor mandibulae* and extends in a lateral direction to a point where the structures involved turn dorsad. The insertion is by fibers and a light aponeurosis on the crista that is situated on the posteroventromedial edge of the lower mandible.

M. depressor mandibulae superficialis lateralis.—The origin is fleshy from the squamosal region, slightly posteroventral to the origin of *M. adductor mandibulae externus superficialis*. A thin aponeurosis lies medial to the muscle fibers. The insertion is by means of an aponeurosis that becomes tendonlike along the posteroventrolateral crista and the posteriormost part of the ventral edge of the lower mandible.

M. depressor mandibulae medialis.—The origin is fleshy from the lateral and ventral surfaces of *Ligamentum depressor mandibulae*. The insertion is fleshy on the posterior surface of the lower mandible, posterodorsal to the insertions of *partes superficialis medialis et lateralis* (figs. [4](#), [9](#), [10](#), [13](#) and [14](#)).

The parts of *M. depressor mandibulae* are difficult to distinguish from one another because of considerable intermingling of fibers.

M. pseudotemporalis superficialis.—The origin is fleshy from the posterior wall of the orbit, dorsal to the foramen of the trigeminal nerve, lateral to the origin of *M. protractor quadrati* and medial to *M. adductor mandibulae externus profundus*. The insertion is by means of an aponeurosis that bifurcates at the point of contact with the mandibular ramus of the trigeminal nerve, which is at the level of the orbital process of the quadrate (except in the Mourning Dove where the division is more anterior), and which inserts as two tendons on the dorsomedial edge of the lower mandible posterior to the insertion of *M. pseudotemporalis profundus*. The lateral tendon is superficial to the dorsomedial edge of *M. adductor mandibulae externus*, and converges with the aponeurosis of *pars profundus* of that muscle and inserts with it on a tubercle near the dorsomedial edge of the mandible anterior to the insertion of *M. adductor mandibulae posterior* as mentioned before. The anterior half of the medial tendon lies ventral to the lateral edge of *M. pseudotemporalis profundus* and the mandibular ramus of the trigeminal nerve. All of the fibers of the muscle insert on the posteroventral surface of the aponeurosis before it divides. Part of *M. pseudotemporalis profundus* also lies ventral to the medial tendon of *M. pseudotemporalis superficialis* and, in effect, the tendon is imbedded in the substance of *M. pseudotemporalis profundus* as it proceeds anteriorly. The trigeminal nerve leaves a slight impression on the ventral surface of the muscle near its origin (figs. [1](#), [3](#), [11](#), [13](#), [14](#), [15](#) and [16](#)).

M. adductor mandibulae posterior.—The origin is fleshy from the anterodorsal and anterior surfaces of the quadrate body, from the anterodorsolateral, medial and anterior surfaces of the orbital process of the quadrate. The muscle also has an origin from the otic process of the quadrate, partly fleshy and partly by a slight aponeurosis. The insertion is fleshy on the dorsal and lateral surfaces of the mandible immediately anterior to the articulating surface. This muscle also has extensive insertion on the medial side of the lower mandible dorsal to the insertion of *M. pterygoideus dorsalis medialis* and posterior to the origin of *M. pseudotemporalis profundus* (figs. [1](#), [3](#), [5](#), [17](#), [18](#), [19](#) and [20](#)).

The fibers of *M. pseudotemporalis profundus* can be distinguished from the fibers of *M. adductor mandibulae posterior* because the pterygoideus nerve passes between the two (Lakjar, 1926:55). Rooth (1953:255-256) considers as part of this muscle the ventral aponeurosis of *pars profundus* of *M. adductor mandibulae externus* and all the fibers ventral to it. But I could not justify the inclusion of that aponeurosis as part of *M. adductor mandibulae posterior* in the doves because none of the fibers of *M. adductor mandibulae posterior* as I have described it were attached to

that particular aponeurosis.

M. protractor quadrati.—The origin is fleshy from the posterior wall of the orbit medial to the foramen of the trigeminal nerve and also medial to the origin of *M. pseudotemporalis superficialis*. The origin describes an arc in the horizontal plane until it reaches the interorbital septum and the optic nerve. The insertion is fleshy on the posteromedial edge of the body of the quadrate and the orbital process of the quadrate and on the otic process of the quadrate. The muscle also inserts on the ventromedial surface of the orbital process of the quadrate and the adjacent area of the body of the quadrate (figs. 5, 7, 9, 11, 13-18).

M. protractor quadrati possesses many fibers that arise from *M. protractor pterygoidei*. Consequently, it is difficult to determine the exact extent of the origin or the insertion of either muscle.

ACTION OF JAW MUSCLES

M. pterygoideus ventralis.—Contraction of this muscle retracts the upper mandible by moving the palatine posteriorly, and simultaneously adducts the lower mandible.

M. pterygoideus dorsalis.—This muscle functions in essentially the same manner as *M. pterygoideus ventralis*. The result of having a part of its origin on the pterygoid as well as on the palatine is to facilitate retraction of the upper mandible.

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M. adductor mandibulae.—This is the chief adductor of the lower mandible and the muscle functions solely in that capacity. In birds having great crushing ability, this muscle is much larger and more powerful and the skull is reinforced behind the quadrate in order to withstand the pressure of the lower mandible against the quadrate during adduction (Sims, 1955:374 and Bowman, 1961:219-222).

M. pseudotemporalis profundus.—With origin and insertion on highly movable bones, this muscle, when it contracts, retracts the upper mandible and adducts the lower mandible. Like the pterygoid muscles, this muscle, by itself, would allow the bird to grasp objects by means of its mandibles. However, *M. pseudotemporalis profundus* could produce a more powerful grip because it takes origin farther anteriorly on the lower mandible.

M. protractor pterygoidei.—Contraction of *M. protractor pterygoidei* pulls the pterygoid anteromedially and causes it to slide forward along the sphenoidal rostrum. This action aids in protraction of the upper mandible.

M. depressor mandibulae.—The depressor of the lower mandible is the sole muscle other than *M. geniohyoideus* involved in the function of abducting the lower jaw of doves. Its size can be correlated especially well with feeding habits of the bird. Other birds that force their closed mandibles into fruit, wood or the earth and then forcibly open them, belong to groups possessing enlarged depressors. Contraction of the muscle pulls the postarticular (retroarticular) process upward with the resultant downward movement of that part of the mandible which is anterior to the articulation. Since there is no "gaping" in doves the muscle is only large enough to overcome the inherent tone of the relaxed adductor muscles.

In some non-passerine species as well as in certain passerines the muscle also serves to raise the upper jaw by acting on the quadrate, which is capable of rotating vertically on its otic process. Especially in the gapers, where resistance is offered near the tip of the lower mandible, contraction of the muscle pulls the entire mandible dorsad thus forcing the jugal and palatal struts forward (Zusi, 1959:537-539). The action supplements that of *Mm. protractor pterygoidei et quadrati* and is enhanced by anterior migration of the origin of *M. depressor mandibulae*.

There is no lifting action involved in contraction of the depressor muscle in doves for two reasons —(A) the origin of the muscle is situated much too far posteriorly on the skull, and, more important, (B) the quadrate is not hinged for vertical movement. As will be discussed later, it moves only in a horizontal plane.

M. pseudotemporalis superficialis.—Like *M. adductor mandibulae*, this muscle performs only the one function of adducting the lower mandible, and like *M. pseudotemporalis profundus* it is a synergist of that muscle.

M. adductor mandibulae posterior.—Although this muscle undoubtedly acts as an adductor of the lower mandible, I believe that, because of its disadvantageous insertion so near the articulation, its main function must be concerned with firming the mandible against the quadrate. This is to say that its function is partially that of a ligament.

M. protractor quadrati.—When *M. protractor quadrati* contracts, the quadrate bone is swung medially. This action, as mentioned previously, results in protraction of the upper jaw, and, as a consequence, its action supplements the action of *M. protractor pterygoidei*.

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CRANIAL OSTEOLOGY

The ability of most birds to protract the upper mandible, and the structure of the skull which enables them to do so are responsible for common reference to the skull as "kinetic" (Beecher,

1951a:412; Fisher, 1955:175). The movement is effected by muscular action on a series of movable bones that exert their forward force on the upper mandible, which in turn swings on a horizontal hinge, the "naso-frontal hinge," at the base of the beak. The bone initiating the movement is the quadrate, which is hinged posteriorly by its otic process and which ordinarily swings up or down depending on the muscle or muscles being contracted at any given moment. The upward swing of the quadrate pushes the jugal bar, which is attached to its lateral tip, along its longitudinal axis, in an anterodorsal direction, and the force is transferred to the upper mandible, which is thereby elevated. A synergetic mechanism is simultaneously initiated by the same bone—the quadrate. Since the quadrate body articulates with the pterygoid, the upward movement forces the pterygoid to slide along a ridge in the ventral midline of the cranium, the sphenoidal rostrum, thus pushing the palatine forward and exerting an upward push on the upper mandible.

In the columbids the quadrate has a bifurcated otic process that functions as the hinge. The posterior tips of the forks are situated almost vertically (one above the other) and the movement of the quadrate is not so much up and down, or vertical, as it is horizontal (fig. 12). When the quadrate moves medially the upper mandible is protracted; a lateral movement results in retraction. There is a slight, almost negligible, upward movement of the quadrate. The movements of the various bony elements were observed on a skull that had been made flexible by boiling in water for a minute as suggested by Beecher (1951a:412).

Also in the columbids the naso-frontal hinge is not constructed in the same manner as it is in many other birds as there is not a simple hinge across the entire base of the beak. In fact, there is no true hinge at all in the area of the nasals, but those bones are extremely thin and they bend or flex under pressure. Actually, the hinge is double or divided. One part is on either side of the nasals. The hinges are situated at the posterodorsal tips of two thin processes of the maxillary bones and the appearance is not unlike that of half a span of a suspension bridge having the hinges at the tops of the towers. Several other species of birds share this type of hinge construction with columbids.

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The movement of the lower jaw is, of course, the primary operation involved in opening the mouth. The lower jaw possesses a deep fossa at its posterior end, or on its posterodorsal surface, which articulates with the body of the quadrate bone. The length of that part of the mandible extending behind the articulation is directly correlated with the resistance offered the mandible in opening, since it is on the posterior extension that the depressor of the lower mandible inserts. The larger the muscle the more surface is needed for attachment. Also the added length of the mandible posterior to the articulation serves as a lever in opening the mandible, and the fulcrum is moved relatively farther forward.

In birds lacking resistance to abduction of the lower mandible, as in doves, it is nevertheless necessary for a slight postarticular process to remain for the insertion of a small depressor muscle which, as mentioned previously, is necessary to counteract the relaxed adductor muscles of the lower jaw.

There are many exceptions to the rule that birds have kinetic skulls, and usually a secondary fusion and reinforcement of bones around the hinge has limited or eliminated all movement. Sims (1955) describes the Hawfinch's immobile upper jaw, which is used as a powerful press in cracking the stones of fresh fruit. Skulls of woodpeckers have been modified somewhat in the same manner as a result of their foraging and nesting habits (Burt, 1930).

The two most distantly related members of the genera under investigation are the White-winged Dove, *Zenaida asiatica*, and the Mourning Dove, *Zenaidura macroura*. They were chosen to demonstrate differences and likenesses in proportions of members of the genera.

Ten measurements were taken on each skull, but simple observation reveals that, in relation to total length of the skull, the beak of the White-winged Dove is longer than that of the Mourning Dove. Tip of upper mandible to base of beak averaged 48.6 and 42.9 per cent of the total length of the skull in the White-winged Dove and Mourning Dove, respectively. The position of the jugal bar has remained about the same with respect to the cranial part of the skull, and the entire cranial part of the skull is almost the same shape in the species studied.

Likewise, in the White-winged Dove the distance from the anterior tip of the lower mandible to the anterior part of *M. adductor mandibulae externus* is relatively longer in relation to the length of the lower mandible than in the Mourning Dove. Finally, the position of the jugal with respect to the naso-frontal hinge is about the same in the two species.

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Measurements and calculations indicate that the longer beak of the White-winged Dove as compared with the Mourning Dove is a function of the beak itself, not of differences in other parts of the skull. Measurements of skulls of Eared and Zenaida doves support this view.

OTHER MORPHOLOGICAL FEATURES

In the species dissected, the only variable muscle that I consider significant in revealing relationships is *M. pseudotemporalis profundus*. It is markedly enlarged in the White-winged Dove in relation to the homologous muscle in the Mourning Dove. The muscle is enlarged in such a manner that a lateral expansion of its mass is apparent in superficial or dorsal view (compare figures 15 and 16). This, of course, indicates a muscle with powerful contraction, which has been

unable to enlarge its circumference symmetrically because the eye is immediately dorsal to the muscle. Therefore it has expanded laterally. Ventral expansion is blocked by the presence of other muscles, and medially there is no surface for the insertion of additional fibers on the orbital process of the quadrate.

The jaw musculature has been known for some time to be highly adaptive (Beecher, 1951a and b, 1953; Bowman, 1961; Burt, 1930; Engels, 1940 and Goodman and Fisher, 1962) and it would not be unreasonable, I think, to expect the jaw muscles of closely related species with similar habits to be similar. The beak of the White-winged Dove is longer in proportion to the length and height of the skull (exclusive of the beak) than is the beak of the Mourning Dove. The lengthened beak is probably an adaptation for nectar-feeding, which has been documented by McGregor, Alcorn and Olin (1962:263-264) while investigating pollinating agents of the Saguaro Cactus (*Cereus giganteus*), and by Gilman (1911:53) who observed the birds thrusting their bills into the flowers of the plant. Gilman indicated, however, that he could not be sure if the birds were seeking insects, pollen, or nectar. In any event the lengthened bill probably facilitates getting food by birds that probe parts of flowers. Hensley (1954:202) noted that both Mourning and White-winged doves were "exceptionally fond of this source of nourishment." But he also points out an "interesting correlation" between the presence of the white-wings in the desert and the flowering of the saguaro. During his studies the appearance of the first white-wing preceded the opening of the first saguaro flower by two days. The flowering and fruiting season lasted until August, the month of termination of the white-wing breeding season.

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Since Hensley makes the correlation solely with the white-wings, I assume that there is no other obvious correlation between plants and birds among the remainder of the avifauna of the desert. Probably the Mourning Dove has failed to adapt to nectar-feeding as yet, and the White-winged Dove is the primary exploiter of this food niche. It should be noted, also, that the head of the Mourning Dove is smaller than the white-wing's, and perhaps there is no need for an elongated beak for reaching deeply into the flowers.

The lengthened bill should produce no difficulties in protraction of the upper mandible and depression of the lower for the reason that in the dove there is no known resistance offered to these movements. The genus *Icterus* furnishes an example wherein resistance is met in the process of opening the mandibles; individuals of this genus thrust their closed bill into certain fruits and forcibly open their mandibles against the resistance of the pulp by strong protraction and depression, thus permitting the juices of the fruit to lake and ultimately to be consumed (Beecher, 1950:53). Beecher refers to the technique used in fruit-eating as "gaping." The result of gaping in *Icterus* should be the presence of a more massive set of muscles concerned with protraction and depression than is found in non-gaping groups. Beecher found the situation to be exactly as expected in that genus and in other genera which also gape. Meadowlarks (*Sturnella*) and caciques (*Archiplanus*) gape and pry in soil and wood respectively (Beecher, 1951a:422 and 426).

The lengthened beak would be a problem when the White-winged Dove attempted to pick up objects such as seeds, which do in fact constitute the largest percentage of its diet in spite of its nectar-feeding habit. A similar situation exists in the genus *Icterus*, which is primarily adapted for gaping even though it shows a preference for insects when they are abundant (Beecher, 1950:53). The lengthened beak could be compensated for by (A) migration of the anterior end of the jugal bar toward the rostral tip of the bill and away from the fronto-nasal hinge with a simultaneous enlargement of the adductor muscles of the lower mandible, or (B) enlargement of the one muscle that functions simultaneously as an efficient retractor of the upper mandible and adductor of the lower mandible, namely *M. pseudotemporalis profundus*. *Mm. pterygoideus dorsalis et lateralis* perform the same function, but because of their position on the lower mandible they, apparently, are stronger retractors of the upper mandible than they are adductors of the lower.

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It will be recalled that the jugal bar bears the same, or nearly the same, relationship to the cranium in the white-wing as it does in the Mourning Dove and that the heads, excluding the beaks of both species, are of nearly the same proportions. Also, *Mm. adductor mandibulae externus* and *pseudotemporalis superficialis*, the chief adductor muscles of the lower mandible, were not noticeably enlarged in the white-wing. It is also important to note that other combinations of migration of bone and/or enlargement of muscles could successfully solve the problem of providing sufficient leverage for the proper functioning of the lengthened mandibles, but it is my thesis that the second alternative sufficed for seed-eating habits and that that is the adaptation that was established; it is, in fact, the only one present in the White-winged Dove.

It is unlikely that this enlarged muscle and beak are the remains of another series of jaw muscles that have converged toward the condition in Mourning Doves. Columbids are almost unquestionably monophyletic, and two lines would have had to diverge and then converge. There is no evidence for such an evolutionary occurrence.

GENERIC RELATIONSHIP

An attempt will be made here to summarize all the available evidence, direct or indirect, which bears on the problem of relationship of these genera. The original dissections which are discussed in this report are only valuable as one more bit of evidence concerning one characteristic that aids in clarification of generic relationship, and it is only in conjunction with

other evidence that any satisfactory conclusion may be forthcoming.

Morphology

My dissections demonstrated that, in relation to the size of the doves, the jaw musculature of all the specimens investigated was so nearly alike that only one major difference was detected. *M. pseudotemporalis profundus* appeared to be enlarged in the White-winged Dove. This might have been predicted, since the white-wing was also shown to possess an elongated beak, presumably an adaptation for nectar-feeding, which would necessitate additional muscle development in order to compensate for the added length. Measurements recorded from several skulls indicated that the heads of the birds (excluding the beak) are nearly proportional.

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Perhaps plumage patterns are the most widely used characters for determining generic relationships of birds. Ridgway (1916:339-385) followed the columbid classification of Salvadori (1893) using plumage patterns and body proportions to distinguish between the genera. In the genus *Zenaidura* he included the unique specimen *Zenaidura yucatanensis*, and he placed *auriculata* in *Zenaida*. The White-winged Dove was referred to a separate genus, *Melopelia*. He described the genus *Zenaidura* in the following manner:

"Plumage of head, neck and under parts soft and blended; bare orbital space moderate, broadest beneath eyes. Coloration plain, the proximal secondaries (sometimes adjacent wing-coverts and scapulars also) spotted with black; rectrices (except middle pair) with a black band across postmedian portion, the apical portion paler gray than basal portion, sometimes white; a small black subauricular spot; adult males with head, neck and anterior under parts more or less vinaceous and sides of neck glossed with metallic purple."

He noted that the plumage of *Zenaida* was almost precisely as described for *Zenaidura*. Also, although all members of *Zenaida* reputedly possessed twelve rectrices, a characteristic of the genus, it was later found that *auriculata* possessed fourteen rectrices. The species was promptly placed in the genus *Zenaidura* by Peters (1934:213-215). In plumage and coloration, *Melopelia* was described as similar to *Zenaida* and *Zenaidura* but without black spots on the wings.

The White-winged Dove also has twelve rectrices, but Bond (1940:53) and Goodwin (1958:330-334) considered the number and shape of rectrices to be of minor importance when compared to the homologous markings of the plumage. Goodwin stated that his conclusion was emphasized by the fact that the tail of *auriculata* is intermediate in length and shape between those of *macroura* and *aurita*. In summary Goodwin "lumped" the genera *Zenaida* and *Zenaidura* under the genus *Zenaida*.

Nidification

It has been adequately documented that members of these genera closely resemble one another in their nesting and egg-laying habits. Bent (1932:407, 417), Davie (1889:157), Goss (1891:242) and Nice (1922:466) have described the two, white eggs of the clutch of the Mourning Dove. They have also noted that their nests are composed mainly of twigs and may be constructed in trees, shrubs or on the ground. The Eared Dove has nearly identical habits (Bond, 1961:104), and a similar situation exists with the Zenaida Dove (Audubon, 1834:356; Bent, 1932:418-419).

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Like the other species, White-winged Doves lay two white or buffy eggs per clutch and build frail nests of sticks (Bent, 1932:431; Wetmore, 1920:141; Baird, Brewer and Ridgway, 1905:377).

The point to be made here is simply this: If the species in question are to be considered congeneric then it might reasonably be expected that they would display some similarity in nidification and egg-laying. If their habits varied considerably it would not necessarily mean that their relationship was more distant, but similarities can usually be considered indicative of affinities because they are the phenotypic expression of the partially unaltered genotype of the common ancestor.

Interbreeding

Intergeneric crosses of columbids in captivity are common, but in nature there is little evidence that even interspecific crosses occur. Only one apparent hybrid between members of the genus *Zenaida* and genus *Zenaidura* has ever been discovered. The individual was taken on the Yucatan peninsula of Mexico, and was described and named as a new species (*Zenaidura yucatanensis*).

Salvadori (1893:373), Ridgway (1916:353) and Peters (1934:213-215) agree that *Zenaidura yucatanensis* Lawrence is a hybrid between *Zenaidura macroura marginella* and *Zenaida aurita yucatanensis*. Ridgway (1916:355), however, notes that "... If *Zenaidura yucatanensis* Lawrence should prove to be really a distinct species, and not a hybrid ... unquestionably *Zenaida* and *Zenaidura* can not be separated generically, since the former is in every way exactly intermediate between the two groups." In the event that the unique type is a hybrid, the very fact of its existence supports the hypothesis that the genera are more closely related than is currently recognized.

Serology

There have been no investigations having as their sole purpose the clarification of the relationship of the genera *Zenaida* and *Zenaidura*. But some work has involved the comparison of the antigenic content of individual columbids with the antigenic content of a member of another species of the same family.

Irwin and Miller (1961) tested, along with other columbids, members of *Zenaida* and *Zenaidura* for presence of, 1) species-specific antigens of *Columba guinea* (in relation to *Columba livia*) which are designated A, B, C and E, and, 2) species-specific antigens of *C. livia* (in relation to *C. guinea*) which are designated A', B', C' and E'.

In the first test all five species of *Zenaida* and *Zenaidura* possessed antigens A and C, and all but *auriculata* possessed E. None of the species gave evidence of the presence of the B antigen of *C. guinea* in their blood. In the latter test only *macroura* had A', only *asiatica* had B' (*aurita* was not tested for B'), and none had C' or E'.

These results would indicate that the five species are similar regarding antigenic content of the blood, and the variation is not consistent within one or the other genus as presently known.

SUMMARY AND CONCLUSION

The avian genus *Zenaida* is currently considered to be distinct from the genus *Zenaidura* by most columbid taxonomists. The jaw muscles of six Mourning Doves (*Zenaidura*) and five White-winged Doves (*Zenaida*) were investigated as to differences and similarities that might clarify the relationships of the genera. The sizes and proportions of skulls were also considered in 37 Mourning and White-winged doves and two Eared Doves. Larger size of *M. pseudotemporalis profundus*, the muscle that functions simultaneously as an adductor of the lower jaw and retractor of the upper jaw, in the White-winged Dove was the character found in the jaw musculature that could be used to support the contention that *Zenaidura* and *Zenaida* represent distinct genera. Larger size of this muscle in the white-wing seems to be related to its elongated beak. The long beak apparently is used for nectar-feeding in flowers of the Saguaro Cactus.

Excluding the beak, skulls of the white-wing and Mourning doves are of nearly the same shape. Previous investigators have shown that in *Zenaida* and *Zenaidura* plumage patterns are similar, nesting habits and eggs are nearly identical, blood proteins are similar, and one "intergeneric" hybridization in nature is known.

Consequently, it is concluded that species of the two alleged genera are congeneric, and I agree with Goodwin (1958) that the genus *Zenaida* (Bonaparte, 1838:41) should include the Mourning Dove, Eared Dove, Socorro Dove, Zenaida Dove, and White-winged Dove. Their Latin binomina are *Zenaida macroura*, *Zenaida auriculata*, *Zenaida graysoni*, *Zenaida aurita*, and *Zenaida asiatica*, respectively.

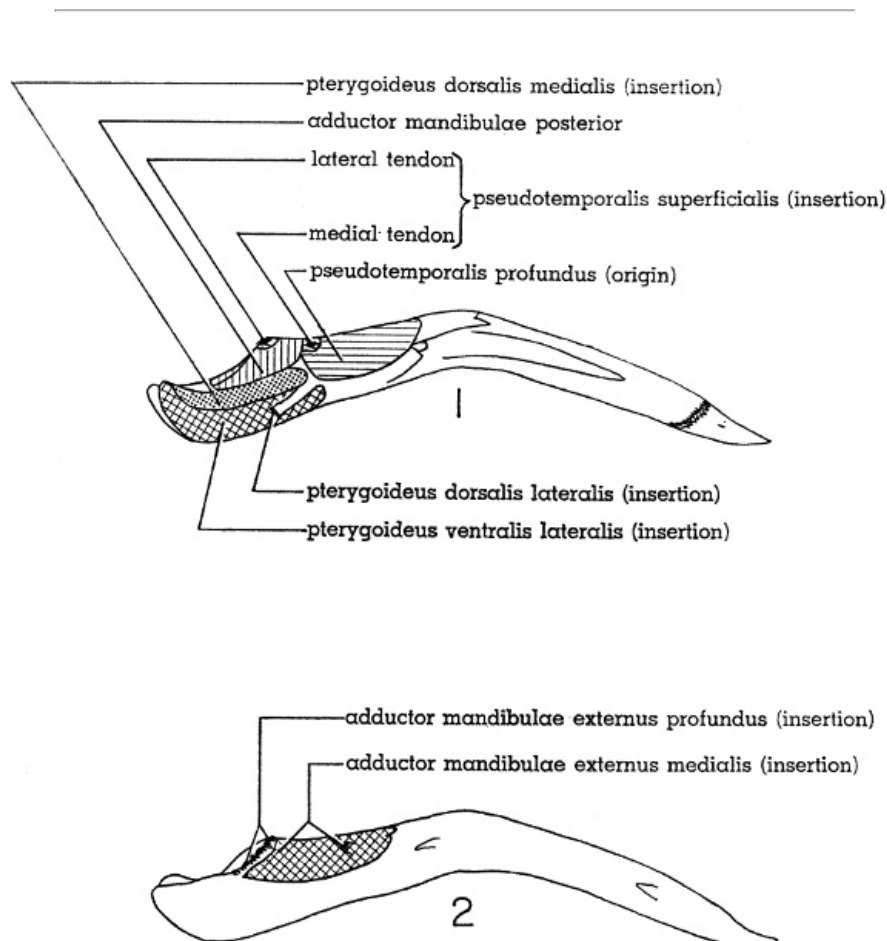


Fig. 1. Medial view of left ramus of lower mandible of Mourning Dove. × 2-1/2.

Fig. 2. Lateral view of right ramus of lower mandible of Mourning Dove. × 2-1/2.

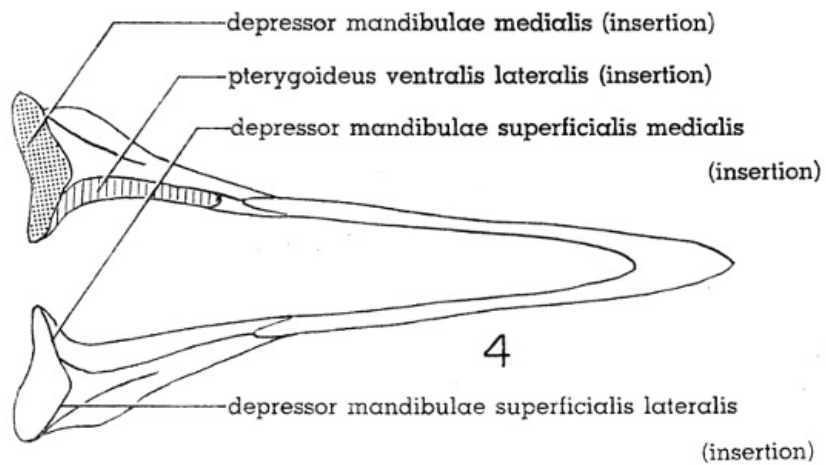
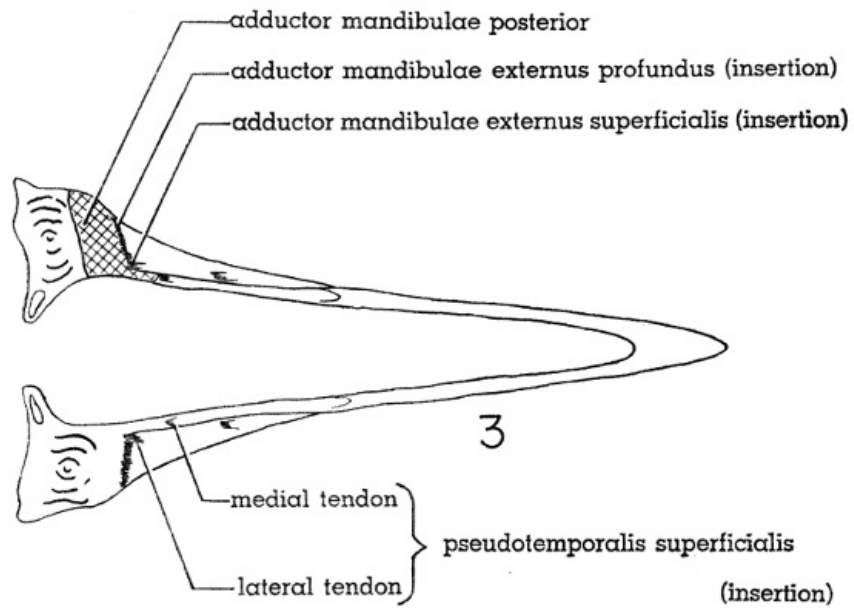


Fig. 3. Dorsal view of lower mandible of Mourning Dove. × 2-1/2.

Fig. 4. Ventral view of lower mandible of Mourning Dove. × 2-1/2.

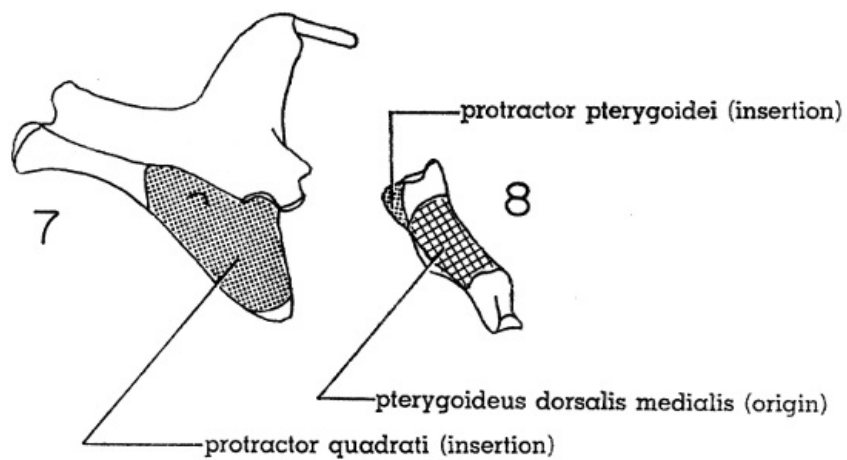
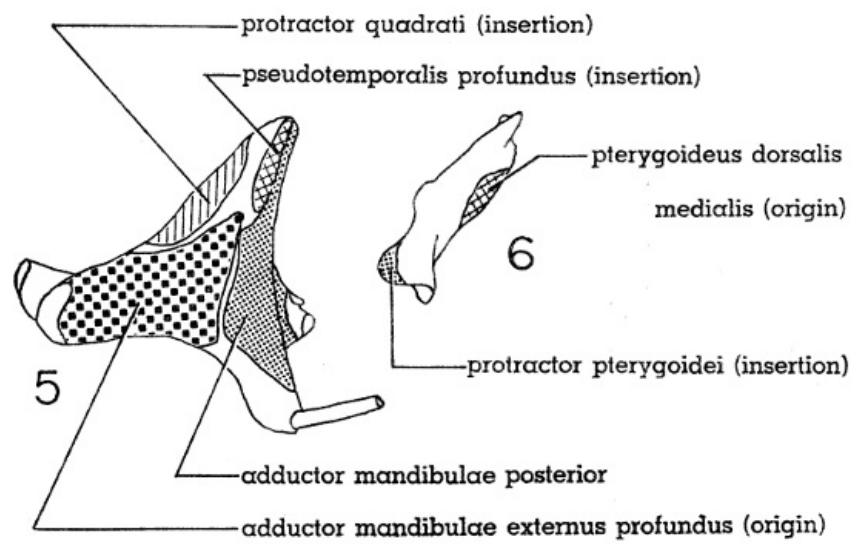


Fig. 5. Dorsal view of right quadrate of Mourning Dove. × 5.

Fig. 6. Dorsal view of right pterygoid of Mourning Dove. × 5.

Fig. 7. Ventral view of right quadrate of Mourning Dove. × 5.

Fig. 8. Ventral view of right pterygoid of Mourning Dove. × 5.

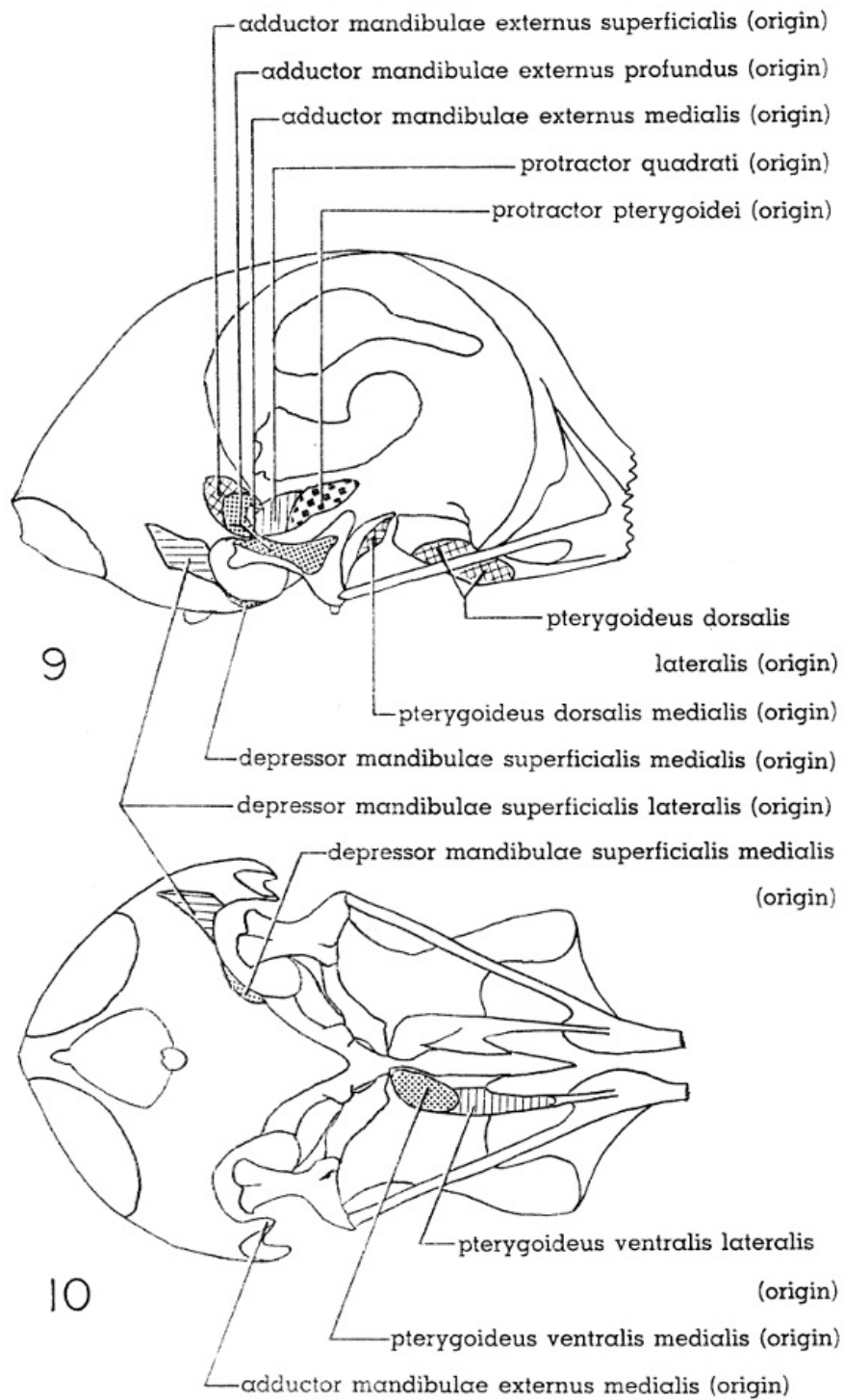


Fig. 9. Right lateral view of skull of Mourning Dove. × 2-1/2.

Fig. 10. Ventral view of skull of Mourning Dove. × 2-1/2.

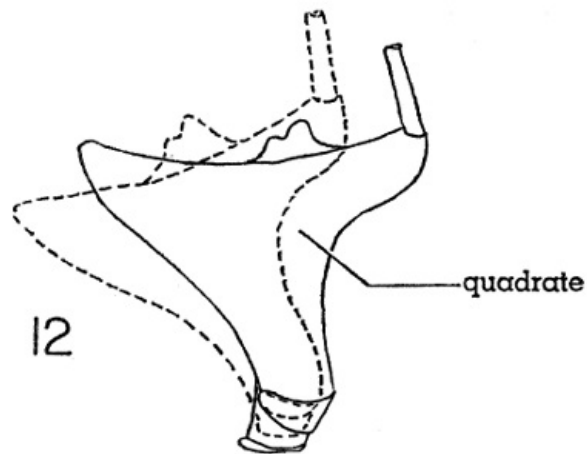
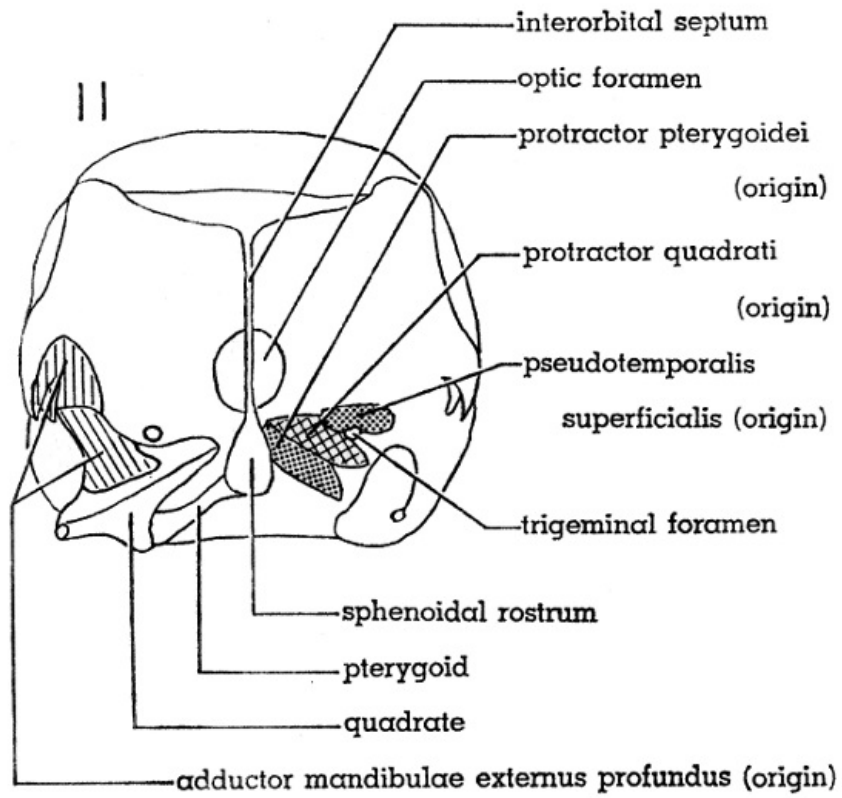


Fig. 11. Cross section of skull of Mourning Dove; anterior view. $\times 2\frac{1}{2}$.

Fig. 12. Dorsal view of right quadrate of Mourning Dove showing movement which protracts the upper mandible (broken line). $\times 5$.

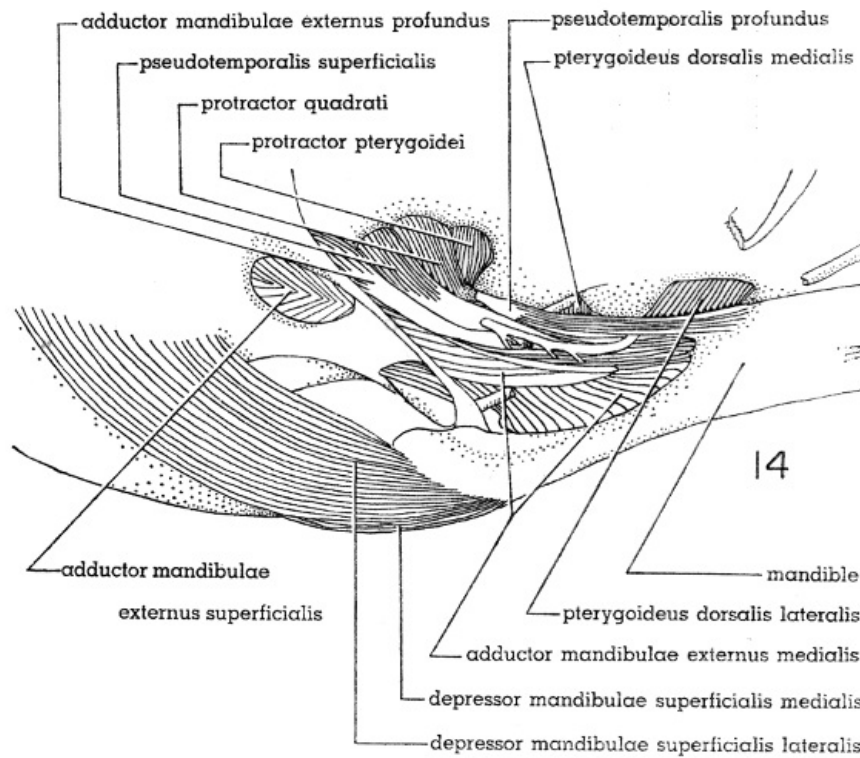
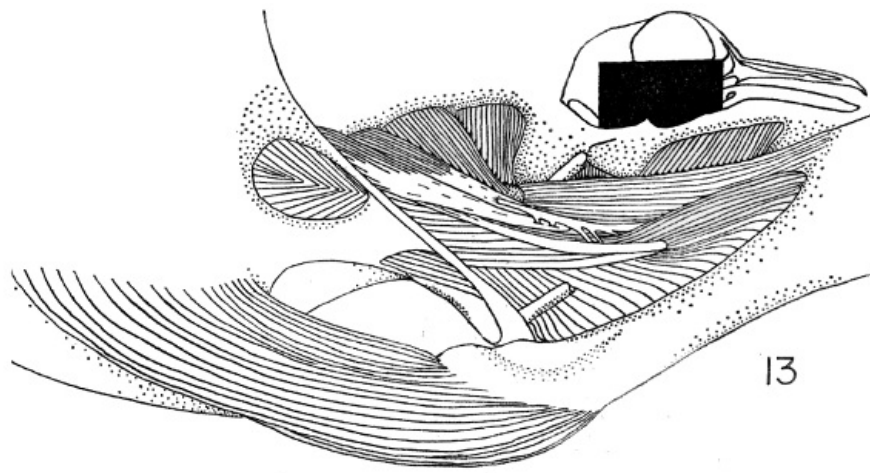


Fig. 13. Right lateral view of the jaw musculature of the White-winged Dove; superficial layer, × 5.

Fig. 14. Right lateral view of the jaw musculature of the Mourning Dove; superficial layer. × 5.

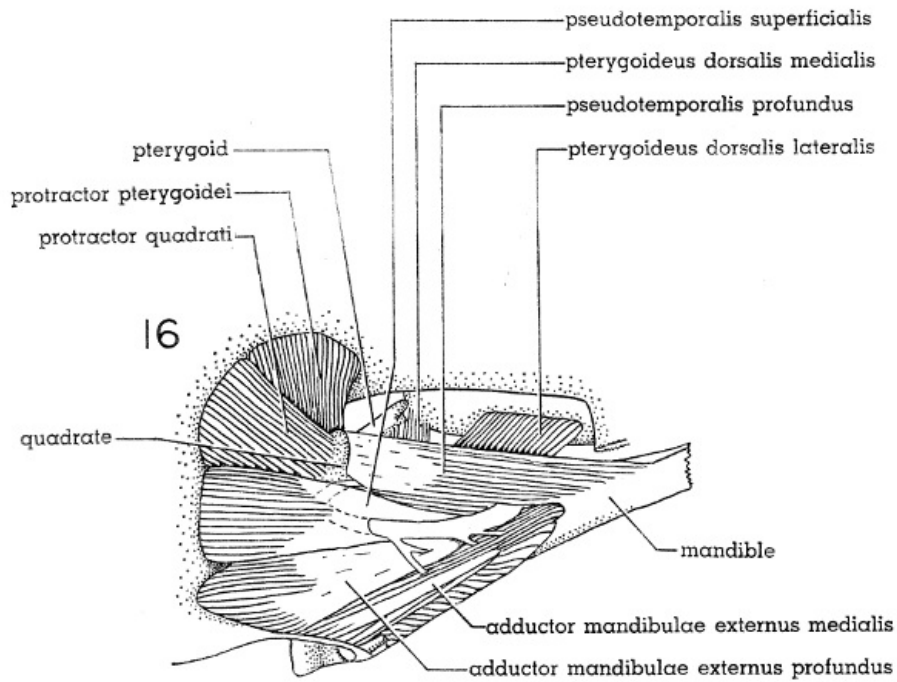
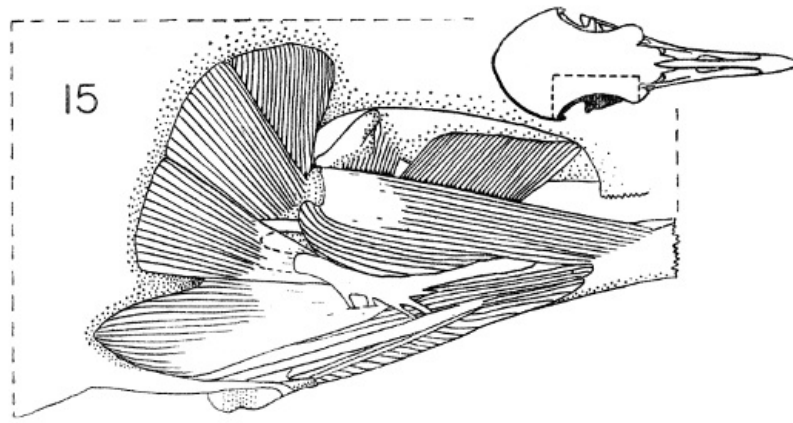


Fig. 15. Dorsal view of the jaw musculature of the White-winged Dove (right side); superficial layer. × 5.

Fig. 16. Dorsal view of the jaw musculature of the Mourning Dove (right side); superficial layer. × 5.

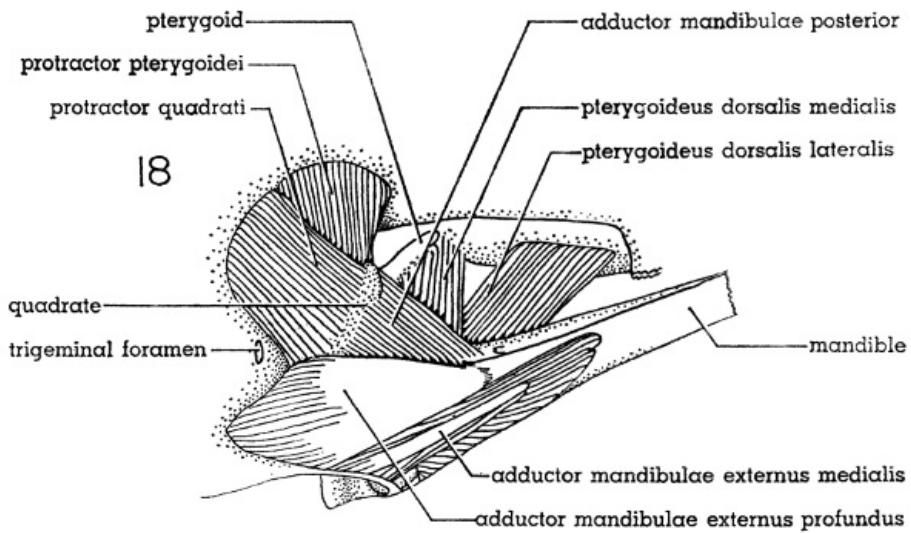
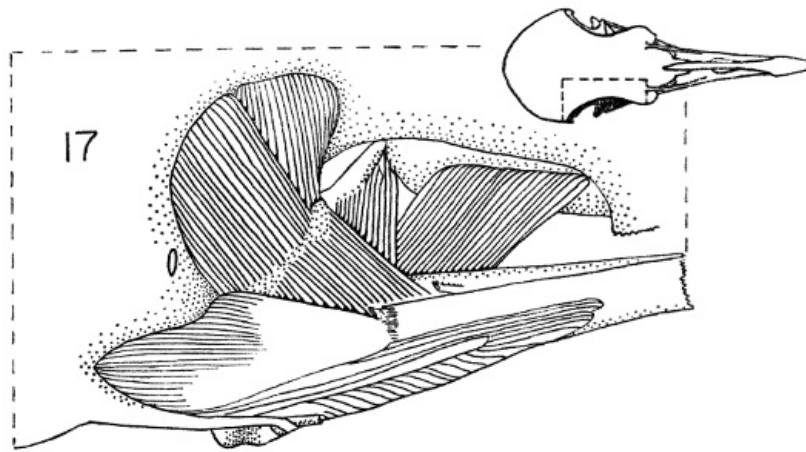


Fig. 17. Dorsal view of the jaw musculature of the White-winged Dove (right side); middle layer. × 5.

Fig. 18. Dorsal view of the jaw musculature of the Mourning Dove (right side); middle layer. × 5.

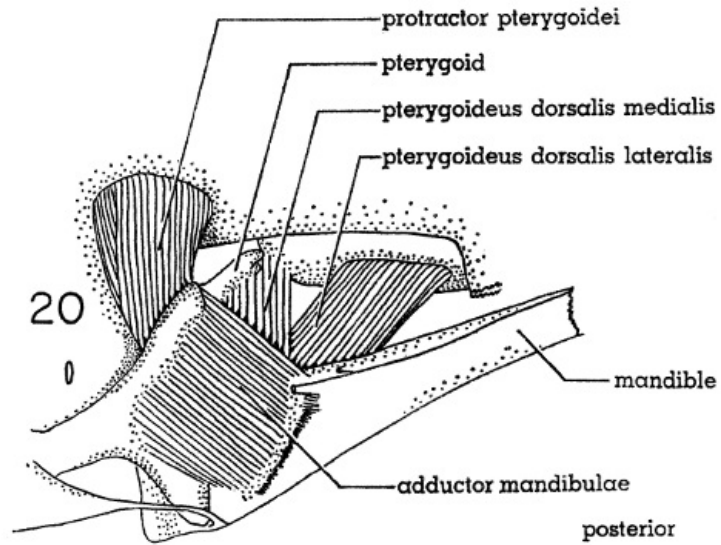
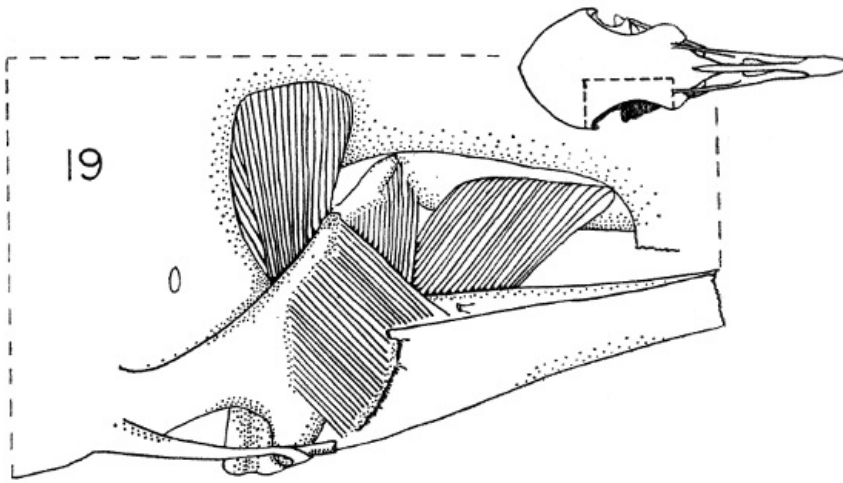


Fig. 19. Dorsal view of the jaw musculature of the White-winged Dove (right side); deep layer. $\times 5$.

Fig. 20. Dorsal view of the jaw musculature of the Morning Dove (right side); deep layer. $\times 5$.

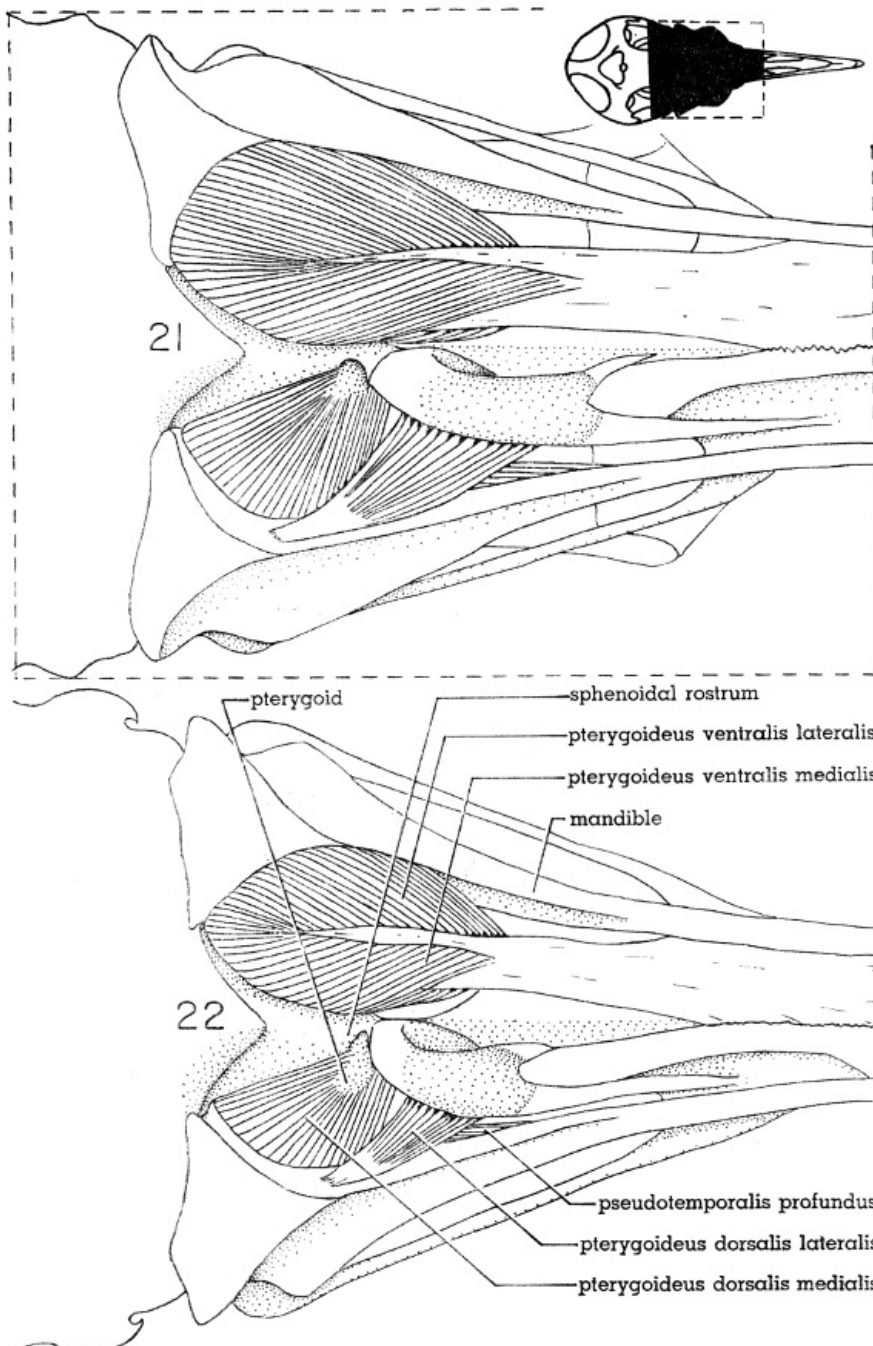


Fig. 21. Ventral view of the jaw musculature of the White-winged Dove (*M. depressor mandibulae* not shown). × 5.

Fig. 22. Ventral view of the jaw musculature of the Mourning Dove (*M. depressor mandibulae* not shown). × 5.

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