The Skeletomuscular System of the Feeding Apparatus of the Noisy Scrub-bird, *Atrichornis clamosus* (Passeriformes: Atrichornithidae)

WALTER J. BOCK

Department of Biological Sciences, Columbia University,
New York, New York 10027, U.S.A.

ABSTRACT. The cranial osteology and the jaw and tongue musculature of *Atrichornis clamosus* are described. Noteworthy are the large, free lacrymal and the distinct dorsal hump or ridge on the basal portion of the maxillary culmen. Aside from the lacrymal, little strong support exists in the cranial osteology for the generally accepted relationship between *Atrichornis* and *Menura*. The considerable differences in skull morphology between these genera are not surprising because of the much larger skull of *Menura*, about three times that of *Atrichornis* in linear measurements. Other than the large, free lacrymal, the skulls of the Menurae differ markedly from those of the bowerbirds, arguing against a close affinity between these two groups. The jaw muscles provide no useful information, at this time, on the possible evolutionary history and the affinities of *Atrichornis*, but the tongue musculature does yield some interesting clues. One feature, partial insertion of the M. trachohyoideus on the ceratobranchiale, is relatively primitive, but one aspect of the hyoid skeleton, lateral flattening of the basihyale, and five features of the tongue musculature are advanced. Most interesting are the vestigial nature of the M. stylohyoideus, a condition otherwise known only in woodpeckers and some meliphagids, and the complete insertion of the M. hypoglossus anterior on the anterior tip of the basihyale, seen also in *Dicaeum*, *Oedistoma*, *Promerops* and a few other passerine birds. These features of the tongue musculature suggest strongly that *Atrichornis* is not primitive among the oscines, but do not, as yet, provide a clear idea of its relationships.

The purpose of this paper is to provide a description of the skeletomuscular system of the jaw and tongue apparatus of *Atrichornis clamosus*. Some comparisons will be made with the skull of *Menura novaehollandiae*; however, full comparison of the cranial morphology of *Atrichornis* and *Menura* must wait until completion of an ongoing study of the latter genus. The available comparisons will permit a few tentative taxonomic conclusions, but more definite ideas on the evolution and relationships of *Atrichornis* to *Menura* and to other passerine birds based on the anatomy of the feeding apparatus must be deferred until detailed analyses are available.

METHODS

Dissections were made with the aid of iodine staining of the musculature, and using a steroscopic dissecting microscope. All illustrations were drawn directly from the dissections with the aid of a drawing tube attached to the microscope, or traced from projected transparencies of the skull. The skull was cleaned by hand after completion of the dissection of the jaw and tongue muscles.

Identification and nomenclature of the jaw and tongue musculature are based on Bock (ms.). The following abbreviations are used in the figures of the musculature.

Glands	
G a o	Glandula angularis oris
G mand	Glandula mandibularis
G max	Glandula maxillaris

Ligaments	
L j m e	L. jugomandibularis externus

L j m i	L. jugomandibularis internus
L p o	L. postorbitalaris

Jaw Muscles

M a m e c	M. adductor mandibulae externus caudalis
M a m e r	M. adductor mandibulae externus rostralis
M a m r e l	M. adductor mandibulae externus rostralis lateralis
M a m e r m	M. adductor mandibulae externus rostralis medialis
M a m e r t	M. adductor mandibulae externus rostralis temporalis
M a m e v	M. adductor mandibulae externus ventralis
M a m p	M. adductor mandibulae posterior
M d m	M. depressor mandibulae
M p p q	M. protractor pterygoidii et quadrati
M ps p	M. pseudotemporalis profundus
M ps s	M. pseudotemporalis superficialis
M pt	M. pterygoideus
M pt i a	M. pterygoideus infundibularis anterior
M pt i p	M. pterygoideus infundibularis posterior
M pt l	M. pterygoideus lateralis
M pt m a	M. pterygoideus medialis anterior
M pt m p	M. pterygoideus medialis posterior
M pt r	M. pterygoideus retractor

Tongue Muscles

M b m	M. branchiomandibularis
M b m p	M. branchiomandibularis anterior
M b m a	M. branchiomandibularis posterior
M c c	M. cucullaris caput portion
M c g	M. ceratoglossus
M c h	M. ceratohyoideus
M cr h	M. cricohyoideus
M d t	M. dermotemporalis
M g g	M. genioglossus
M hg a	M. hypoglossus anterior
M hg o	M. hypoglossus obliquus
M m h	M. mylohoideus
M s h	M. serpihyoideus
M st h	M. stylohyoideus
M tr h	M. tracheohyoideus
M tr l	M. tracheolateralis

DESCRIPTION

Skull

The skull of *Atrichornis* (Figs 1 and 2) has few features distinctly different from those usually present in small, insectivorous passerine birds. The brain and orbits are large, and dominate the total structure of the skull. The brain case of this specimen is fully ossified. Jaws are relatively short and straight with a large external nares and no ossification within the nasal cavity. The dorsal edge of the upper jaw rises gradually to a distinctive hump over the posterior end of the external nares, then drops off rapidly to the nasal-frontal hinge.The brain case is bulbous with a slightly projecting occipital region and an indistinct temporal fossa. The postorbital process is small and the zygomatic process almost nonexistent. Quadrates have distinct medial and lateral condyles and a moderate orbital process that terminates in a point. The ptergyoids are stout with well developed anterior feet embracing the basisphenoid rostrum. Palatines are straight and parallel with short transpalatine processes and strong prepalatine bars running forward to the upper jaw. A long slit separates the two halves of the bony palate with articulates with the basisphenoid rostrum only at the palatine-pterygoid junction. This slit extends to the anterior half of the vomer which has a narrow anterior plate and almost straight anterior edge. The maxillopalatines have moderately expanded medial plates.

The most unusual feature of the skull is the large, free lacrymal (or prefrontal) which extends from the frontal to the jugal bar (Fig. 1B). The dorsal head of this bone is small, and contacts the frontal along a narrow rim. A large gap separates the dorsal half of the lacrymal from ectethmoid plate, but the ventral halves of these two bones are in broad contact. The lacrymal does not fuse with any of the bones with which it articulates.

The mandible is straight with a narrow ramus and a moderate mandibular fossa. A distinct groove forms the articular surface for the medial condyle. Both the retroarticular process and the internal process of the mandible are short.

Jaw Ligaments

The four major avian jaw ligaments — the postorbital, the internal jugomandibular, the external jugomandibular and the occipitomandibular — are all present and well developed with the external jugomandibular being slighter weaker than the other. These ligaments have the normal passerine attachments and configurations (Fig. 3B; the occipitomandibular ligaments is not shown).

Salivary Glands

A special search was not made for the salivary glands so only the largest were noted. The G. angularis oris (Fig. 3B) lies medial and ventral to the jugal bar, ending just anteriorly to the postorbital ligament. The G. maxillaris (Fig. 6) lies along the choanal slit, medial to the M. pterygoideus, and covers the shelf of the palatine bone. The G. mandibularis (probably a combination of the mandibular and sublingual glands, Fig. 6) lies along the lateral edge of the M. pterygoideus, covering the lateroventral surface of the muscle. The ducts of these glands were not traced.
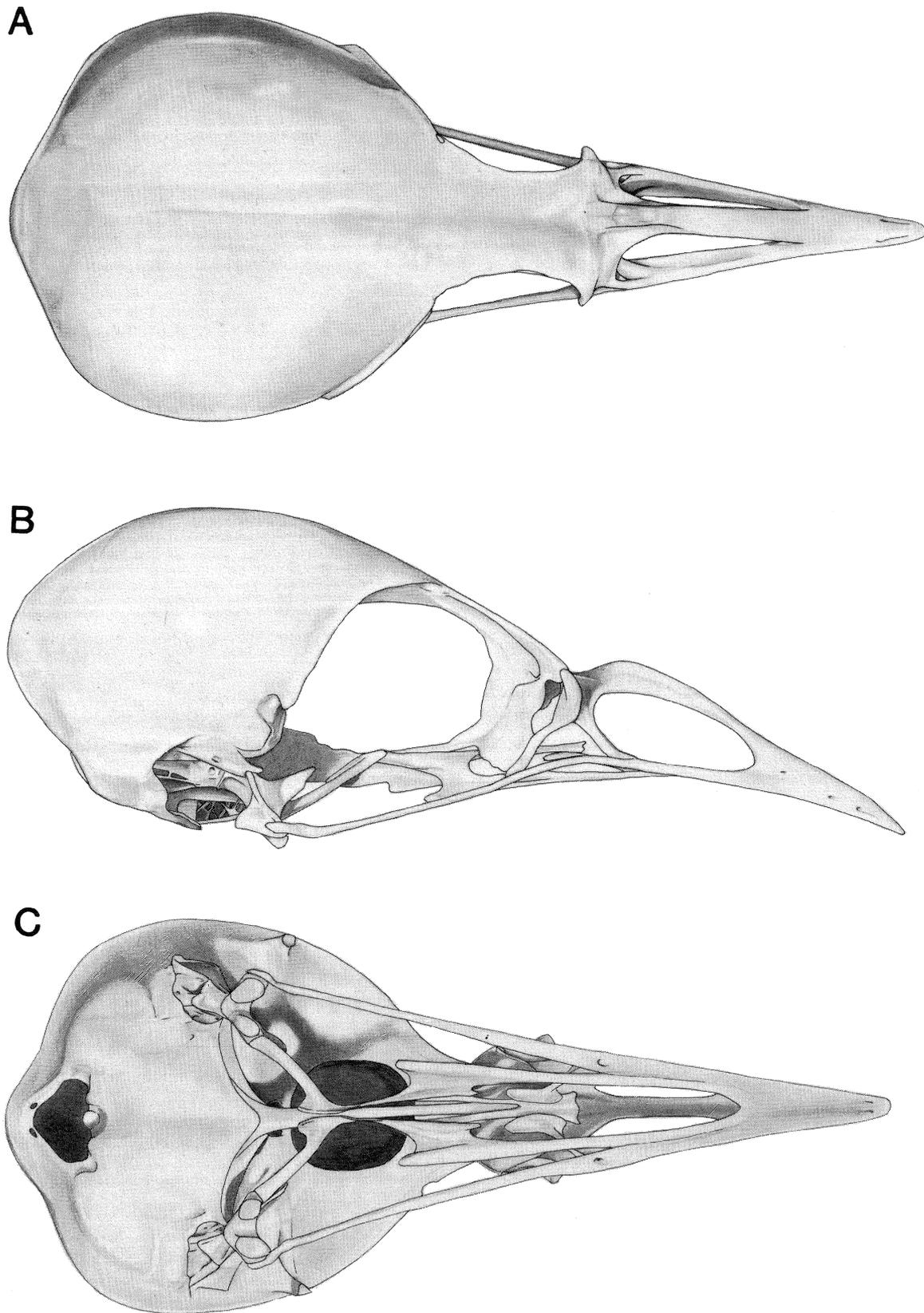
Fig. 1. Skull of *Atrichornis clamosus* seen in dorsal (A), lateral (B) and ventral (C) views. Note the large unfused lacrymal (l) articulating dorsally with the frontal.

A
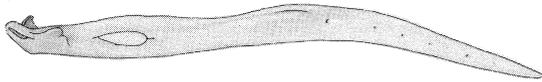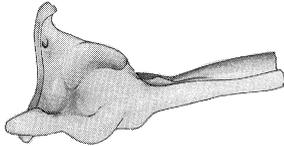
Fig. 2. Mandible of *Atrichornis clamosus* seen in lateral (A) and enlarged dorsal (B) views.

Jaw Muscles

The jaw muscles of *Atrichornis* (Figs 3, 4, 5, 6, 7 and 8) do not show any special features, being reasonably typical for an insect-eating passerine bird. Each muscle will be described individually but without special reference to the figures. See Bock (ms.) for discussion of the functions of these muscles.

M. depressor mandiulae (M d m).   Origin is from the lateroposterior surface of the brain case and the lateral edge of the occipital plate. Insertion is on the posterior end of the mandibular ramus, the short retroarticular process and the posterior surface of the internal process of the mandible. The muscle is almost purely parallel-fibred with a fleshy origin and insertion.
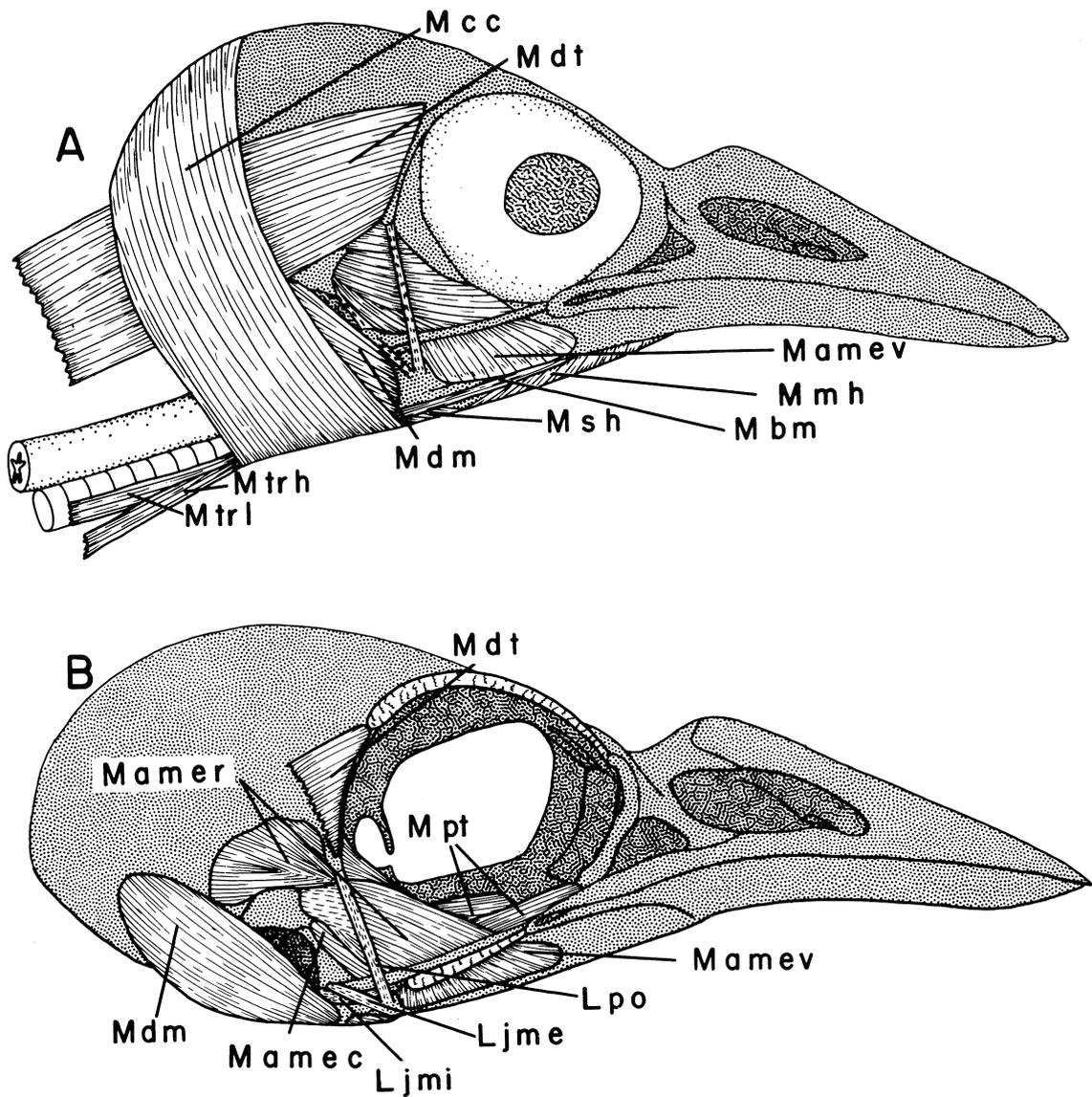
Fig. 3. Jaw and tongue musculature of *Arichornis clamosus* with (A) and without (B) the superficial M. cucullaris caput portion (M c c), M. dermotemporalis (M d t) and eye. See Methods section for abbreviations used in this and following figures.
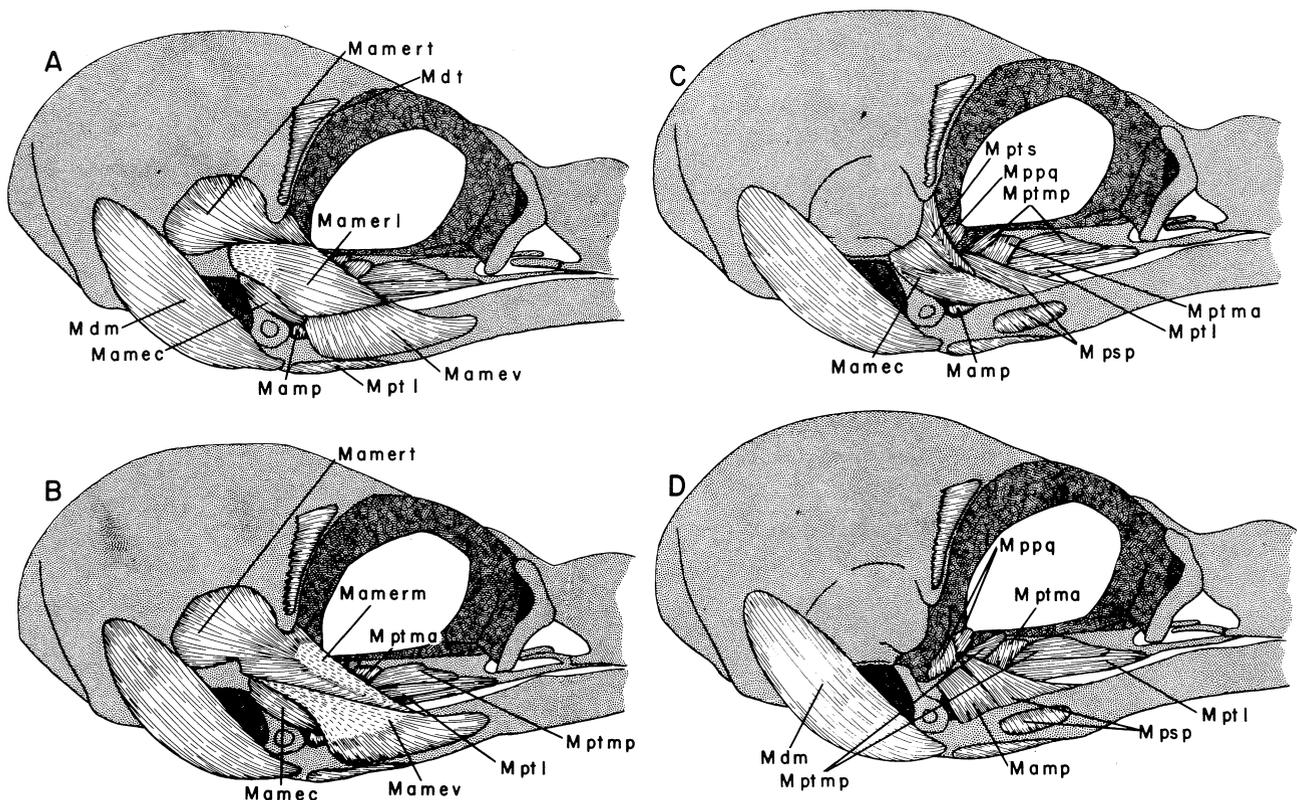
Fig. 4. Jaw muscles of *Atrichornis clamosus* seen in lateral view in successively deeper layers (A–D).

Longest fibres are 10 mm long with the shortest fibres (the medioventral portion) being only 3 mm long; most fibres are 6–7 mm long. The muscle is 3 mm wide, measured aong the lateral surface, and about 1.5 mm thick, given a fibre (= physiological) cross-sectional area (CSA = total cross-sectional area of all fibres) of about 4.5 mm². The occipitomandibular ligament lies buried in the medial part of the muscle.

M. adductor mandibulae externus. This is the largest and most complex component of the dorsal adductors; it is subdivided into three parts which merge somewhat into one another deep within the muscle. Each of the subdivisions will be described separately.

M. ADDUCTOR MANDIBULAE EXTERNUS ROSTRALIS (M a m e r). This portion of the adductor mandibulae externus has three reasonably distinct divisions — the temporalis (M a m e r t), the medialis (M a m e r m) and the lateralis (M a m e r l) — which will be described separately; however it must be stressed that these divisions merge into one another even more than do the parts of the adductor mandibulae externus. The temporalis originates from the temporal fossa and from the area medial to the postorbital process where it merges without a break into the medialis. Its fibres are arranged from fan-shaped to slightly bipinnately. Fibre length varies from short anterior fibres (2 mm) to longest posterior ones with an average of about 3 mm. The muscle width (surface measurement) is approximately 4 mm and thickness about 2 mm with a fibre CSA of 8 mm². The lateralis is the most

superficial portion of the muscle and originates from the surface of a broad aponeurosis arising from the skull between the temporal fossa and the otic head of the quadrate. This position has a flat spindle shape with the fibres arranged unipinnately. Fibres are 3–4 mm long with the muscle being 4 mm wide and 0.75 mm thick for a fibre CSA of 3 mm². The medialis is the deepest part of the muscle and can only be seen in oblique view or when the superficial parts are dissected away. It arises from the lateral edge of the posterior wall of the orbit (lateral to the mandibular ramus of the trigeminal nerve), from the dorsal edge and medial surface of the aponeurosis of origin of the M a m e lateralis and from a broad aponeurosis forming the medial surface of the muscle; the last aponeurosis arises from the brain case just medial to the quadrate articulation. The muscle is bipinnate with a deep central tendon of insertion. Fibres are 3–4 mm long with the fibre CSA being 20 mm² (5 mm × 4 mm), making the medialis the largest segment of the rostralis. All three parts insert via a common tendon of insertion that attaches to the dorsal edge of the mandibular ramus at the anterior point of the muscle. The tendon lies deep within the muscle with fibres of the lateralis attaching to its lateral side, of the medialis to its medial and ventral surfaces, and of the temporalis to its free, posterior end.

M. ADDUCTOR MANDIBULAE EXTERNUS VENTRALIS (M a m e v). Origin is from the medial surface and the ventral edge of a broad aponeurosis arising from the tip of the short zygomatic process. Insertion is fleshy
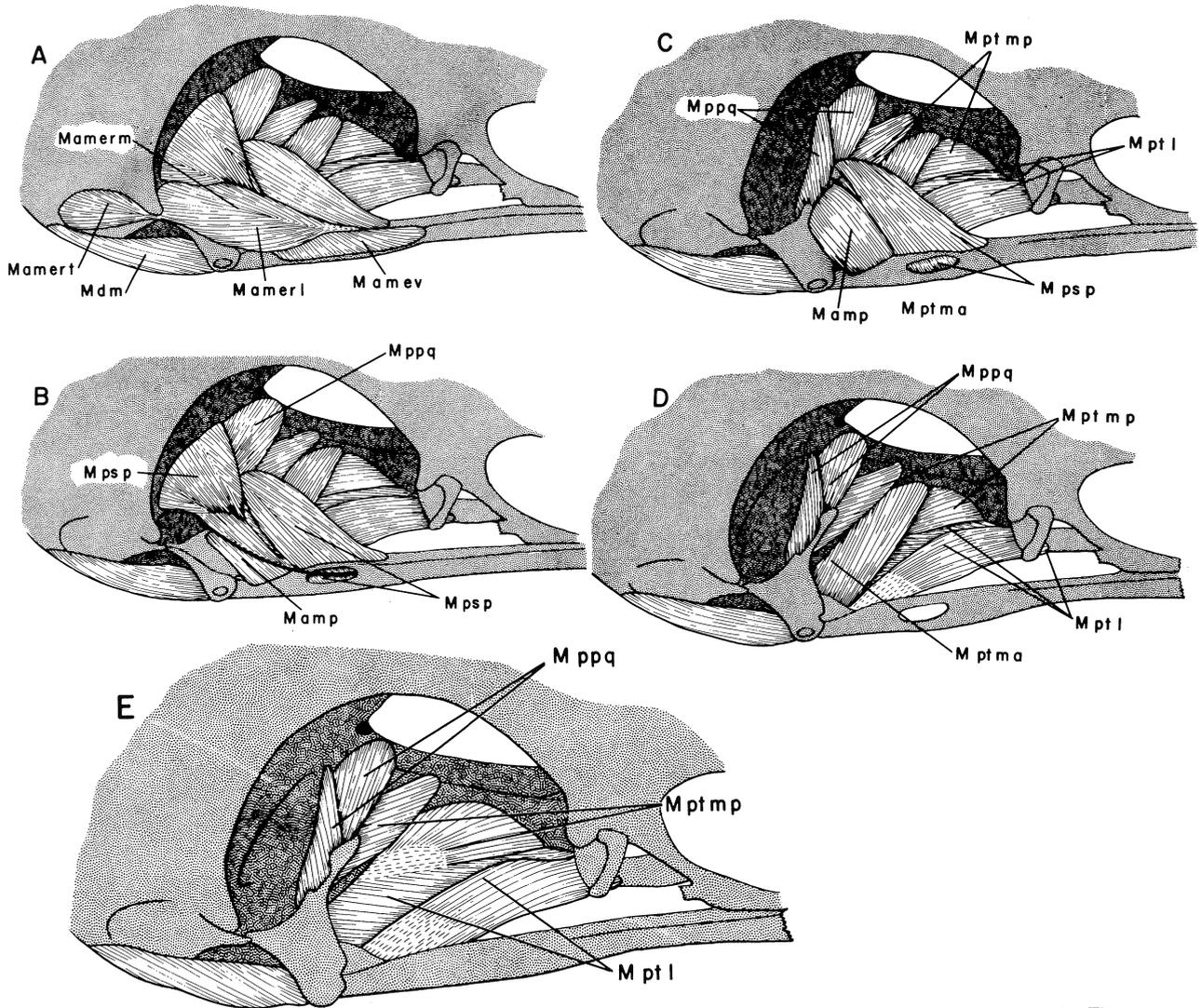
Fig. 5. Jaw muscles of *Atrichornis clamosus* viewed obliquely through the orbit in successively deeper layers (A–E).
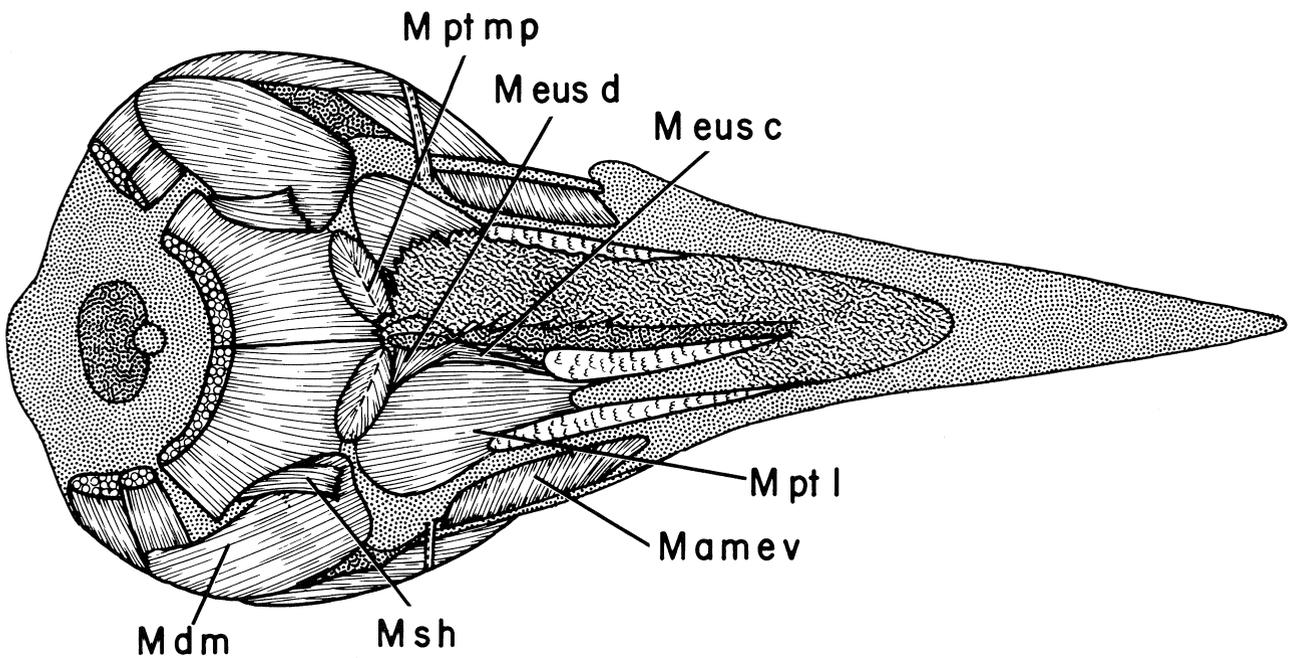
Fig. 6. Jaw muscles of *Atrichornis clamosus* in ventral view showing a general overview and the position of the major glands.
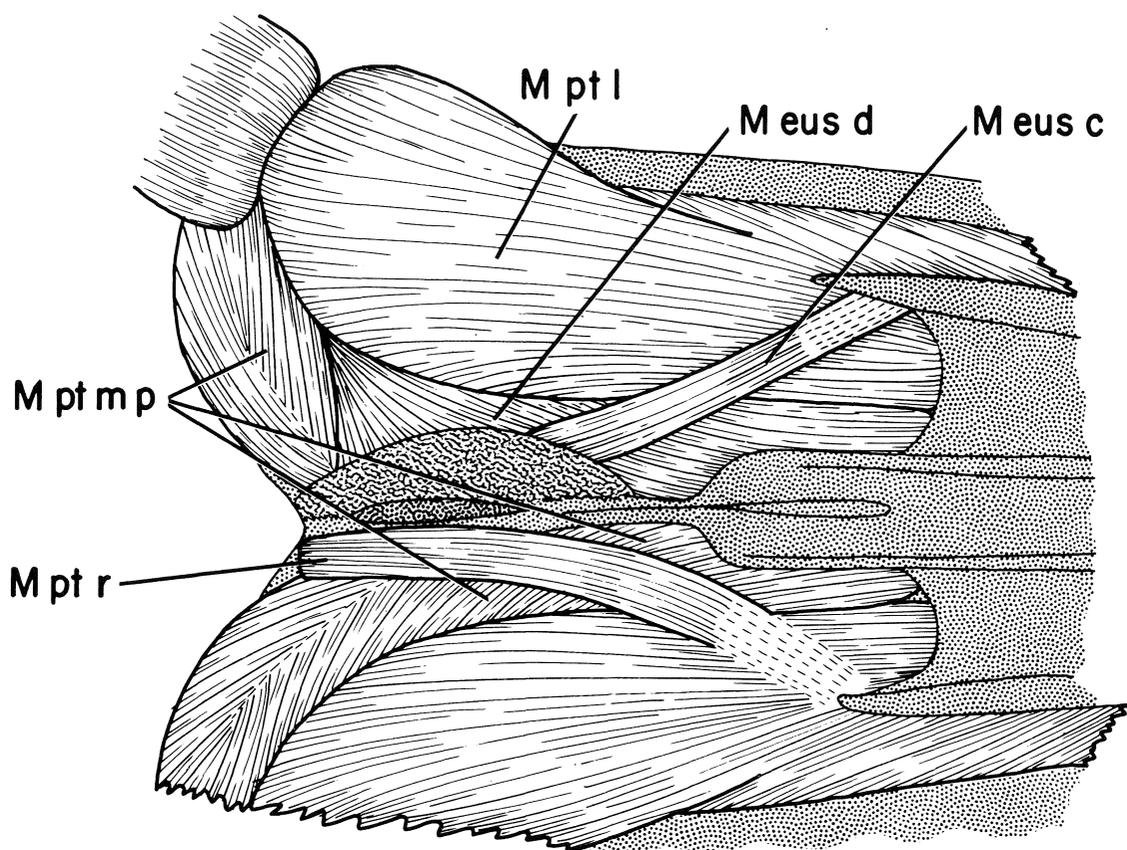
Fig. 7. Jaw muscles of *Atrichornis clamosus* in ventral view showing details of the muscles to the infundibulum and of the neighbouring position of the M. pterygoideus.

over a broad area of the lateral surface of the ramus around the mandibular fossa extending from the insertion of the M a m posterior to a point well anterior of the insertion of the M a m e rostralis. The ventralis is an unipinnate, fan-shaped muscle. Fibres vary from 2 mm (posterior) to 4 mm (anterior) long with a fibre CSA of 10 mm² (5mm × 2mm). Fibres in the medio-dorsal part of this muscle merge with those of the M a m e rostralis, especially the medialis portion.

M. ADDUCTOR MANDIBULAE EXTERNUS CAUDALIS (M a m e c). Origin is from the brain case ventral and medial to the zygomatic process, from the posterior wall of the orbit medial to the quadrate articulation and from the dorsal end of the otic process of the quadrate; some fibres arise from a short aponeurosis on the medial surface of the muscle. Insertion is on the dorsal edge of the ramus, dorsal to the posterior end of the mandibular fossa, partly fleshy but mainly via a superficial aponeurosis covering the anteromedial surface of the muscle. The dorsomedial fibres from the braincase are arranged unipinnately, and attach to the anterior aponeurosis while the ventroposterior fibres from the quadrate attach partly fleshy, but mainly unipinnately, on the aponeurosis of insertion. Fibre length is 2-3 mm with the shorter fibres arising from the quadrate; the fibre CSA is approximately 8 mm² (4 mm × 2 mm). The caudalis lies posterior and deep to the rest of the M a m externus, and is relatively short

and thick compared to the other parts of the externus.

M. pseudotemporalis superficialis (M ps s). Originates from the posterior wall of the orbit extending medially from the origin of the M a m externus almost to the foramen for the optic nerve. Insertion is by a single tendon to the medial surface of the mandibular ramus just anterior to the quadrate articulation. The m ps superficialis is complexly pinnate with a faint indication of three parts (trifed) with a lateral and two internal tendons of origin. The superficial fibres of the muscle appear to be arranged in a parallel fashion, but the true pinnate configuration of the muscle is revealed by dissection. The muscle is 5 mm wide at its base and 10 mm long. Most fibres are 2-3 mm long with a fibre CSA of at least 20 mm² and possibly 25 mm². The inserting end of the M ps superficialis separates the M ps profundus and the M a m posterior.

M. pseudotemporalis profundus (M ps p). Origin is from the distal half of the orbital process of the quadrate; the entire origin is fleshy. Insertion is fleshy and mainly on the medial surface of the ramus about the mandibular fossa, but also along the dorsal edge of the ramus between the insertions of the M a m e rostralis and the M a m e caudalis. The M ps profundus is parallel-fibred and fan-shaped. Fibres are 6 mm, or more, long with a fibre CSA of 6 mm² (2 mm × 3 mm). The separation of the M ps profundus from the M a m posterior is quite arbitrary, being determined
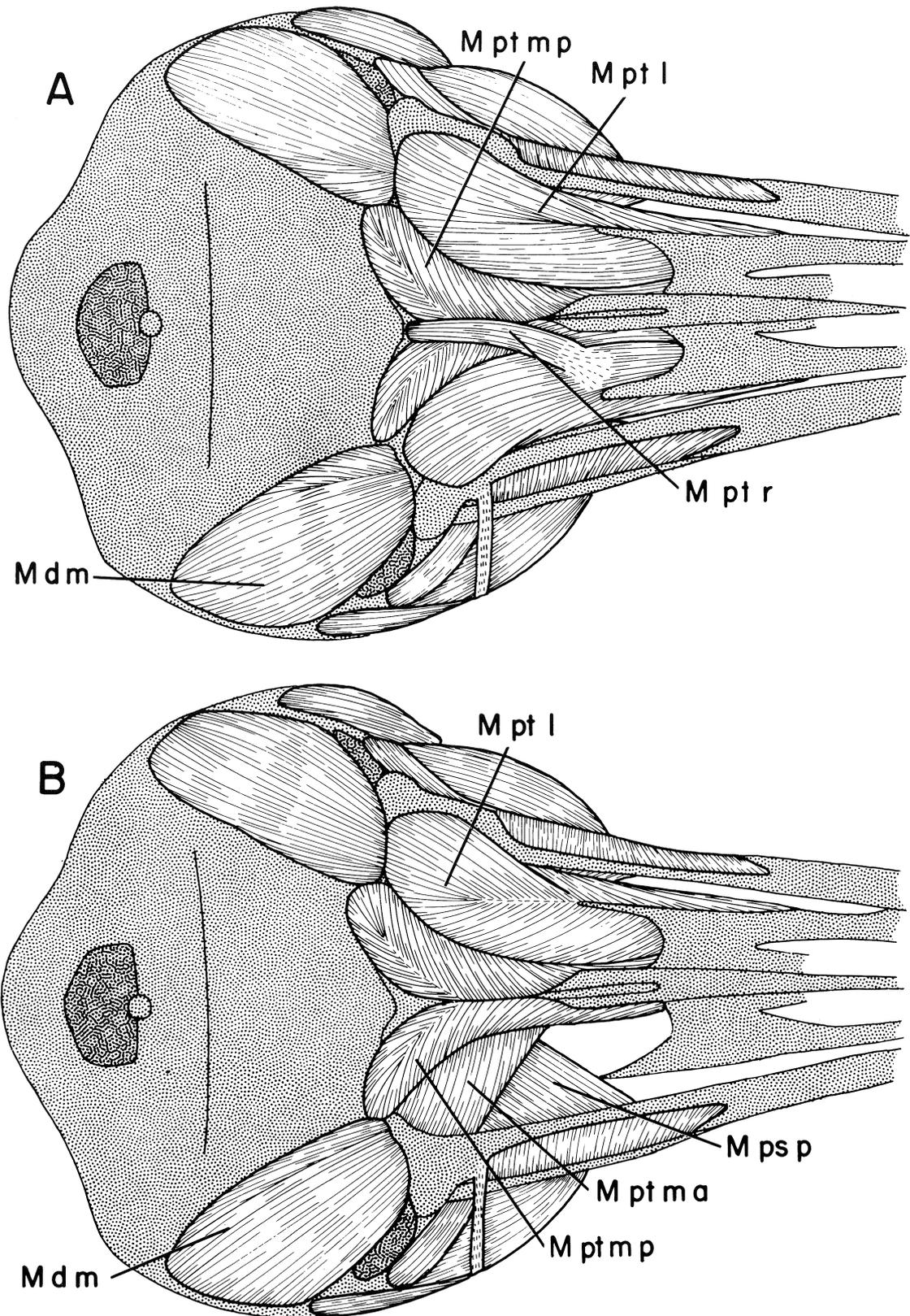
Fig. 8. Jaw muscles of *Atrichornis clamosus* in ventral view showing the M. pterygoideus in successively deeper layers (A–B).

mainly by the position of the pterygoid branch of the trigmeninal nerve. These two muscles are best merged into a single muscle, the M. quadromandibularis, which cannot even be subdivided into two parts in the passerine birds (Bock, ms.).

M. adductor mandibulae posterior (M a m p). Origin is from the basal half of the orbital process of the quadrate and ajoining part of the quadrate body. Insertion is on the lateral surface and dorsal edge of the mandibular ramus from the quadrate articulation to the insertion of the M ps profundus, and on the broad shelf forming the anterior edge of the quadrate articulation of the mandible; the insertion of the M ps superficialis separates those of the M a m posterior and of the M ps profundus. It is a parallel-fibred muscle with fibres 2-3 mm long and a fibre CSA of 4 mm^2 (2 mm × 2 mm). The M a m posterior is a rather large muscle which cannot be seen until the M. adductor mandibulr externus and the M. pseudotemporalis superficialis are removed.

M. protractor pterygoidii et quadrati (m p p q). Originates from the ventral part of the posterior wall of the orbit, from a point just medial to the quadrate articulation to a point anterior and ventral to the orbital foramen. Part of its origin is ventral to the origin of the M ps superficialis. Insertion is on the posterodorsal surface of the pterygoid, close to its quadrate articulation, and on the posterior surface of the orbital process of the quadrate and adjoining body of the quadrate. A few fibres attach to the anterior surface of the orbital process. The muscle appears to have two distinct parts but this results only from the arrangement of the superficial fibres; the deeper fibres merge together without a break. The muscle is mainly parallel-fibred but some of the fibres attaching to the pterygoid are unipinnate. Fibre length ranges from 4 mm (longest anteromedial) to 2 mm (shortest lateroposterior). The fibre CSA is about 8 mm^2 (5 mm wide × 1-2 mm thick).

M. pterygoideus. This large ventral adductor of the jaws is comprised of several parts which are reasonably distinct from one another; they will be described separately.

M. PTERYGOIDEUS INFUNDIBULARIS ANTERIOR (M pt i a) and M. PTERYGOIDEUS INFUNDIBULARIS POSTERIOR (M pt i p). These two small superficial slips on the ventral surface of the muscle are derived from, and are incompletely separated from, the adjoining parts of the M. pterygoideus. These muscles were first described by Richards & Bock (1973:66–67, based on the unpublished Ph.D. thesis of Richards) and described under the name "fan-like part" of the M pt medialis which is the M pt i posterior; the M pt i anterior was not described. A full description of these muscles is provided by Bock (ms.). The strap-like M pt i anterior arises from the medial surface of the transpalatine process, along with the M pt retractor, and inserts on the lateroanterior edge of the infundibular slit. It serves to close the opening of the infundibular slit by pulling the two lips forwards and thereby straightening them

against each other. The fan-shaped M pt i posterior originates along most of the lateral edge of the infundibular lip and inserts via a thin tendon on the tip of the internal process of the mandible, along with the large tendons of the M pt medialis posterior. It serves to open the infundibular slit by pulling the two lips laterally and away from one another. Both muscles are very thin slips and are easily damaged or destroyed when removing the mucosa lining the roof of the mouth prior to the dissection of the M. pterygoideus.

M. PTERYGOIDEUS LATERALIS (M pt l). This muscle was frequently divided into a ventral and dorsal portion but recent study (Bock, ms) suggests that this is an artificial division along the plane of an aponeurosis of origin. Origin is from the dorsal surface of the transpalatine process and the palatine shelf, and from a tendon arising from the tip of the transpalatine process. Two aponeuroses of insertion exist — one on the dorsal surface of the muscle that attaches to the corner between the ramus and internal process of the mandible and one on the medial surface (in common with the M pt m posterior) that attaches to the tip of the internal process of the mandible. Fibres spread out from the origin of the muscle to these several areas of insertion. Most fibres are about 3 mm long with a total fibre CSA of 24–28 mm^2 (4 mm × 6-7 mm). The M pt lateralis merges with the M pt m posterior along its medial border.

M. PTERYGOIDEUS MEDIALIS POSTERIOR (M pt m p). Earlier studies had divided the medial part of the M. pterygoideus into a ventral and a dorsal portion, and further subdivided the dorsal portion into anterior and posterior divisions. Recent analysis (Bock, ms.) suggested that the division of the medialis into ventral and dorsal parts is artificial and that the primary division is whether the portion arises from the anterior or the posterior surface of the pterygoid. The posterior part usually extends ventral to the pterygoid to originate from a major part of the mediopalatine process and even from the shelf of the palatine. Thus, much of the posterior part of the M pt m posterior may be anterior to the M pt m anterior. The M pt m posterior originates from the lateral surface of the mediopalatine process, bipinnately from a tendon arising from the posterior end of the mediopalatine process and from the posterior surface of the pterygoid. It inserts on an aponeurosis lying along the lateral surface of the muscle (in common with the M pt lateralis), on an aponeurosis along the posterior surface of the muscle and, by a few fibres, directly on the tip of the internal process of the mandible; the inserting aponeuroses attach to the tip of the internal process of the mandible. It is mainly unipinnate, but the posterior third is bipinnate. Fibres are 1–2 mm long (average about 1.5 mm) with a fibre CSA of about 10 mm^2 (1 mm × 10 mm). The M pt m posterior lies mainly ventral to the pterygoid except for the portion that takes origin from this bone.

M. PTERYGOIDEUS MEDIALIS ANTERIOR (M pt m a). Origin is from the anterior surface of the pterygoid and from a small area on the lateral surface of the
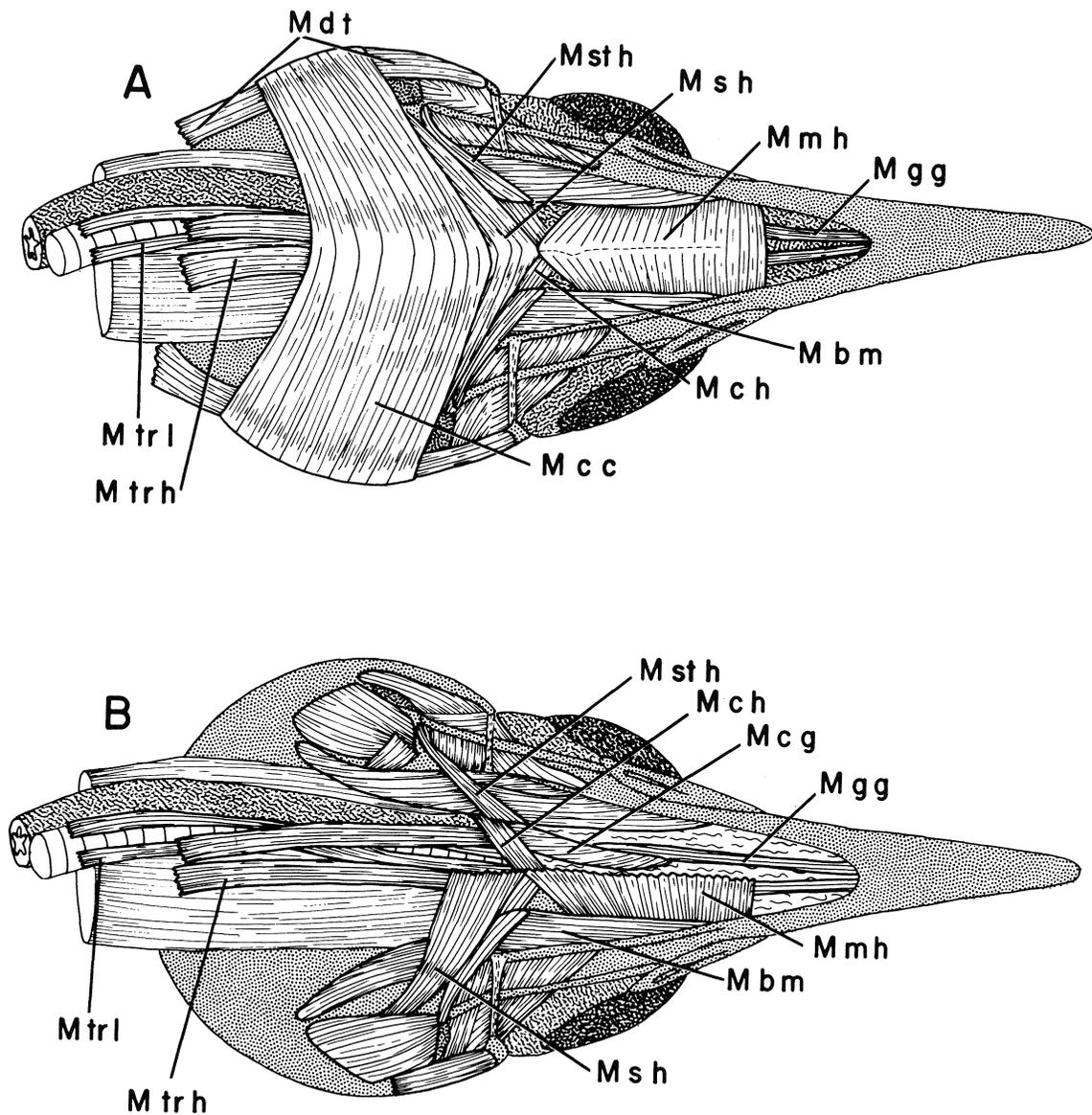
Fig. 9. Tongue muscles of *Atrichornis clamosus* in ventral view with (A) and without (B) the superficial M. cucullaris and M. dermotemporalis. The M. mylohyoideus and M. serpihyoideus have been removed from the right side in Figure B. In this and following drawings, the muscles and other structures of the neck have been extrapolated posterior from the level of the occipital condyle (apprximately at the posterior border of the M. cucullaris) where the head was severed from the neck.

mediopalatine process just anterior to the pterygoid articulation. Insertion is at the corner of the ramus and internal process of the mandible medial to that of the M a m posterior; insertion is mainly fleshy. It is mostly parallel-fibred, but a few fibres may be unipinnate. Fibres are 5-6 mm long with a fibre CSA of 2 mm^2 (4 mm × 0.5 mm).

M. PTERYGOIDEUS RETRACTOR (M pt r).   Origin is from the transpalatine process and from the superficial ventral aponeurosis of the M pt lateralis. Insertion is on the basitemporal plate just lateral to the midline. The M pt retractor is thin, parallel-fibred and strap-like with fibres 5-6 mm long and a fibre CSA of about 0.20 mm^2 (0.88 mm wide × 0.25 mm thick).

Tongue

The tongue (Fig. 10A) is slightly concave dorsally (Fig. 10C) with its anterior tip divided into two by a short medial cleft. Each of the two tips bears a number of short laciniae giving the tongue tip a frilled appearance. The extent of this frilling in *Atrichornis* is no greater than that seen in many insectivorous birds. It does not resemble in any special way the tongue of the Meliphagidae.

Tongue Skeleton

The bones of the hyoid in *Atrichornis* are typical for passerine birds with the exception of the basihyale. This

Fig. 10. Tongue and tongue musculature of *Atrichornis clamosus* in dorsal (A) and lateral (B) views, and cross section (C) of the tongue at the indicated level.

Fig. 11. Tongue of *Atrichornis clamosus* in dorsolateral view to show details of the insertion of the M. genioglossus into the mucosa between the tongue and the larynx.
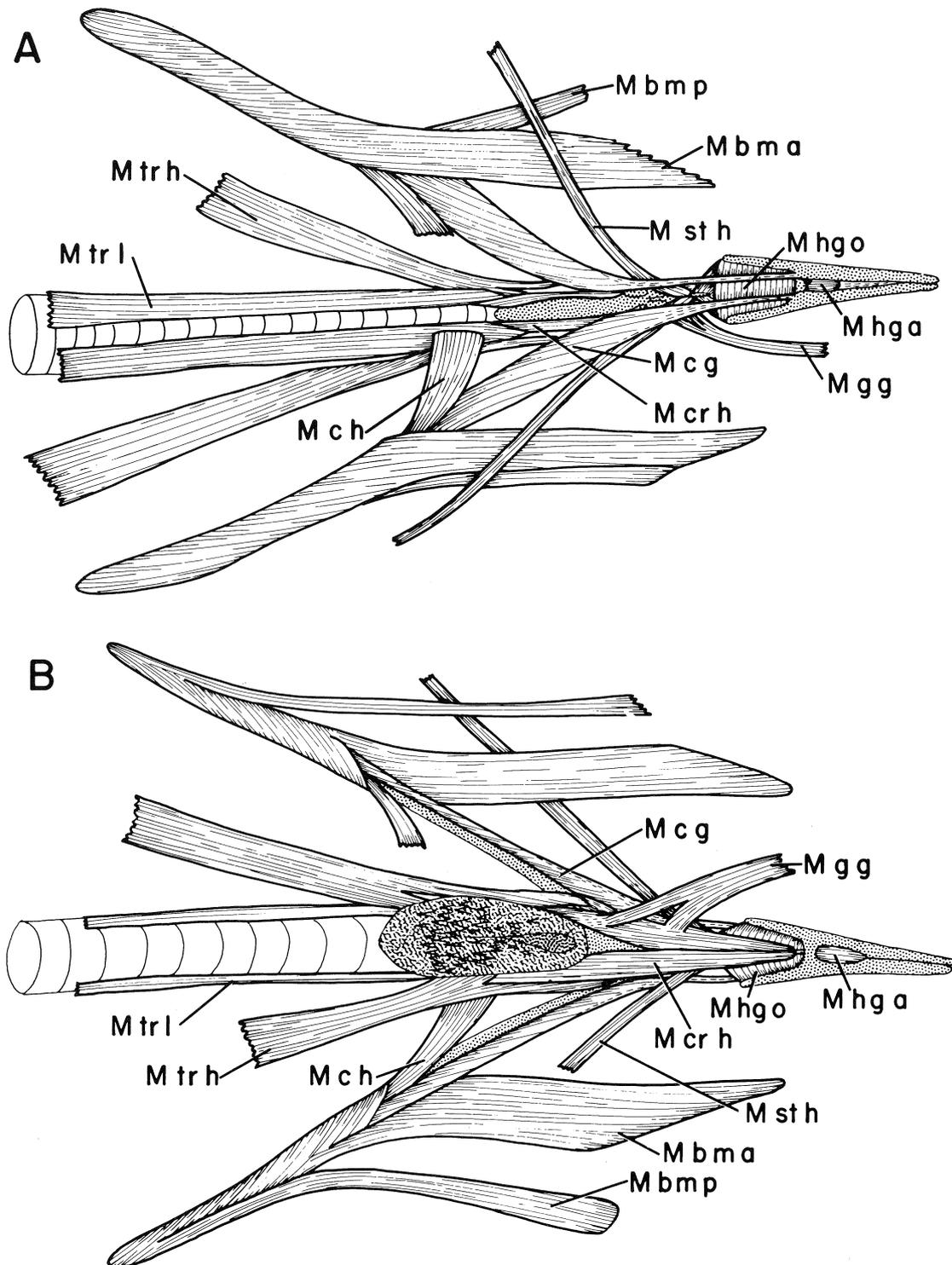
Fig. 12. Tongue muscles of *Atrichornis clamosus* in ventral (A) and dorsal (B) views. The M. mylohyoideus and M. serphihyoideus have been removed, the tongue and trachea dissected from the floor of the mouth and the structures spread out from the midline to show the individual muscles in greater detail.
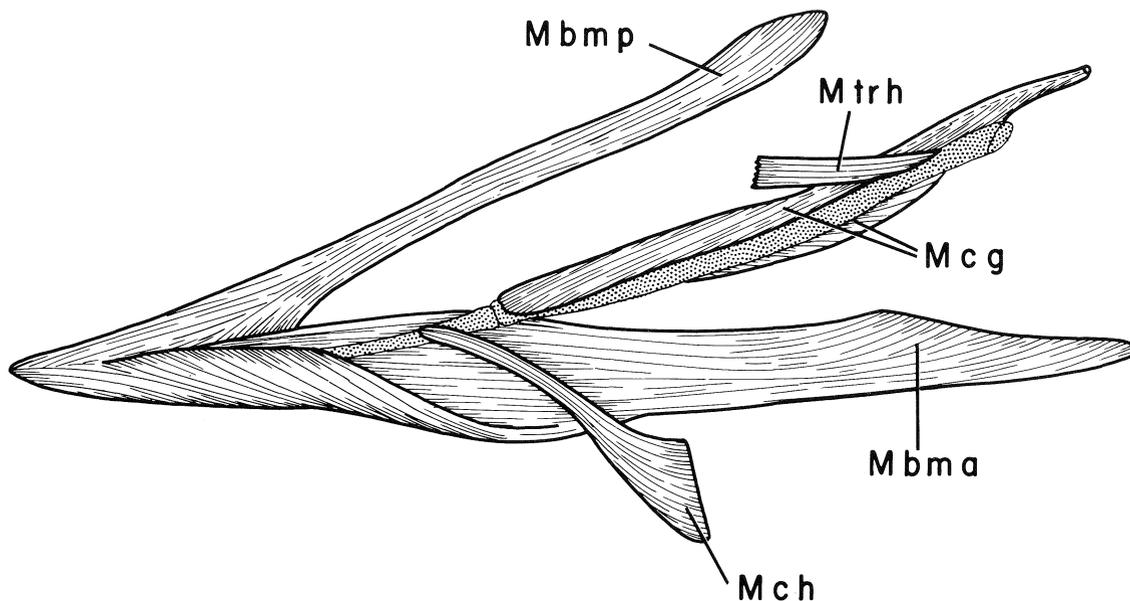
Fig. 13. Tongue muscles of *Atrichornis clamosus* in dorsal view to show the details of the muscles attaching to the hyoid horn; the muscles have been dissected and spread out for greater detail.

bone is slightly flattened laterally and has a distinct, sharp, ventral keel at its midpoint (Fig. 15).

Tongue Muscles

Atrichornis possesses all of the tongue muscles known for other passerine birds (Figs 3, 9, 10, 11, 12, 13, 14, 15 and 16). Two other muscles — the M. cucullaris and the M. dermotemporalis — will be described here because their dissection was done with that of the tongue muscles. The head of the *Atrichornis* specimen was severed from the neck before I received it. The cut was made at the occipital condyle at a level near the posterior edge of the M. cucullaris caput portion; hence it was not possible to trace any of the muscles into the neck. Most likely, the noncranial attachment of these muscles do not differ from those seen in other passerine birds. For purposes of drawing, the structures in the neck were extrapolated back for a short distance. Each muscle will be described individually but without special reference to the figures. See Bock (ms.) for a discussion of the functions of these muscles.

M. dermotemporalis (M dt). Origin is from the lateral surface of the brain case just behind the orbital rim (Fig. 3). The muscle runs posteriorly down the neck. It is covered by the M. cucullaris caput portion. The M. dermotemporalis is a parallel-fibred strap-like muscle with very long fibres. The fibre CSA is 2 mm² (4 mm wide × 0.5 mm thick).

M. cucullaris caput portion (M c c). Origin is from the dermis near the middorsal line of the posterior end of the brain case (Fig. 3). Insertion is on the contralateral muscle along the ventral midline of the head; actually, the fibres run continuously from origin to origin. The M. cucullaris is the most superficial

muscle of the head and difficult to separate from the overlying skin. It is about 8 mm wide and very thin, about 0.1-0.2 mm thick; giving a fibre CSA of about 1 mm². Fibres on each half of the muscles are about 35 mm long for a total length of 70 mm.

M. mylohyoideus (M m h). Origin is from the medial surface of the mandibular ramus just below its dorsal edge. Insertion is on a midventral raphe with the contralateral muscle. The muscle is 10 mm wide, measured at the midventral line, and is 0.1-0.2 mm thick for a fibre CSA of 1-1.5 mm². Fibre length (for each muscle) varies from 3 mm for the short anterior fibres to 6 mm for the longest posterior fibres.

M. serpihyoideus (M s h). Origin is from the lateral edge of the basitemporal plate, medial to the origin of the M d mandibulae. Insertion is on the contralateral muscle at the ventral midline with the anterior end of the muscle attaching to the posterior end of the M. mylohyoideus. Fibres are 10 mm long with a fibre CSA of 3.0-0.6 mm² (3 mm wide × 0.1-0.2 mm thick).

M. stylohyoideus (M st h). Half of the muscle originates from the basitemporal plate, along with the M. serpihyoideus, and half from the lateral edge of the mandibular ramus just anterior to the insertion of the M d mandibulae. It inserts on the ventral surface of the basihyale just anterior to the ceratobranchial articulation. Fibres are 15-18 mm long with a fibre CSA of 0.03 mm²-0.05 mm² (0.3-0.5 mm × 0.1 mm). The M. stylohyoideus is a thin, narrow, strap-like muscle and is vestigal in *Atrichornis*.

M. branchiomandibularis (M b m). This muscle has two parts — an anterior and a posterior — but they can be described together. The M b m anterior originates from the medial surface of the mandibular ramus, ventral to the origin of the M. mylohyoideus. The
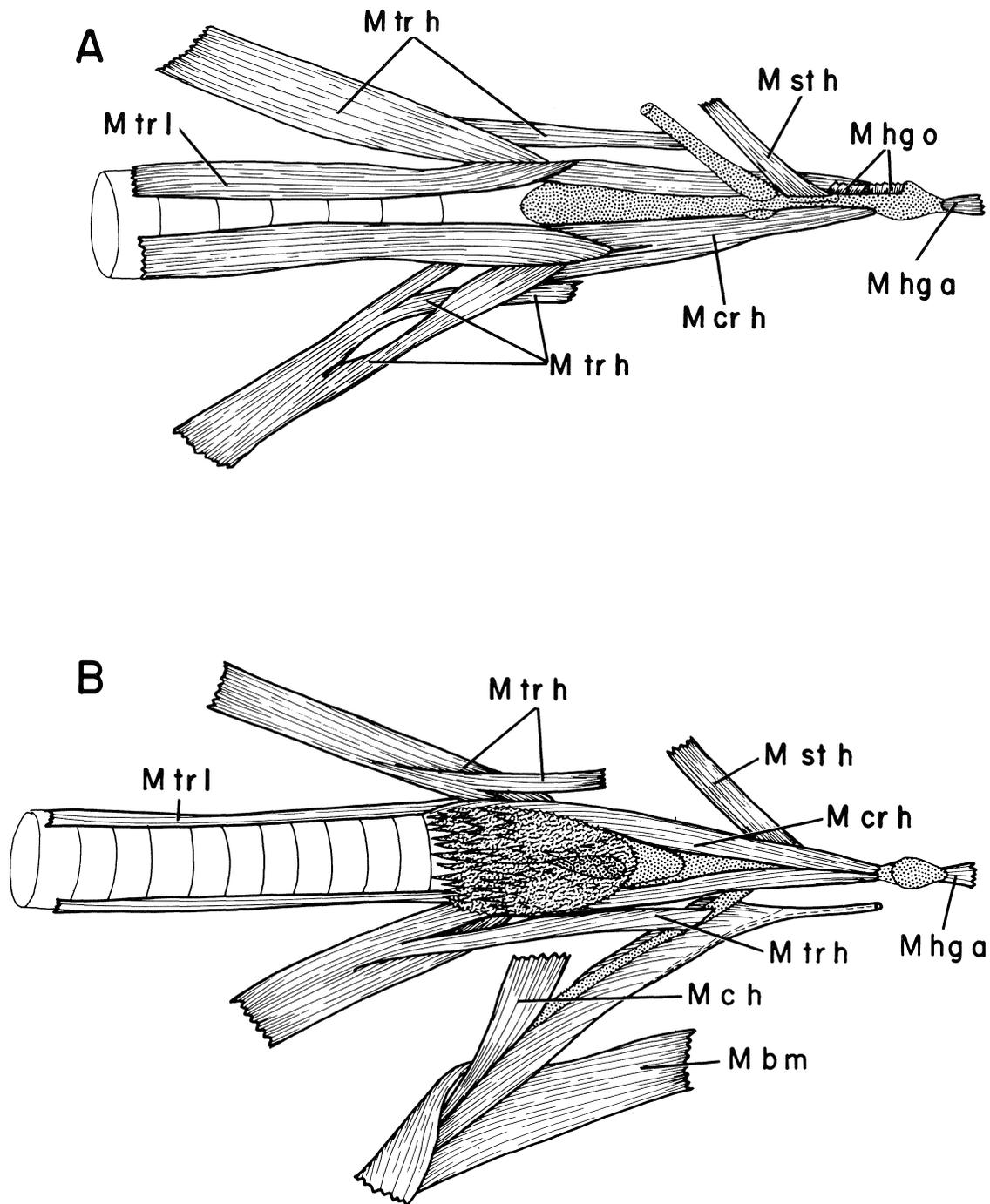
Fig. 14. Tongue muscles of *Atrichornis clamosus* in ventral view (A) and dorsal view (B) to show the details of the muscles attaching to the basihyale and the larynx. The paraglossalia and the left hyoid horn have been removed.

M b m posterior originates from the ventral edge of the mandible, ventral to the anterior half of the M a m e vetralis. Both parts merge and insert on the distal end of the epibranchiale. The M. branchiomandibularis is a parallel-fibred muscle which wraps about the hyoid horn to encase these bones completely. Fibres are 20–25 mm long with a fibre CSA of 1 mm² (2 mm × 0.5 mm) for the larger anterior part and 0.55 mm² (0.75 mm × 0.75 mm) for the smaller posterior portion.

M. ceratahyoideus (M ch). Origin is from the dorsolateral surface of the epibranchiale just above the ceratobranchial articulation. Insertion is with the contralateral muscle on the midventral line, dorsal to the posterior end of the M. mylohyoideus. The insertion of the M. ceratohyoideus is bound to that of the overlying M. mylohyoideus and M. serpihyoideus. The M. ceratohyoideus passes dorsal to the epibranchiale as it extends from its origin to insertion. It is a parallel-
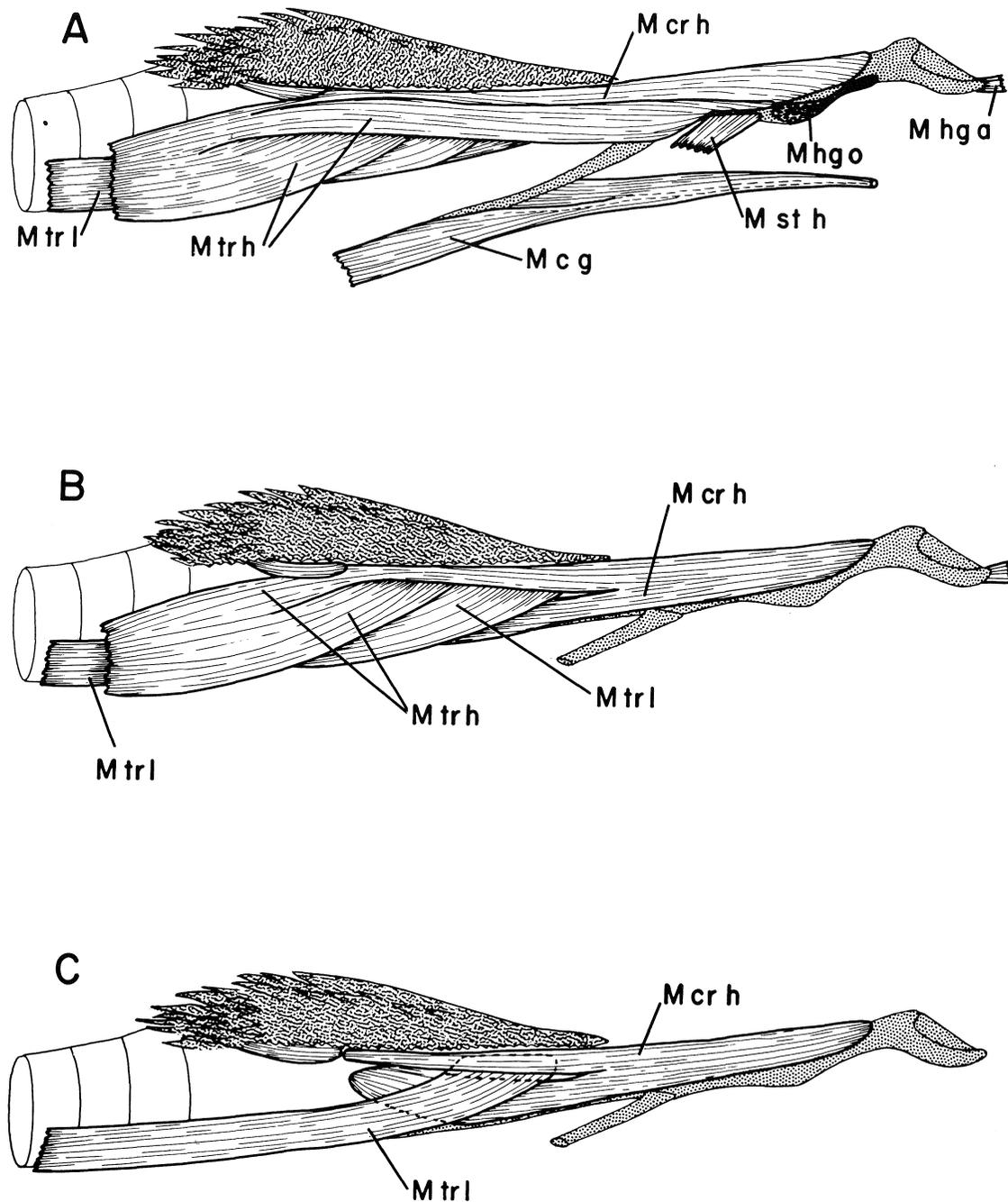
Fig. 15. Tongue muscles of *Atrichornis clamosus* in lateral view in successively deeper levels (A–C) to show the details of the muscles attaching to the basihyale and the larynx. The paraglossalia and most of the hyoid horn have been removed.

fibred, strap-like muscle (slightly fan-shaped) with fibres 7 mm long and a fibre CSA of 0.18–0.28 mm² (maximum, 0.3–0.4 mm × 0.6–0.7 mm). The muscle is 2 mm wide at its insertion.

M. genioglossus (M g g). Origin is from the posterior edge of the mandibular synthesis (Fig. 10B). Insertion is by several slips into the mucosa between the tongue and the glottis (Fig. 11), but not to the paraglossale. The M. genioglossus lies superficial to other tongue muscles at its insertion. Parallel fibres of

this strap-like muscle are 10–12 mm long and have a fibre CSA of 0.06–0.08 mm² (0.3–0.4 mm × 0.2 mm).

M. ceratoglossus (M c g). Origin is along the whole length of the ceratobranchiale, mainly from the ventral surface but partly from the lateral surface. All fibres attach pinnately to a stout tendon lying on the ventrolateral edge of the muscle and attaching to the medioventral corner of the paraglossale just anterior to the basihyale articulation. The M c hyoideus is a unipinnate, two-joint muscle 16 mm long, 1.5 mm wide
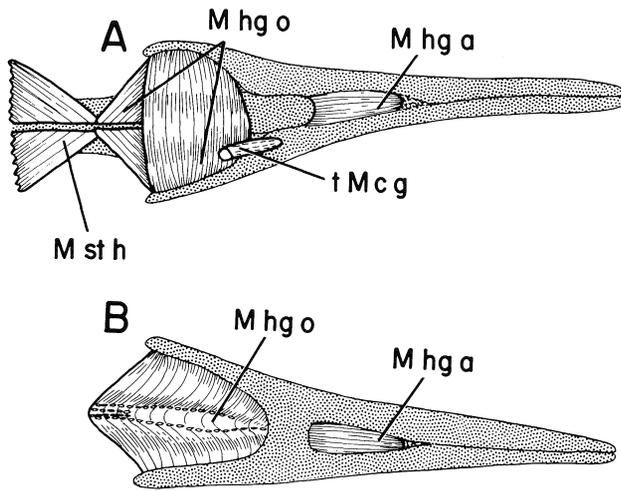
Fig. 16. Tongue muscles of *Atrichornis clamosus* in ventral (A) and dorsal (B) views to show the details of the muscles attaching to the paraglossalia.

and 0.8–1.0 mm thick. Fibres are 4–5 mm long and the fibre CSA is approximately 15 mm² (10 mm × 1.5 mm).

M. hypoglossus obliquus (M hg o). Origin is from the medioventral surface of the entire posterior process of the paraglossale. The ventral fibres pass ventral to the basihyale from origin to origin, while the deeper (dorsal) fibres insert on the basihyale; perhaps one-fourth of the M. hg obliquus inserts on the basihyale. The M hg obliquus has two indistinctly separable parts. Most fibres are parallel and lie transversely to the longitudinal axis of the tongue. A posterior portion has fibres lying sharply obliquely to the anterior fibres. Although this posterior part appears to be very distinct in ventral view (Fig. 16A), this distinction fades when one dissects through the muscle or examines the muscle in dorsal view (Fig. 16B). Fibre length is 3 mm (origin to origin) or 1–1.5 mm from origin to insertion on basihyale. The fibre CSA is 1–1.5 mm² (2 mm wide × 0.5–0.75 mm thick).

M. hypoglossus anterior (M hg a). Origin is from the ventral tendinous sheath that binds the two paraglossalia together. All fibres insert on the anterior tip of the basihyale between the two paraglossalia; no fibres insert on the paraglossale. The M hg anterior is a single medial muscle with no signs of a division into two muscles as in most passerine birds. All fibres are parallel to the longitudinal axis of the tongue. Fibres are 1.55 mm long with a fibre CSA of 0.15 mm² (0.55 mm wide × 0.03 mm thick).

M. cricohyoideus (M cr h). Origin is from the dorsolateral edge (small head) and from the ventrolateral surface (large head) of the cricoid (Fig. 15). The two heads of origin of the M cr hyoideus are separated by the insertion of part of the M tr hyoideus and the insertion of the M tr lateralis. The larger ventral head of the M cr hyoideus passes deep (medially) to the inserting end of the M tr lateralis. A few fibres from

the dorsal edge of the M tr hyoideus merge into the dorsal head of the M cr hyoideus. The two heads of the muscle merge close to the anterior end of the cricoid and insert on the dorsal surface of the basihyale just off the middorsal line and just posterior to the paraglossale articulation. It is a parallel-fibred, strap-like muscle with fibres 19–20 mm long and a fibre CSA of about 1 mm² (1 mm × 1 mm). The M. cricohyoideus is the main retractor of the tongue in *Atrichornis* because of the vestigial nature of the M st hyoideus.

M. tracheohyoideus (M tr h). Origin was severed from head in this speicmen, but is presumably similar to that seen in other passerine birds, i.e., from the surface of the M. pectoralis or from the furcula. It inserts via three different slips. The largest slip, which comprises approximately the ventral three-fourths of the muscle, inserts on the ventrolateral surface of the cricoid, just posterior to the insertion of the M tr lateralis. The second slip, about one-fourth of the muscle, runs forward to insert on the lateral surface of the proximal end of the ceratobranchiale, with a few fibres running forward to insert on the basihyle. A small number of fibres from the dorsal edge of the muscle comprise the third slip and merge into the dorsal head of the M cr hyoideus. This strap-like, parallel-fibred muscle has very long fibres that extend from the furcula to the anterior end of the trachea, and has a fibre CSA of 0.5–1.0 mm² (2 mm wide × 0.3–0.5 mm thick).

M. tracheolateralis (M tr l). Origin was severed from head in this specimen, but presumably is from the syringeal aponeurosis as in *Menura* (see Ames, 1971). Insertion is on ventrolateral surface of the cricoid, approximately at the level of the anterior end of the glottis; it lies over the ventral head of the M cr hyoideus (Fig. 15C). This strap-like, parallel-fibred muscle has very long fibres (same approximate length as those of the M tr hyoideus) and has a fibre CSA of 0.6–1.00 mm² (2 mm wide × 0.3–0.5 mm thick).

DISCUSSION

Only limited comparisons could be made between *Atrichornis* and *Menura*, and no meaningful ones between *Atrichornis* and other passerine birds because of time restrictions; these studies have been planned and will be reported on in the future. A few conclusions can be presented now on the cranial osteology and on the tongue musculature.

Comparison of the skull of *Atrichornis* with that of *Menura* shows a number of similarities as well as differences; most are hard to evaluate. Most of the similarities could be as easily attributed to general passerine resemblance as to a reflection of close affinity of these genera. Many of the differences may be associated with the much larger size of *Menura* which has a skull about 3 times that of *Atrichornis* in linear measurements.

One feature that is shared by the two birds is the large, free lacrymal that articulates dorsally with the frontal, ventrally with the jugal and medially with the ectethmoid plate; it is not fused with any of these neighbouring bones. The morphology of the lacrymal does differ in these two genera, with the bone being smaller and with a much reduced dorsal head in *Atrichornis*. The large, free lacrymal of *Atrichornis* and *Menura* is very unusual for passerine birds; otherwise found only in the bowerbirds (Ptilonorhychidae; Stoner, 1937; Bock, 1963). Although the lacrymal of *Menura* is quite similar to that seen in the bowerbirds, as first pointed out by Stoner, the lacrymal of *Atrichornis* differs considerably from that of the bowerbirds. Moreover, aside from the lacrymal, the overall morphology of the skull of both *Atrichornis* and *Menura* differs markedly from that of the bowerbirds, compared to the range of variation of skull morphology seen in all passerine birds, in spite of the claim by Sibley (1974) that the skull of *Menura* is, overall, similar to that of the bowerbirds.

A reasonable functional-adaptive explanation for the large lacrymal in *Menura*, *Atrichornis* and the bowerbirds cannot be offered at present.

The morphology of the skull provides support, although not very strong, for the close relationship of *Atrichornis* to *Menura*. Granting the close similarity of the lacrymal in *Menura* and in the bowerbirds, the cranial osteology does not offer, at this time, any special support for the conclusion postulated by Sibley (1974, 1976; Sibley & Ahlquist, 1985, in press) that lyrebirds are close relatives of the bowerbirds and are part of the Australian 'corvine assemblage'.

The jaw muscles offer almost no information on the possible evolutionary history and on the affinities of *Atrichornis* at the current state of our knowledge; however, the tongue muscles exhibit several peculiar attributes and permit some comments on the status of *Atrichornis*. These conclusions depend upon a broad comparative study of the tongue musculature that I have made, but is mainly unpublished (Bock, ms.). They will not permit an assessment of the taxonomic position of *Atrichornis*, only an indication of the evolutionary change in its tongue morphology from that of other oscine birds. I will not give reasons supporting conclusions on the primitiveness versus advancedness of different configurations of the tongue musculature, or of possible reversals of change, largely because most of my conclusions are not based on really convincing arguments (see Bock, 1977 for a discussion of methods and Bock, ms. for a discussion of the diversity seen in passerine tongue muscles).

The M. genioglossus has two slips of insertion in most passerine birds, one to the psoterolateral surface of the paraglossale and one to the mucosa between the tongue and the glottis. The former insertion is lacking in a number of species, some with very different feeding habits as, for example, *Coccothraustes* and *Arachnothera*. I suspect that presence of the paraglossal insertion is primitive in passerine birds and that its loss

is advanced, but cannot eliminate the possibility of reevolving the paraglossal insertion once it has been lost.

The M. stylohyoideus is the main retractor of the tongue in passerine birds, but has become vestigial in a few genera in the Meliphagidae with the M. cricohyoideus or a digastric M. stylohyoideus-serpihoideus becoming the main tongue retractor. These forms are nectarivorous with relatively long protrusion and retraction of the tongue. The vestigial M. stylohyoideus in *Atrichornis* is puzzling because this bird has a short tongue with no evidence of long protraction and retraction. The vestigial condition of this muscle would be advanced, but reversed evolutionary change would be easily possible so long as the muscle does not disappear completely.

In most passerine birds possessing a M. hypoglossus anterior, this muscle arises from the midventral connective tissue between the paraglossalia and inserts on the paraglossale, anterior to the attachment of the M. ceratoglossus. Insertion to this muscle to the anterior end of the basihyale is one of the several advanced states of the M hg anterior and is seen in *Dicaeum*, *Oedistoma* and *Promerops*. Usually, only part of the muscle inserts on the basihyale. Complete insertion of the M hg anterior on the basihyale in *Atrichornis* is advanced, but reversed evolution to an insertion on the paraglossale appears to be easily possible.

Generally, in passerine birds, the M. hypoglossus obliquus passes beneath the basihyale without inserting on this bone; the muscle forms a sling between the two paraglossalia. Insertion of the M hg obliquus on the basihyale is found in *Dicaeum*, *Passer*, *Coereba*, some emberizines, fringillids and drepanidids among others. (In most New World nine-primaried oscines, the M hg obliquus *does not* insert on the basihyale.) Insertion of the M hg obliquus on the basihyale appears to be advanced and I suspect that reversed evolutionary change to the sling-like structure is improbable because the inserting muscle appears to have all the functions and adaptive advantages of the sling-like arrangement. The partly inserting arrangement in *Atrichornis* would be advanced. The semidivision of this muscle is probably also advanced.

Typically, in passerine birds, the M. ceratohyoideus originates from the medial surface of the posterior end of the ceratobranchiale; this appears to be the primitive condition. In a few genera, e.g. *Corvus* and *Moho*, part or all of this muscle arises from the lateral surface of the ceratobranchiale. In a few, the origin of the muscle extends to the epibranchiale. The origin of the M c hyoideus from the dorsolateral surface of the epibranchiale in *Atrichornis* appears to be advanced.

Insertion of the M. tracherhyoideus, in part or completely, on the anterior end of the ceratobranchiale is found in a few passerine birds, e.g. *Corvus*, *Nucifraga* and other corvoids, and appears to be the primitive condition. In most passerines, most or all of the M tr hyoideus inserts on the cricoid, with few or no fibres extending to the ceratobranchiale; this appears to be the advanced condition. It is unclear whether a

ceratobranchial insertion of this muscle can reevolve once it has been lost. The condition in *Atrichornis* thus appears to be relatively primitive, but has almost reached the advanced stage seen in most other passerine birds.

The other tongue muscles in *Atrichornis* do not have a structure that can be assigned clearly to a primitive or an advanced state. In addition to the musculature, it should be mentioned that the flattened keel of the basihyale is most likely advanced compared to the cylindrical basihyale seen in most passerine birds.

Thus, *Atrichornis* possesses five aspects of the tongue musculature and one of the tongue skeleton which appear to be advanced, and one which is somewhat primitive. These advanced features of the tongue morphology are not consistent with the widely held belief (see Bock & Clench, 1985) that the *Menurae*, the suborder of suboscines to which *Atrichornis* has been placed, is a primitive group of passerine birds compared to the other oscines. Indeed, the tongue musculature of *Atrichornis* is remarkably advanced compared to that seen in most other genera of passerine birds which I have examined.

CONCLUSIONS

Skull morphology, namely the large free lacrymal that articulates with the frontal, provides some, but not very strong support for the generally accepted conclusion that *Atrichornis* is closely related to *Menura* (Bock & Clench, 1985). Little support exists from the osteology of the skull to support the hypothesis that these genera are closely related to *Menura* (Bock & Clench, 1985). Little support exists from the osteology of the skull to support the hypothesis that these genera are closely related to the bowerbirds (Ptilonorhynchidae). The morphology of the skeletomuscular system of the tongue suggests that *Atrichornis* has undergone considerable evolutionary change from the primitive passerine condition, but the functional and adaptive reasons for these advances are obscure.

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A female Noisy Scrub-bird *Atrichornis clamosus* at nest (photo G. Chapman, CSIRO Wildlife Research).