

Original Article

Myology and osteology of the Whooper Swan *Cygnus cygnus*
(Aves : Anatidae)

Part 2. Muscles of the jaws, tongue and anteriormost neck

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Abstract: This is the second paper on the myology and osteology of the Whooper Swan *Cygnus cygnus* and deals with the muscles of the cranium and most anterior neck. The material is the same dead swan used in the first paper (Matsuoka and Hasegawa, 2007). All major muscles and ligaments were examined to check the attachments (origin and insertion) on the bones. The skull and mandible of the Bewick's Swan *Cygnus columbianus* were used to check the relationship between the bone structure and the attaching muscles and ligaments. The detailed osteology of the Whooper Swan is figured as the result of this study.

Key Words: Anatidae, Whooper Swan, *Cygnus cygnus*, Myology, Osteology, cranial muscles

Introduction

The cranial anatomy of the waterfowl (Anatidae) was described in detail by Goodman and Fisher (1962). Nevertheless, a study of the detailed cranial osteology is still required because the book by Goodman and Fisher (1962) does not include good osteological figures. Furthermore, a description of the tongue muscles should cover all the elements, yet Goodman and Fisher (1962) only include the superficial ones.

Here, the authors continue the research of Matsuoka and Hasegawa (2007), in which the anatomy of the pectoral and humeral regions of the Whooper Swan were described. In this second paper the cranial muscles and their attachment to the bones are examined and figured.

The material used in the present study is the same individual as in the previous paper: a male *Cygnus cygnus* which died in a zoo aged at least 21 years, pickled in a solution of approximately 5 % formalin, and housed in the Gunma Museum of Natural History (specimen number VA-04-02).

In this study, the ligaments and muscles were removed one by one from the surface to the deeper layers of the skinned head. An osteological specimen of the skull and mandible of the Bewick's Swan *Cygnus columbianus* was used to check the relationship between bone structure, such as muscle attachment scars, and the attaching soft tissues during the examination. The osteological figures of the Whooper Swan and the Bewick's Swan are shown in Fig. 7. As the result of this study, Fig. 8 is prepared to see the origins and insertions of all cranial muscles.

The nomenclature of the muscles of the jaw follows Goodman and Fisher (1962). For the other muscles (muscles of the tongue and anteriormost neck) and ligaments, the terminology of Baumel (1979a, b) and Vanden Berge (1979) is used. Where there is a difference in nomenclature between authors, alternatives are indicated as synonyms. Alternative names used by George and Berger (1966) are included in the latter. Osteological nomenclature is adapted from Howard (1929) and Baumel (1979).

Muscles of the jaw

(Figs. 1, 2, 3-A)

M. adductor mandibulae externus superficialis

A-portion. : The most posterodorsal of the three portions (Figs. 1, 2). The Ia (*levator anguli oris*) portion of Goodman and Fisher (1962). The origin is aponeurotic dorsally in the lateral surface and is fleshy in the deeper fibers. Arises from a wide area in the ventral edge of the postorbital process, the temporal fossa (Fig. 2-b; area 2 of Fig. 8), and the dorsoanterior margin of the soft tissue around the external acoustic meatus. Inserts on a small area of the dorsolateral surface of the lower jaw (area 14 of Fig. 8), which is anterodorsal to the lateral coronoid process. The lateral surface of the lateral coronoid process is covered by the tendon of this muscle.

B-portion. : Anteroposteriorly, the central portion among the three portions (Figs. 1, 2). The Ib (inner part) portion of

Goodman and Fisher (1962). The dorsal half (the region which is above the level of the jugal when the jaws are closed) is deeper than the A- and C-portions in their anterior and posterior borders, respectively. This state of the posterior border is different to that noted by Goodman and Fisher (1962).

Arises tendinously from the ventral surface of the tip (but slightly posterior because the origin of the C-portion attaches to the anteriormost region) of the postorbital process. Inserts by fleshy fibers on the lateral surface of the mandible anterior to the lateral coronoid process (Fig. 2-b; area 12 of Fig. 8). *Ramus mandibularis* emerges on the lateral surface of this muscle in the mid-anterior region of the muscle's insertion point.

C-portion. : The Ic (*retractor anguli oris*) portion of Goodman and Fisher (1962). The anteriormost superficial adductor muscle and as wide as the B-portion (Figs. 1 and 2). Arises tendinously and by fleshy fibers from the tip of the ventral surface of the postorbital process, anterior to the origin of the B-portion. Inserts

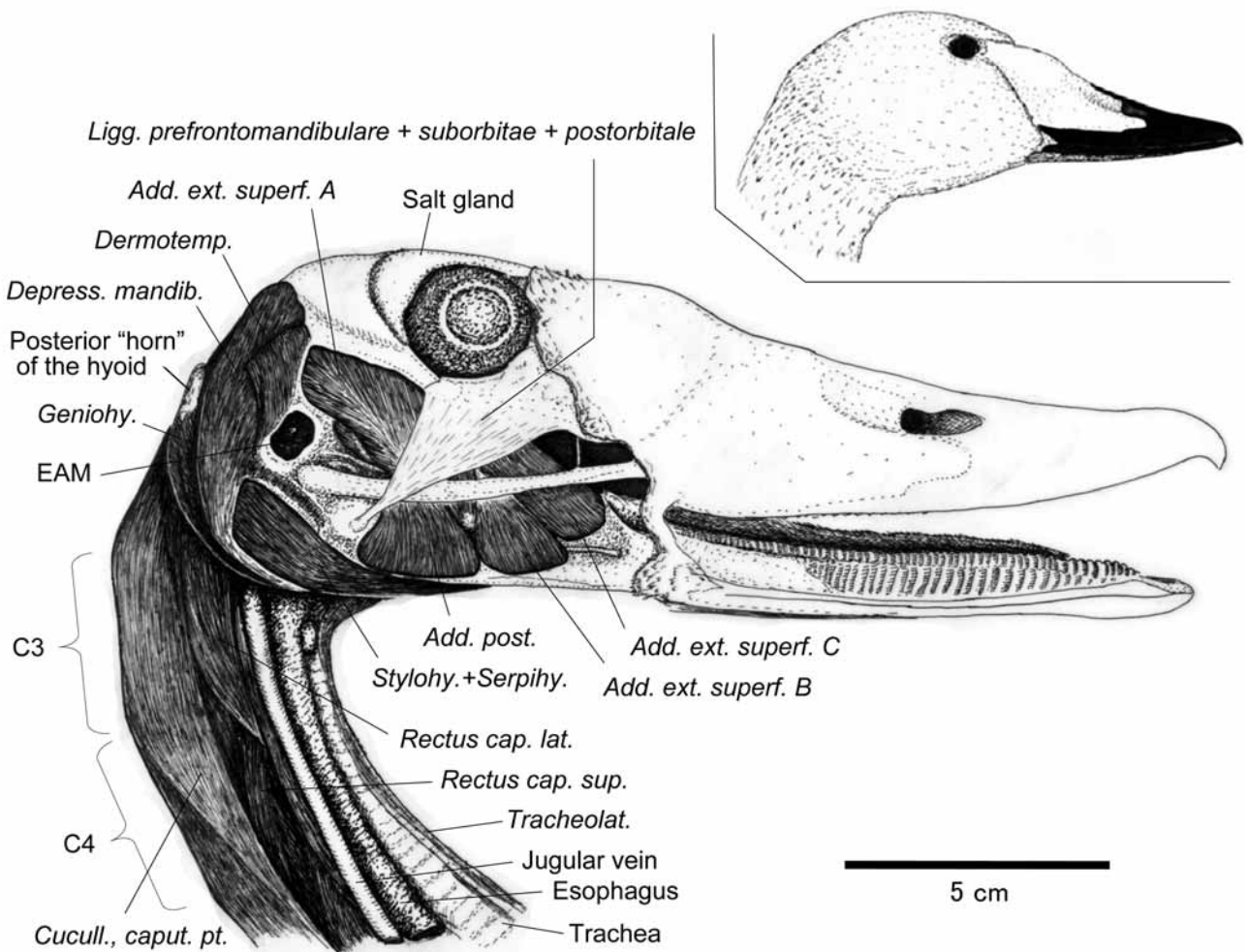


Figure 1 The feathered head (top right) and the skinned head (the main figure with scale bar) of the Whooper Swan *Cygnus cygnus*.

Abbreviations: Add. ext. superf. : *M. adductor mandibulae externus superficialis*, A-C: A- to C-portions of this muscle. Add. post. : *M. adductor mandibulae posterior*. C3, C4: the positions of 3rd and 4th cervical vertebrae. Cucull. caput. pt. : *M. cucullaris caput part*. Depress. mandib. : *M. depressor mandibulae*. Dermotemp. : *M. dermatemporalis*. EAM: External acoustic meatus. Geniohy. : *M. geniohyoideus* = *M. branchiomandibularis*. Rectus cap. lat. : *M. rectus capitis lateralis*. Rectus cap. sup. : *M. rectus capitis superior*. Serpihy. : *M. serpihyoideus*. Stylohy. : *M. stylohyoideus*. Tracheolat. : *M. tracheolateralis*.

by tendon on the dorsal margin of the anterior region of the coronoid process and by fleshy fibers on the lateral surface of the lower jaw (area 11 of Fig. 8). Its tendinous insertion on the coronoid process forms the anterior corner (*Angulus mandibulae* by Baumel, 1979a) of this process.

M. adductor mandibulae externus medialis

Deeper than the A- and B-portions of *M. adductor mandibulae externus superficialis* (Fig. 2-B). Arises by fleshy fibers from the boat-shaped depression in the roof of the ventral surface of the postorbital process (area 20 of Fig. 8). Inserts tendinously on the dorsal margin and lateral surface of the posterior region of the coronoid process (area 13 of Fig. 8). Its tendinous insertion on the coronoid process forms the posterior projection of this process. The wide insertion on the lateral surface is also strong and creates lines for the tendinous attachment on the surface of the coronoid process.

Goodman and Fisher (1962) labeled this muscle "M. II" in

their text and figures.

M. adductor mandibulae posterior

Synonym : *M. adductor mandibulae caudalis* (Vanden Berge, 1979).

Triangular in lateral view when the superficial A-portion of *M. adductor mandibulae externus superficialis* covering the dorsal region is removed (Fig. 2-B). This muscle and the *M. adductor mandibulae externus profundus* appear almost fused and are therefore difficult to separate.

Arises tendinously from the anterior edge of the tip of the orbital process of the quadrate (Fig. 3-A; area 9 of Fig. 8). Inserts by fleshy fibers on the lateral surface of the mandible posterior to the lateral coronoid process (area 15 of Fig. 8).

M. adductor mandibulae externus profundus

Arises by fleshy fibers from the lateral side of the dorsal margin of the quadrate (Figs. 2-B, 3-A), between the tips of the

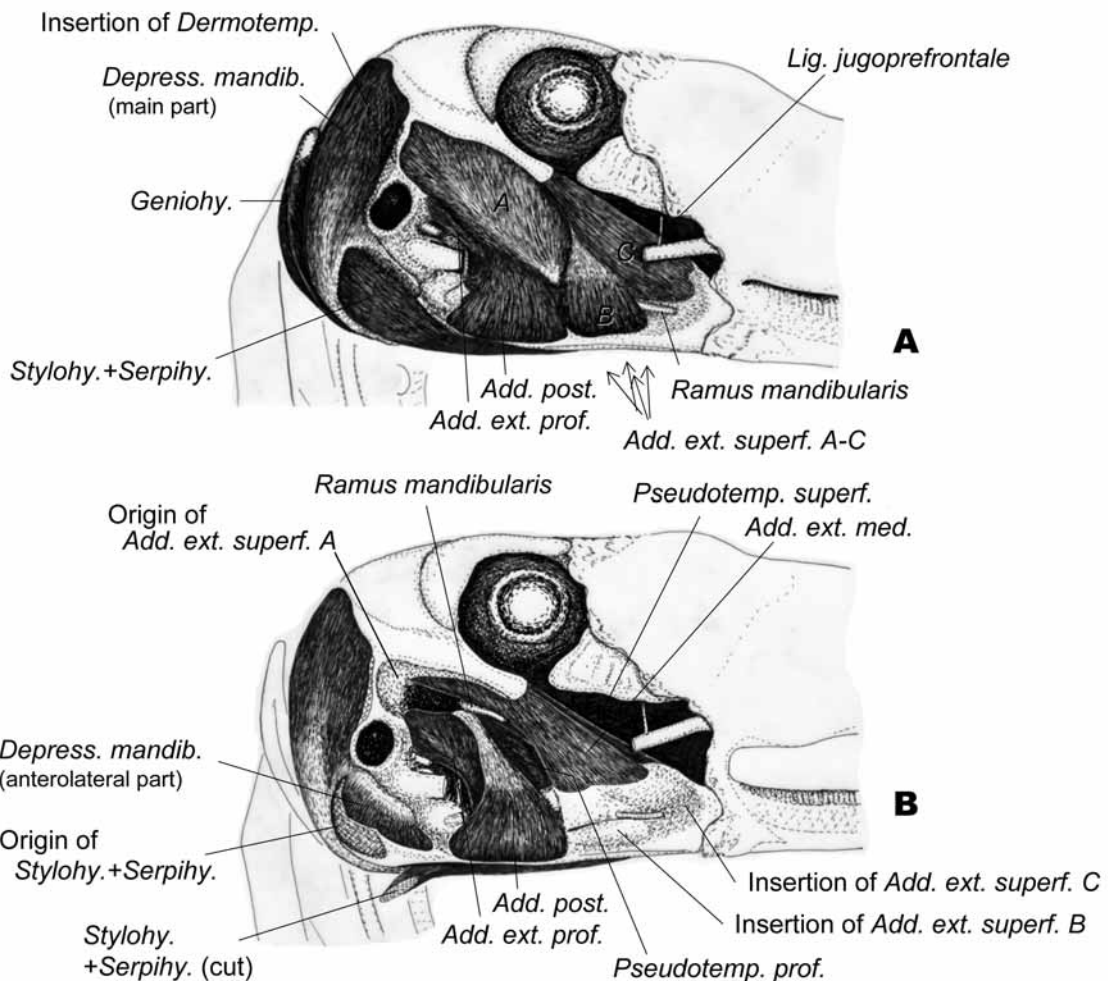


Figure 2 The superficial (A) and deeper (B) jaw muscles of the Whooper Swan *Cygnus cygnus*.

Abbreviations: Add.ext.med.: *M. adductor mandibulae externus medialis*. Add.ext.prof.: *M. adductor mandibulae externus profundus*. Add.ext.superf.: *M. adductor mandibulae externus superficialis*, A-C: A- to C-portions of this muscle. Add.post.: *M. adductor mandibulae posterior*. Depress.mandib.: *M. depressor mandibulae*. Dermotemp.: *M. dermotemporalis*. Geniohy.: *M. geniohyoideus* = *M. branchiomandibularis*. Pseudotemp.superf.: *M. pseudotemporalis superficialis*. Serpiphy.: *M. serpihyoideus*. Stylohy.: *M. stylohyoideus*.

orbital process and the otic process (area 10 of Fig. 8). The belly attaches widely on the lateral surface of the quadrate. Inserts both tendinously and by fleshy fibers on a small area just anterior to the glenoid of the mandible, where it faces dorsolaterally (area 16 of Fig. 8). Goodman and Fisher (1962) labeled this muscle "M. III" in their text and figures.

M. pseudotemporalis superficialis

Deeper than the C-portion of *M. adductor mandibulae externus superficialis* and *M. adductor mandibulae externus medialis*.

Arises by fleshy fibers and tendinously from the ventromedial surface of the postorbital process (Fig. 3-A; area 21 of Fig. 8). Inserts tendinously on the dorsal region of the medial surface of the entire coronoid process (area 30 of Fig. 8).

M. pseudotemporalis profundus

Deep to *M. adductor mandibulae posterior* for the most part

and to *M. adductor mandibulae externus medialis* in its anterior region (Fig. 2-B).

Arises by fleshy fibers from the anterior marginal surface of the quadrate (Fig. 3-A; area 8 of Fig. 8). Inserts by fleshy fibers on the dorsal margin and on the dorsal region of the medial surface of the lower mandible, the area anterior to the insertion of *M. pterygoideus dorsalis medialis* and posterior to the course of *Ramus mandibularis* (area 34 of Fig. 8).

M. pterygoideus ventralis lateralis

The pterygoideus muscle portions are superficial on the ventromedial view of the head when the spinose epidermis of the deep mouth is removed. *M. pterygoideus ventralis lateralis* is much more slender than the *medialis* portion.

Arises by fleshy fibers from the basal (relatively lateral) region of the ventral surface of the internal articular process of the lower jaw (area 37 of Fig. 8). Inserts by a long tendon on the

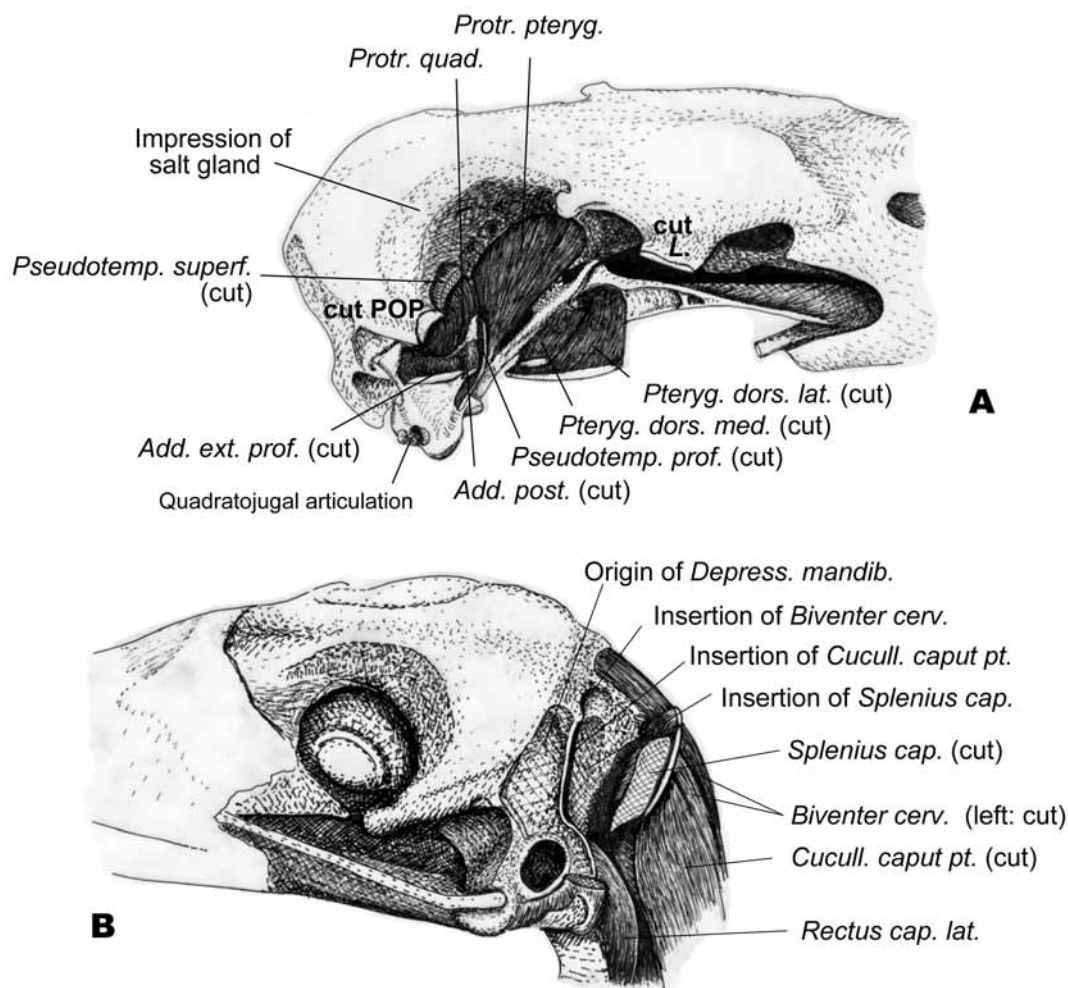


Figure 3 The deep muscles of jaw (A) and the anterior-most neck muscles (B) of the Whooper Swan *Cygnus cygnus*.

Abbreviations: Add. ext. prof. : *M. adductor mandibulae externus profundus*. Add. post. : *M. adductor mandibulae posterior*. Biventer cerv. : *M. biventer cervicis*. Cucull. caput pt. : *M. cucullaris, caput part.* Depress. mandib. : *M. depressor mandibula*. Protr. pteryg. : *M. protractor pterygoideus*. Protr. quad. : *M. protractor quadratus*. Pseudotemp. prof. : *M. pseudotemporalis profundus*. Pseudotemp. superf. : *M. pseudotemporalis superficialis*. Pteryg. dors. lat. : *M. pterygoideus dorsalis lateralis*. Pteryg. dors. med. : *M. pterygoideus dorsalis medialis*. Rectus cap. lat. : *M. rectus capitis lateralis*. Splenius cap. : *M. splenius capitis*.

epidermal tissue in the area lateral to the internal nares (Fig4-B) .

M. pterygoideus ventralis medialis

Arises by fleshy fibers from the medial region of the dorsal surface of the internal articular process, where it is strongly impressed (area 38 of Fig. 8) . Inserts by fleshy and aponeurotic fibers on the ventromedial surface of the entire length of the pterygoid and of the caudal one-third of palatine bones (area 28 of Fig. 8) .

M. pterygoideus dorsalis lateralis

A large muscle visible in the medial surface of the mandible when the tongue and trachea complex has been removed (Figs. 3-A, 4-B) . The caudal margin is in contact with the insertion of the ventromedial part of *M. depressor mandibulae*.

Arises by fleshy fibers and tendinously from the laterodorsal surface and lateroventral margin of the caudal one-fifth of the palatine (area 6 of Fig. 8) and by aponeurotic fibers from the anterior end of the lateroventral margin of the pterygoid. Therefore, the main origin is on the palatine bone, although it is called the *pterygoideus*. Inserts by fleshy fibers and tendinously on the medial surface of the lower jaw, on the area of the ventral region anterior to the caudal border of the internal articular process and is caudal to the origin of *M. geniohyoideus* (area 35 of Fig. 8) . The insertion mostly by fleshy fibers is wide but the tendon attaches only on its ventrocaudal corner.

M. pterygoideus dorsalis medialis

A smaller portion deeper than the *lateralis* portion (Fig. 3-A) . Arises tendinously from the ventral region of the anterior half of

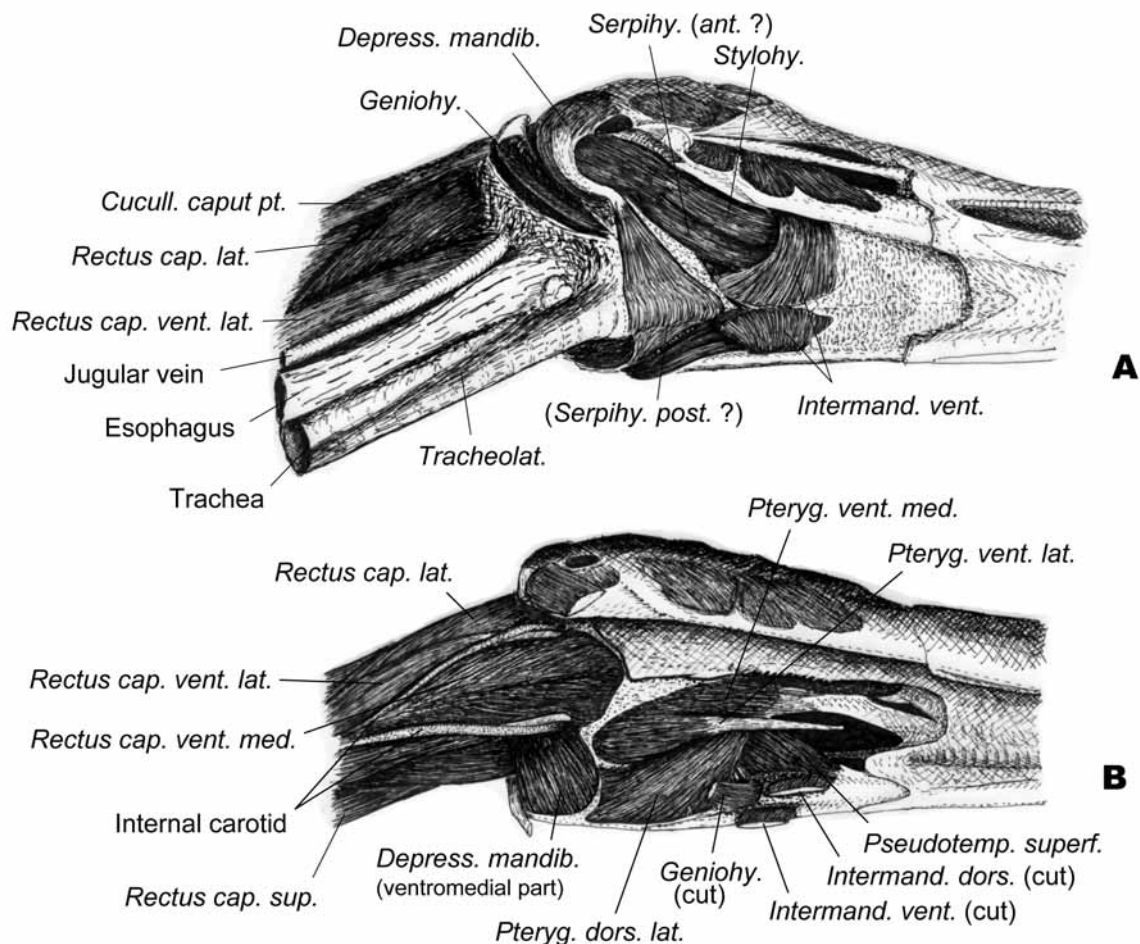


Figure 4 The superficial muscles in the ventrolateral view of the skinned head (A) and the deep jaw and anterior-most neck (B) of the Whooper Swan *Cygnus cygnus*.

Abbreviations: Cucull. caput. pt. : *M. cucullaris caput part.* Depress. mandib. : *M. depressor mandibulae.* Geniohy. : *M. geniohyoideus* = *M. branchiomandibularis.* Intermand. dors. : *M. intermandibularis dorsalis.* Intermand. vent. : *M. intermandibularis ventralis.* Pseudotemp. superf. : *M. pseudotemporalis superficialis.* Pteryg. dors. lat. : *M. pterygoideus dorsalis lateralis.* Pteryg. vent. lat. : *M. pterygoideus ventralis lateralis.* Pteryg. vent. med. : *M. pterygoideus ventralis medialis.* Rectus cap. lat. : *M. rectus capitis lateralis.* Rectus cap. sup. : *M. rectus capitis superior.* Rectus cap. vent. lat. : *M. rectus capitis ventralis lateralis.* Rectus cap. vent. med. : *M. rectus capitis ventralis medialis.* Serpihy. : *M. serpihyoideus.* Stylohy. : *M. stylohyoideus.* Tracheolat. : *M. tracheolateralis.*

the lateral surface of the pterygoid (area 7 of Fig. 8) . Inserts by fleshy fibers on the area under the *cotyla medialis* of the medial surface of the lower jaw (area 36 of Fig. 8) .

M. protractor pterygoideus

Vanden Berge (1979) considered this muscle and *M. protractor quadratus* as two parts of one muscle, *M. protractor pterygoidei et quadrati*. This paper follows Goodman and Fisher (1962) , as the origins of these two muscles are distinguishable.

M. protractor pterygoideus is a large muscle in the bottom of the orbit, visible when the eyeball has been removed (Fig. 3-A) . Arises by fleshy fibers widely from the interorbital septum (the area 22 of Fig. 8) . Inserts tendinously on the caudal end of the dorsomedial surface of the pterygoid.

M. protractor quadratus

Caudal to *M. protractor pterygoideus*. Arises widely by fleshy fibers from the area between the *Foramen n. ophthalmici* and *F. n. maxillomandibularis*, where it faces anterolaterally and is the most ventral area of the orbit (area 23 of Fig. 8) . Inserts by fleshy fibers on the entire medial surface of the orbital process of the quadrate and the impression is deep and large (area 29 of Fig. 8) .

M. depressor mandibulae

A large muscle in the laterocaudal region of the skinned head. In this paper, this muscle is subdivided into three parts which are named the main, anterolateral and ventromedial parts (Figs. 2, 4) .

The main part arises widely by fleshy fibers from the laterocaudal surface of the cranium (area 4 of Fig. 8) and continues ventrally on the lateral surface of the base of the opisthotic process, then inserts tendinously on the caudal margin of the posterior articular process of the lower jaw.

The anterolateral part arises aponeurotically from the lateral surface of the lateral part of *Lig. occipitomandibulare*. The insertion of the anterolateral part sandwiches the dorsal part of the base of the posterior articular process. Its lateral part inserts by fleshy fibers on the area 17 of Fig. 8. The fibers on the other side, the medial insertion of the anterolateral part, were not able to be distinguished from the inserting ventromedial part.

The ventromedial part arises by fleshy fibers from the medial surface of the opisthotic process (area 27 of Fig. 8) . It inserts by fleshy fibers on the entire area of the medial surface of the posterior articular process (area 39 of Fig. 8) , and the insertion extends into the large and deep "cave" which is under the jaw articulation. This part of the *M. depressor mandibulae* surrounds the *Lig. occipitomandibulare*.

Muscles of the tongue

(Figs. 4-A, 5, 6)

M. intermandibularis ventralis

Synonym : *M. mylohyoideus* (George and Berger, 1966) .

A superficial, very thin muscle. The anterior border does not cover the anterior region of *M. intermandibularis dorsalis*. Anterior to this muscle, the superficial layer of the skinned lower jaw in ventral view is formed by fatty fibers.

Arises by fleshy fibers from just above the ventral border of the medial surface of the lower jaw in the region anteroposterior to the level of the coronoid process (area 32 of Fig. 8) . The right and left sheets of this muscle connect by aponeurosis in the midline for insertions. The posterior end of this inserting aponeurosis is in touch with the anterior end of the insertion of *M. serpihyoideus*.

M. intermandibularis dorsalis

Synonym : *M. mylohyoideus* (George and Berger, 1966) .

Arises by fleshy fibers from the medial surface of the lower jaw, the small area dorsoanterior to the origin of *M. branchiomandibularis* and ventral to the insertion of *M. pseudotemporalis superficialis* (area 31 of Fig. 8) . Inserts by fleshy fibers on the cartilage which is ventral to the anterior half of the urohyal.

M. serpihyoideus

M. serpihyoideus and *M. stylohyoideus* are fused in their origins. The large fleshy muscle arises from the lateral surface of the posterior articular process of the lower jaw and turns to the inserting ventral aspect of the head in the position of roughly under the external articular process. The *M. serpihyoideus* is ventral to the *M. stylohyoideus* in the originating lateral aspect of the head and is medial in the ventral aspect. The bellies of *M. serpihyoideus* and *M. stylohyoideus* are independent in the ventral aspect of the head.

Arises by fleshy fibers from the lateral surface of the posterior articular process (area 18 of Fig. 8) . The caudal margin of the posterior articular process itself is the insertion of the main part of *M. depressor mandibulae* and the origin of this muscle plus the fused *M. stylohyoideus* is just anterior to the margin. Inserts by aponeurosis on the ventral surface of the junction of the posterior basihyal and the anterior urohyal and ceratobranchial, where it is deeper than the ventral and dorsal elements of *M. intermandibularis* and *M. hypoglossus obliquus*.

Note : A superficial, extremely thin muscle is found posterior to the above described recognizable muscle and superficial *M. intermandibularis ventralis*. This vestigial muscle sheet arises tendinously from the ventral corner of the ventrocaudal margin

of the posterior articular process of the lower jaw (area 18 of Fig. 8). The other part of the originating tendinous fibers extend caudomedially and connect with the inserting main part of *M. depressor mandibulae*. The right and left sheets of this muscle connect by aponeurosis in the midline for insertions and the insertion wraps around the larynx. This is the most posterior muscle that contributes to raising the tongue and trachea. The authors could not find a name or related description of this muscle. This is possibly the posterior portion of *M. serpihyoideus*, which means that the above described muscle should be labeled as *M. serpihyoideus anterior*, but this muscle needs to be investigated further.

M. stylohyoideus

Fused with *M. serpihyoideus* in the origin on the lateral aspect of the head, but is separate where it inserts on the ventral aspect of the head. *M. stylohyoideus* is anterior to *M. serpihyoideus* in the originating lateral aspect of the head and is lateral in the ventral aspect.

Arises by fleshy fibers from the lateral surface of the PAP of

the lower jaw (area 19 of Fig. 8). In the ventral aspect of the head, this muscle passes longitudinally the position lateral to *M. serpihyoideus* and the deeper *M. ceratoglossus*, ventromedial to the inserting *M. branchiomandibularis*, and dorsomedial to *M. intermandibularis dorsalis*. Inserts by fleshy fibers on the dorsal surface of the anterior part of urohyal bone, where is anterior to the ceratobranchial articulation (area 5 of Fig. 6).

M. branchiomandibularis

Synonym : *M. geniohyoideus* (George and Berger, 1966; Goodman and Fisher, 1962).

An easily recognizable muscle which wraps around the base of the posterior "horn" of the hyoid. The belly, arising from the medial surface of the mandible, passes dorsally to *M. stylohyoideus* and appears on the postero-caudal part of the head, between the insertions of *M. depressor mandibulae* and *M. rectus capitis lateralis*.

Arises by fleshy fibers from the prearticular area of the medial surface of the lower jaw (area 33 of Fig. 8). Inserts on the circumference of the entire epibranchial except for the tip (area 9 of Fig. 6).

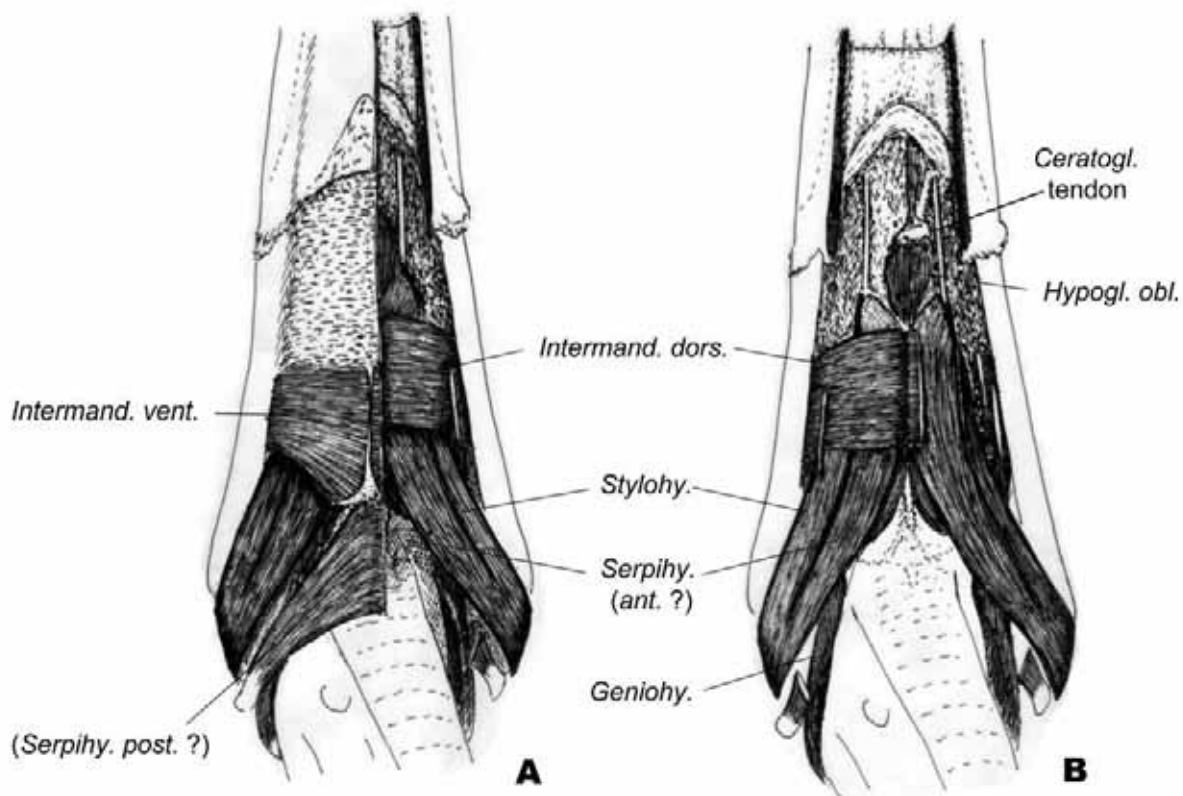


Figure 5 The muscles of the tongue of the Whooper Swan *Cygnus cygnus*: the superficial (A) and shallow (B) layers.

Abbreviations: Ceratogl. : *M. ceratoglossus*. Geniohy. : *M. geniohyoideus* = *M. branchiomandibularis*. Hypogl. obl. : *M. hypoglossus obliquus*. Intermand. vent. : *M. intermandibularis ventralis*. Intermand. dors. : *M. intermandibularis dorsalis*. Serpihy. ant. : *M. serpihyoideus anterior*. Serpihy. post. : *M. serpihyoideus posterior*. Stylohy. : *M. stylohyoideus*.

M. interceratobranchialis

Synonym : *M. ceratohyoideus* (George and Berger, 1966; Goodman and Fisher, 1962) .

Arises by fleshy fibers from the almost entire ventromedial surface of the ceratobranchial and the anteriormost part of epibranchial (area 8 of Fig. 6) . Inserts the ventral surface of the urohyal (area 6 of Fig. 6) .

M. ceratoglossus

A long muscle lateral to the *M. interceratobranchialis* . Arises by fleshy fibers from the dorsolateral surface of the entire ceratobranchial and the anterior-most 10 mm or so of the epibranchial (area 7 of Fig. 6) . Anterior to the anterior end of ceratobranchial, this muscle connects to a strong tendon and inserts

on the lateral margin of the basihyal .

M. hypoglossus obliquus

A small, shallow muscle in the position of the ventral base of the tongue. Arises tendinously from the ligament connecting the anterior tips of the ceratobranchial and urohyal bones. Inserts by fleshy fibers on the anterior end of the ventral surface of the urohyal .

M. hypoglossus rostralis

Synonym : *M. hypoglossus anterior* (George and Berger, 1966) .

The caudal origin of this muscle is in connection with the anterior insertion of *M. hypoglossus obliquus* . Arises tendinously from the caudal end of the ventral surface of the basihyal .

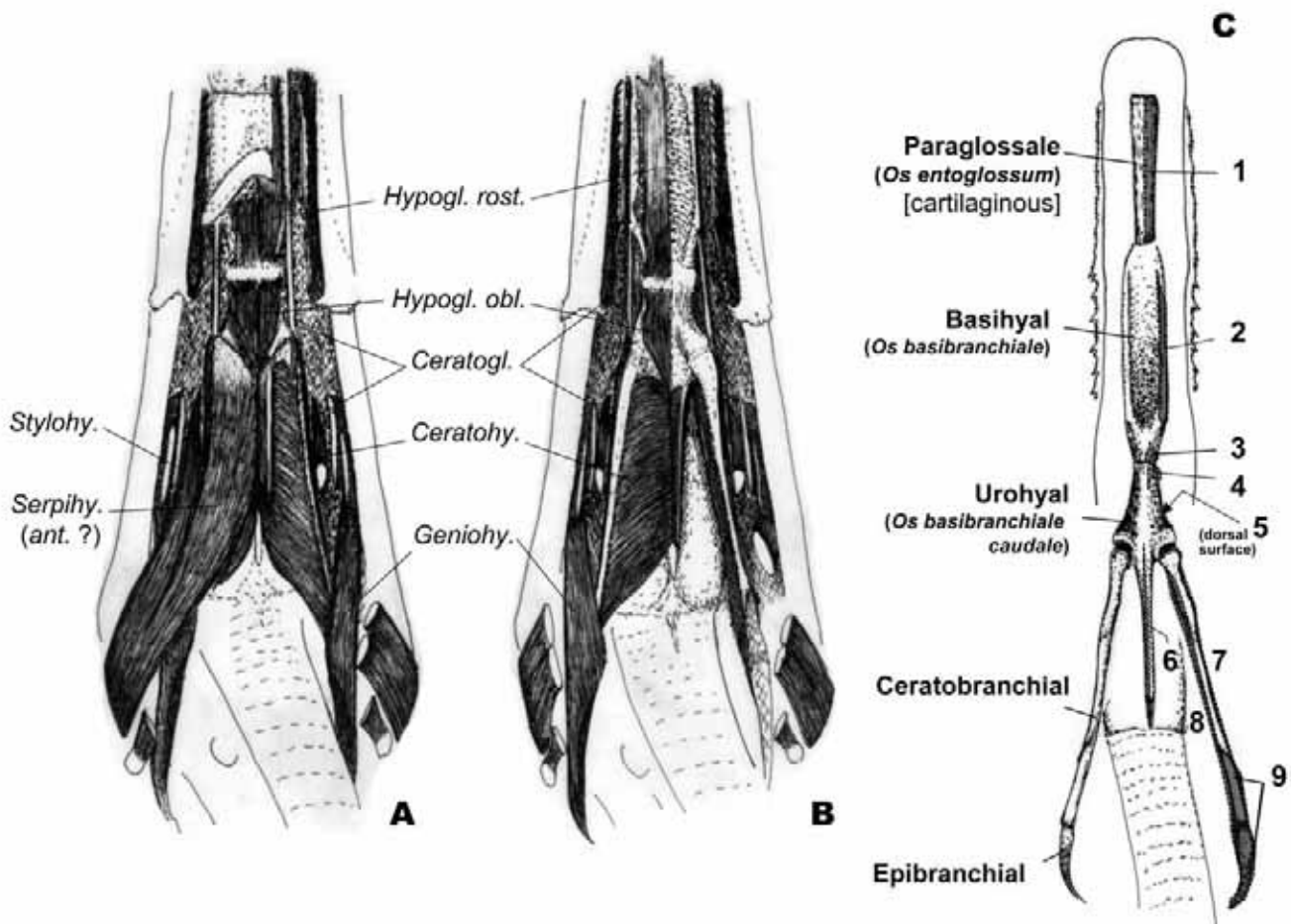


Figure 6 The muscles of the tongue, the deep (A) and deepest (B) layers, and the ventral view of the bones of tongue (C) of the Whooper Swan *Cygnus cygnus* .

1: Insertion of *M. hypoglossus rostralis* . 2: The anterior continuation of the tendinous insertion of *M. ceratoglossus* . 3: Origin of *M. hypoglossus rostralis* . 4: Insertion of *M. hypoglossus obliquus* . 5 (the dorsal surface of the anterior part of urohyal bone) : Insertion of *M. stylohyoideus* . 6: A strong tendon that acts as the origin of *M. hypoglossus obliquus* and the insertion of *M. interceratobranchialis* . 7 (the lateral surface of entire ceratobranchial) : Origin of *M. ceratoglossus* . 8 (the dorsomedial surface of entire ceratobranchial and the anterior end of epibranchial) : Origin of *M. interceratobranchialis* . 9 (the ventral surface of the posterior end of ceratobranchial and around the epibranchial) : Insertion of *M. branchiomandibularis* (= *M. geniohyoideus*) .

Abbreviations: Ceratogl. : *M. ceratoglossus* . Geniohy. : *M. geniohyoideus* = *M. branchiomandibularis* . Hypogl. obl. : *M. hypoglossus obliquus* . Hypogl. rostr. : *M. hypoglossus rostralis* . Serpihy. ant. : *M. serpihyoideus anterior* . Stylohy. : *M. stylohyoideus* .

Passes the ventral surface of the basihyal and inserts by a strong tendon on the anterior cartilaginous midline hyoid.

Muscles of the anterior most neck

(Figs. 1, 3-B, 4)

M. cucullaris capitis

Synonym : *M. dermatemporalis* (Goodman and Fisher, 1962) .

This is the most superficial muscle of the neck and is closely connected with the skin. The origin of this muscle is from the skin. A more thorough dissection should reveal that this muscle covers the muscles of the neck. However, only the anterior (insertion) portion was removed from the skin and figured in this study. The cut portion covers the anterior part of *M. depressor mandibulae* in the area dorsal to the external acoustic meatus. Inserts by fleshy fibers to the crest between the temporal fossa and the impression of the origin of *M. depressor mandibulae* (dorsal half) and the continuous soft tissue around the external acoustic meatus.

M. cucullaris, caput part (Goodman and Fisher, 1962)

A superficial, flat and wide muscle which rises from the anterior cervical vertebrae. Inserts laterally to the insertion of *M. biventer cervicis*. The insertion is on the conspicuous crest, which is posterior to the impression of the origin of *M. depressor mandibulae* and runs dorsoventrally in the middle of the parietal area.

M. biventer cervicis

A long and slender muscle in the dorsal midline of the neck. Superficial only anterior to and in the region around the third vertebra, caudally being placed in between the right and left *M. cucullaris, caput part*. Inserts by fleshy fibers on the medial region, just lateral to the sagittal line, of the dorsal-most part of the cranium.

M. splenius capitis

A thick muscle generally deeper than *M. cucullaris, caput part*. Arises from the dorsal surface of the two anterior vertebrae, the

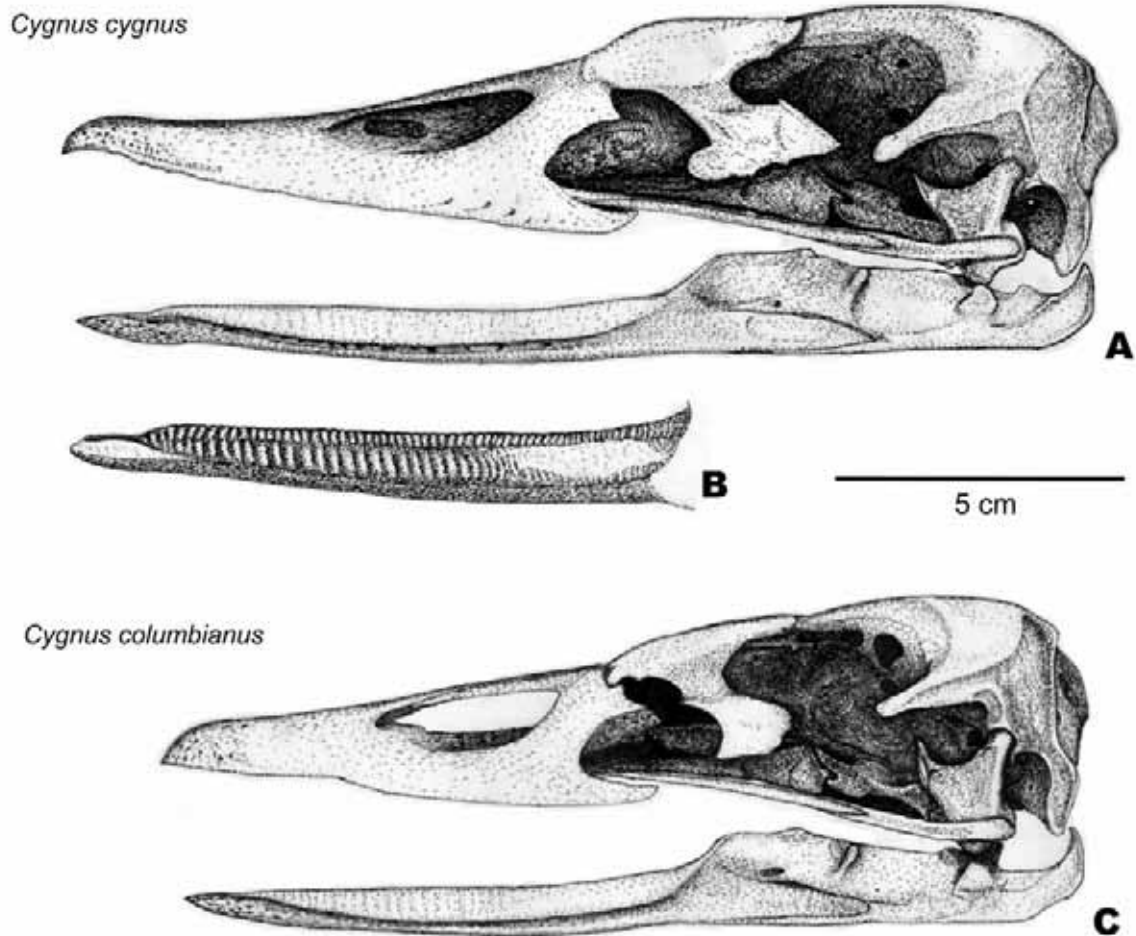


Figure 7 The skulls of swans. The skull (A) and epidermal lower bill (B) of the Whooper Swan *Cygnus cygnus*. C: The skull of Bewick's Swan *Cygnus columbianus*.

dorsal surface of the atlas and the anterior edge of the neural crest of the axis. Inserts by fleshy fibers widely on the area posterior to the conspicuous crest which is the insertion point of *M. cucullaris, caput part*. The area of insertion of *M. splenius capitis* is the lateral two-thirds or more of the posterior surface

of the cranium, and the supraoccipital region does not include the attachment points for any muscles.

M. rectus capitis lateralis

A superficial muscle in the ventrolateral region of the anterior

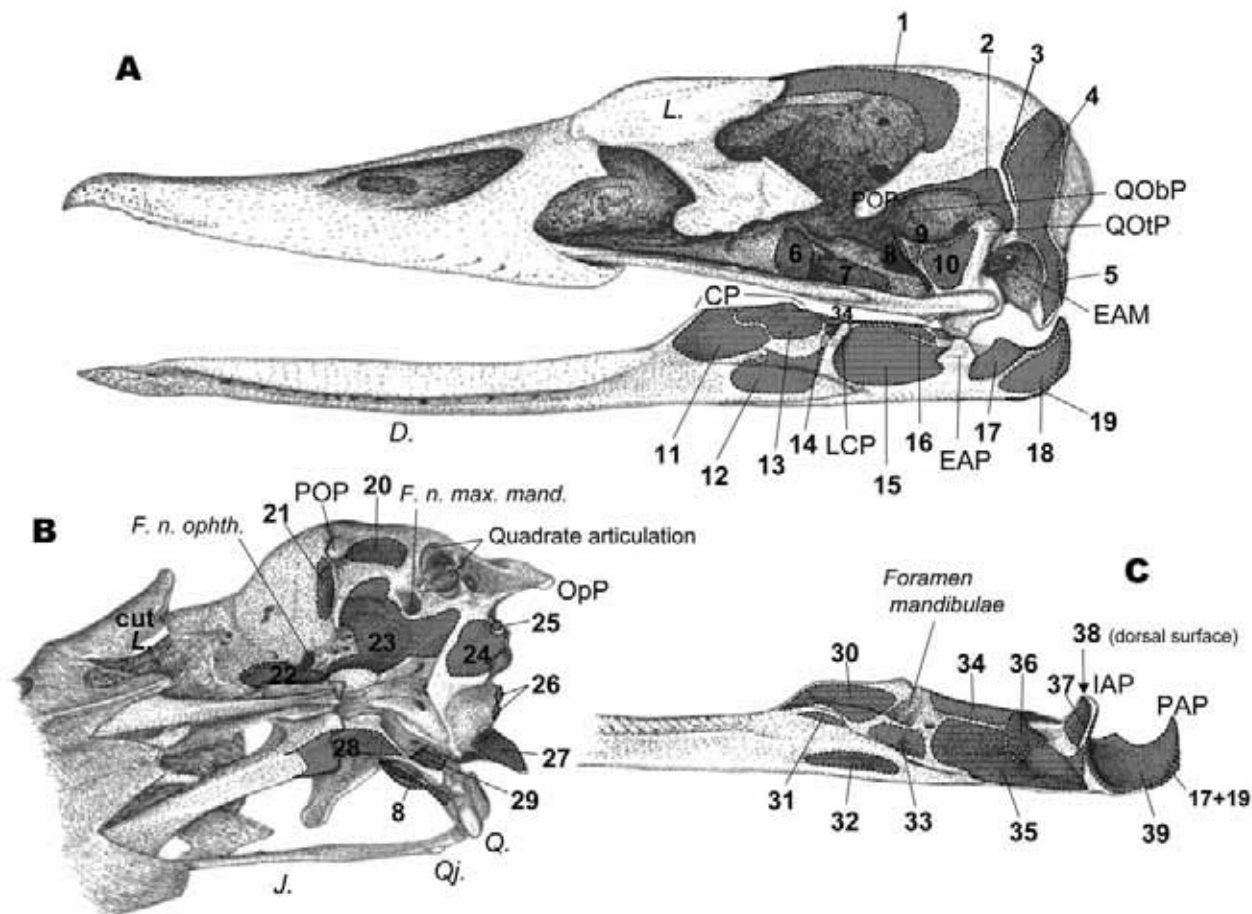


Figure 8 The cranial osteology of the Whooper Swan *Cygnus cygnus*.

1: Impression of the salt gland (*Glandula nasalis*). 2: Origin of the A-portion of *M. adductor mandibulae externus superficialis*. 3: Insertion of *M. dermatotemporalis*. 4: Origin of *M. depressor mandibulae*. 5: Insertion of *M. rectus capitis lateralis* on the caudal surface. 6: Origin of *M. pterygoideus dorsalis lateralis*. 7: Origin of *M. pterygoideus dorsalis medialis*. 8: Origin of *M. pseudotemporalis profundus* from the marginal anterior surface of quadrate. 9: Origin of *M. adductor mandibulae posterior*. 10: Origin of *M. adductor mandibulae externus profundus*. 11: Insertion of the C-portion of *M. adductor mandibulae externus superficialis*. 12: Insertion of the B-portion of *M. adductor mandibulae externus superficialis*. 13: Insertion of *M. adductor mandibulae externus medialis*. 14: Insertion of the A-portion of *M. adductor mandibulae externus superficialis*. 15: Insertion of *M. adductor mandibulae posterior*. 16: Insertion of *M. adductor mandibulae externus profundus*. 17: Insertion of the anterolateral part of *M. depressor mandibulae*. 18: Origin of *Mm. serpihyoideus + stylohyoideus*. 19: Origin of *M. ? serpihyoideus posterior*. 20: Origin of *M. adductor mandibulae externus medialis*. 21: Origin of *M. pseudotemporalis superficialis*. 22: Origin of *M. protractor pterygoideus*. 23: Origin of *M. protractor quadratus*. 24: Insertion of *M. rectus capitis ventralis medialis*. 25: Insertion of *M. rectus capitis ventralis lateralis*. 26: Insertion of *M. rectus capitis superior*. 27: Origin of the ventromedial part of *M. depressor mandibulae*. 28: Insertion of *M. pterygoideus ventralis medialis*. 29 (the medial surface of quadrate): Insertion of *M. protractor quadratus*. 30: Insertion of *M. pseudotemporalis superficialis*. 31: Origin of *M. intermandibularis*. 32: Origin of *M. intermandibularis ventralis*. 33: Origin of *M. branchiomandibularis (= M. geniohyoideus)*. 34: Insertion of *M. pseudotemporalis profundus* (partly continuous to the lateral surface). 35: Insertion of *M. pterygoideus dorsalis lateralis*. 36: Insertion of *M. pterygoideus dorsalis medialis*. 37: Origin of *M. pterygoideus ventralis lateralis*. 38: Origin of *M. pterygoideus ventralis medialis*. 39: Insertion of the ventromedial part of *M. depressor mandibulae*.

Abbreviations: CP: Coronoid process. D.: Dentary. EAP: External articular process. F. n. max. mand.: *Foramen nervus maxillomandibularis*. F. n. ophth.: *Foramen nervus ophthalmici*. IAP: Internal articular process. J.: Jugal. L.: Lachrymal. LCP: Lateral coronoid process. OpP: Opisthotic process. PAP: Post articular process. POP: Postorbital process. Q.: Quadrate. QObP: Orbital process of quadrate. QOtP: Otic process of quadrate.

of the neck. Arises from the hypophyses of the anterior cervical vertebrae. Inserts on the posterior (caudal) surface (Fig. 3:6) of the opisthotic process.

M. rectus capitis superior

Deep muscle in the lateroventral neck. The origins that are from the lateral processes of the several anterior most cervical vertebrae were not well examined in this study and only the insertion on the cranium was dissected. This muscle inserts by two adjacent tendons on the posterolateral edge, where there is a two-knobbed basitemporal plate (area 26 of Fig. 8).

M. rectus capitis ventralis

This ventral neck muscle consists of two portions: *pars lateralis* and *pars medialis*. *Pars lateralis* inserts by tendon on the lateral knob of the basitemporal plate (area 25 of Fig. 8). *Pars medialis* inserts by fleshy fibers on the entire surface of basitemporal plate (area 24 of Fig. 8).

Some ligaments and membranes

Ligg. prefrontomandibulare + suborbitae + postorbitale

The Whooper Swan has a wide, triangular sheet of ligament

on the lateral surface of the skinned head (Fig. 1). This comprises of the *Lig. prefrontomandibulare* (*Lig. lacrimomandibulare* by Goodman and Fisher, 1962), *Lig. suborbitae* and *Lig. postorbitale* ligaments fused together.

This subcutaneous, wide ligament connects between the two anterodorsal attachments and tapers towards the external articular process of the lower jaw. One of the two anterodorsal attachments is on the lateral surface of the ventral part of the lachrymal, where the attachment surface is broad, while the other is on the tip of the postorbital process of the frontal. The *Ligg. prefrontomandibulare + postorbitale* keeps the lower jaw from being retracted against the cranium. *Lig. suborbitae* is the ventral border of the orbit and reinforces the lacrimal bone.

Lig. jugoprefrontale

The lacrimo-jugal ligament of Goodman and Fisher (1962). A short ligament attaching dorsally on the medial surface of the lacrimal and caudally on a point in the anterior jugal.

Lig. occipitomandibulare

The *neurocranio-mandibular* ligament of Goodman and Fisher (1962). As its medial part, the strong sheet of this ligament

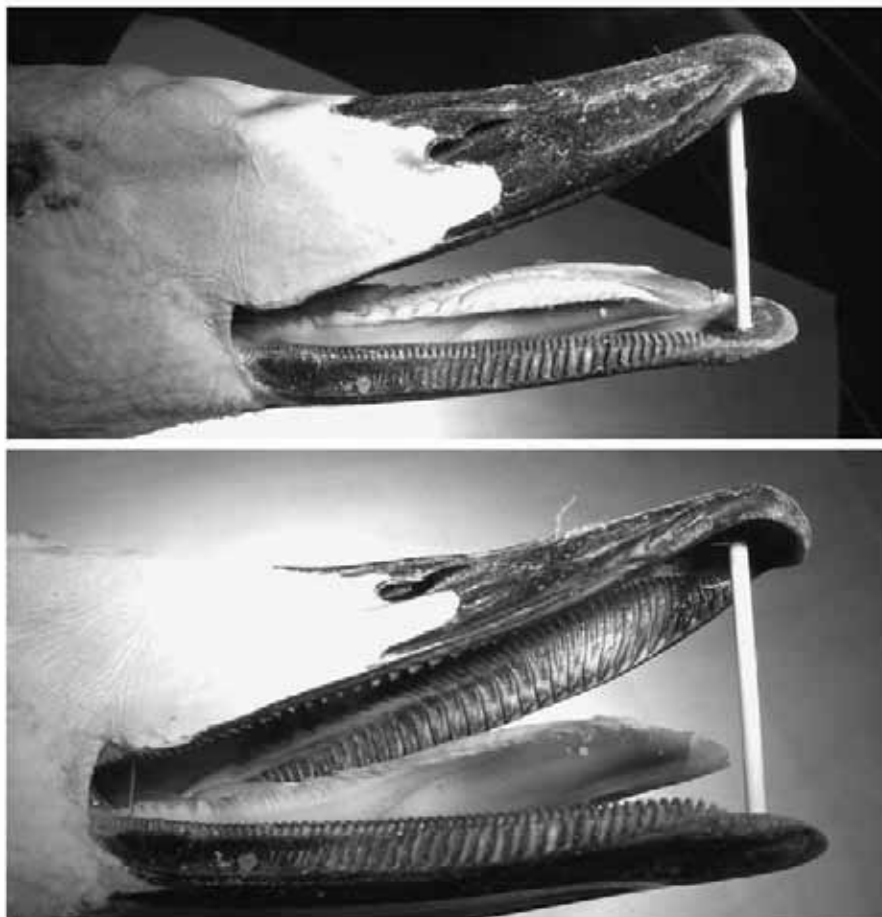


Figure 9 Two views of the lamellated upper and lower bills.

Photographs were taken before the feathers and skin were removed.

connects between the ventral tip of the opisthotic process of the cranium and the ventral extension of the internal articular process on the medial surface of the lower mandible. This part of the ligament is covered by the inserting *M. depressor mandibulae*. The lateral part connects the median crest on the lateral surface of the opisthotic process and the caudal border of the external articular process on the lateral surface of the lower jaw; the ligament serves as the ventral floor of the external acoustic meatus. This part of the ligament is covered laterally by the soft tissue forming the external acoustic meatus and this soft tissue covers the surface of the caudal quadrate and the lateral surface of the external articular process continuously. This ligament keeps the lower mandible from being displaced forward.

Membrana atlantooccipitales dorsalis

This membrane is wide and obvious in the dorsal view after all muscles are removed. Connects between the dorsal margin of the foramen magnum and the dorsal arch of the atlas.

Membrana atlantooccipitales ventralis

Connects between the small area just lateral to the occipital condyle on the cranium and the neurapophysis of the atlas.

Concluding remarks

Some important osteological structures

After the dissecting work described above, the authors could clearly identify the detailed osteology, scars and projections on the bones, as well as the impressions of muscles (tendons), ligaments and other soft tissues. The result is summarized in Fig. 8. Some prominent and important osteological structures are as follows.

Postorbital process (POP)

The postorbital process is the anteriorly prominent process of the frontal bone in the cranium, which borders the posteroventral part of the orbit.

The entire ventral margin is the origin of the a-portion of *M. adductor mandibulae externus superficialis*. Its B- and C-portions arise from the ventromedial surface of the tip of this process. *Lig. prefrontomandibulare* attaches to the lateral surface of this tip.

The weak ridge, running entirely from the tip of POP to the region above the temporal fossa on the lateral surface of the frontal is not an attachment point for any muscles or major ligaments. This ridge seems, to the authors at least, to have no role in the mechanics of the cranium.

Opisthotic process (OpP)

The anatic birds have a ventrally developed opisthotic process (Howard, 1929). This is the highly developed *Ala tympanica* of *Os exoccipitale* (Baumel, 1979) that forms a part of the boundary of the tympanic cavity. The *Lig. occipitomandibulare* attaches to the crest on the lateral surface. The lateral surface and its posterior margin of OpP is part of the ventral region of the origin of *M. depressor mandibulae*. The caudal surface of the laterocaudal edge of OpP is the insertion of *M. rectus capitis lateralis*.

Coronoid process (CP)

The anatic birds have a long and well-developed coronoid process (CP) anteroposteriorly in the lower jaw. Among the adductor muscles attached to the coronoid process, *M. adductor mandibulae externus medialis* is the strongest one and forms the posterior peak on the dorsal margin. The weaker peak of the anterior region of CP is the attachment point for the tendinous fibers of the c-portion of *M. adductor mandibulae externus superficialis*. The entire medial surface of CP forms the insertion point of *M. pseudotemporalis superficialis*.

Lateral coronoid process (LCP)

In the Whooper Swan studied here, the lateral surface of LCP is not covered by muscular fibers (as the insertion of the A-portion of *M. adductor mandibulae externus superficialis*), as noted by Goodman and Fisher (1962) on the Mute Swan and some other species. It seems that the insertion of the A-portion of *M. adductor mandibulae externus superficialis* on the dorsal surface of LCP, rather than the lateral surface as is common in anatic birds, is a genetic character of the *Cygnus* species.

The LCP divides the adductors of the lower jaw into the anterior ones (B- and C- portions of *M. adductor mandibulae externus superficialis*, *M. adductor mandibulae externus medialis* and *M. pseudotemporalis superficialis*) and posterior ones (*M. adductor mandibulae posterior* and *M. adductor mandibulae externus profundus*). The A-portion of *M. adductor mandibulae externus superficialis* is located in the middle. The origin of the anterior adductors on the cranium are always caudal to the insertions on the lower jaw. These anterior muscles appear to waste energy during adduction.

The posterior adductors, on the contrary, are efficient, since they have their origins and insertions at even distances from the quadrate-mandible junction. The posterior adductors are also the retractors of the upper jaw. Therefore the muscles inserted on the area posterior to the LCP are much more efficient in closing the mouth.

Internal articular process (IAP)

The anteriorly curved IAP is the sole origin of the *M. pterygoideus ventralis* portions: the *lateralis* portion arises from the ventral surface and the *medialis* portion arises from the dorsal surface.

External articular process (EAP)

This is a large projection on the lateral surface of the mandible. The EAP is the structure that receives the glenoid on the dorsal surface, and is not an attachment point for any muscle. The only major tissue which attaches to the lateral surface of EAP is the large sheet of ligament, which impresses a small notch on it.

Posterior articular process (PAP)

The well developed sword-like PAP is characteristic in anatid birds. The bone PAP is sandwiched between the medial *M. depressor mandibulae* and the lateral *Mm. stylohyoideus + serpihyoideus*.

Sulcus gl. nasalis

A luminescent, wide but thin salt gland (*Glandula nasalis*) lies on the dorsal surface of the supraorbital margin of the frontal bone. This gland is impressed on the dorsal surface of the frontal with a shallow but clear impression (area 1 of Fig. 8).

On the quadrate

The knob (area 9 of Fig. 8) on the lateral surface on the base of the orbital process (QObP) is the origin of *M. adductor mandibulae posterior*. The lateral surface of the quadrate, including the dorsal margin between QObP and the otic process (QOtP) (area 10 of Fig. 8), is the origin of *M. adductor mandibulae externus profundus*. The anterior marginal surface of the quadrate (area 8 of Fig. 8), including the tip of QobP, is the origin of *M. pseudotemporalis profundus*. The entire medial surface, which is deeply concave, is the insertion of *M. protractor quadratus* (area 29 of Fig. 8).

On the rostrum region

On the horny rostrums, the medial surface of the upper bill and the lateral surface of the lower bill are lamellated and washboard-like, while the ventromedial edge of the upper bill and dorsal edge of the lower bill are serrated (Figs. 1, 7-B, 9). These epidermal structures of the bill are essential parts of the feeding apparatus. The serrations on the dorsal edge of the lower bill, as well as the large wear facets on the tip region and the posterior region of the lamellated surface of the bill, are worn. Therefore, the serrated edge seems to have a function like

that of teeth, catching and crushing food in the mouth. The lamellae on the medial surface of the upper bill and the lateral surface of the lower bill show a characteristic "ratchet structure". This is a repeated series of triangular "steps" which ensures food only moves in one direction before it is swallowed. After entering the mouth, therefore, food is automatically moved deeper into the mouth.

After the horny layer is removed, however, the surface of the bones is mostly smooth and the foramina and canals for vessels are striking, although these epidermal structures are seldom impressed on the bony surface. On the lower jaws, only a small area on the anterior part of the laterodorsal surface of the dentary retains a trace of horny lamellae (Fig. 7). These traces are very shallow. They correspond to the bottom of the lateral lamellae. The horny serrations on the dorsal edge are unrecognizable on the dentary bone.

The tongue with inward-facing strong hairs also acts to carry the food deeper, along with the lamellated surface of the rostrums. The developed tongue itself is recognizable by the large basihyal bone. The existence of hairs, however, is impossible to determine from the osteological structures of the hyoid bones.

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オオハクチョウの筋学と骨学 その2：頭部および最前位頸部の筋

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要旨：本報告はMatsuoka and Hasegawa (2007) が開始したオオハクチョウ*Cygnus cygnus* (ガンカモ目カモ科) の筋学と骨学の記載の第2報である。前報と同一の群馬県立自然史博物館で入手後ホルマリン固定されている個体 (VA-04-02) を用い、頭骨に付着する筋、靭帯、および舌筋類について表層から順次切りはずしながら記載、図示した。解剖にあたってはコハクチョウ*Cygnus columbianus*の頭骨標本と対比しながらすすめ、骨格要素の表面に見られる諸構造と軟組織の付着との関係を確認した。筋類をすべて取り去ったオオハクチョウの頭部を頭骨標本化し、骨学的特徴と筋の付着について図示した。

キーワード：カモ科, オオハクチョウ, *Cygnus cygnus*, 筋学, 骨学, 頭部筋