

## CHAPTER 3: RESULTS

As defined here, the laryngeal apparatus of *B. acutorostrata* and *C. marginata* begins anteriorly with the nasopharynx (Quayle 1991) and ends posteriorly with the trachea supported by tracheal rings (Plate 3). The larynx in mysticetes is hereby defined as a muscular sphincter which separates the oral from the nasal passageways and which includes the epiglottis, glottis and aryteno-epiglottic folds.

### 3.1 Gross anatomy of *Balaenoptera acutorostrata*

Lengths of the laryngeal apparatus' (measured from nasopharynx to end of tracheal rings) of *B. acutorostrata* ranged from 57.7 cm in the juvenile female (Plate 4), 57.8 cm in the juvenile male (Plate 5) to 85.5 cm and 1.1 m in the adult male (Plate 6) and female (Plate 3), respectively. These measurements are approximate bearing in mind that most of the nasopharynges of the various specimens were lost during their initial removal.

#### a) Bones

From a ventral perspective, the most outstanding features on the surface of the apparatus of *B. acutorostrata* are the hyoid and sternum bones (Plate 7), the latter covering more or less the posterior third of the apparatus and the former lying in close association with the tracheal area. These bones provide points of attachment for various muscles and upon removal of the styloid bones and os hyoides, the muscular character of the ventral surface of the laryngeal apparatus is evident.

The hyoid bones described in this study include the tympanohyal, stylohyal-epihyal, basihyal and thyrohyals referred to by Mead (1997, pers. comm.), with the stylohyal-epihyals being synonymous with the styloid bones and the basihyal and thyrohyals being synonymous with the os hyoides.

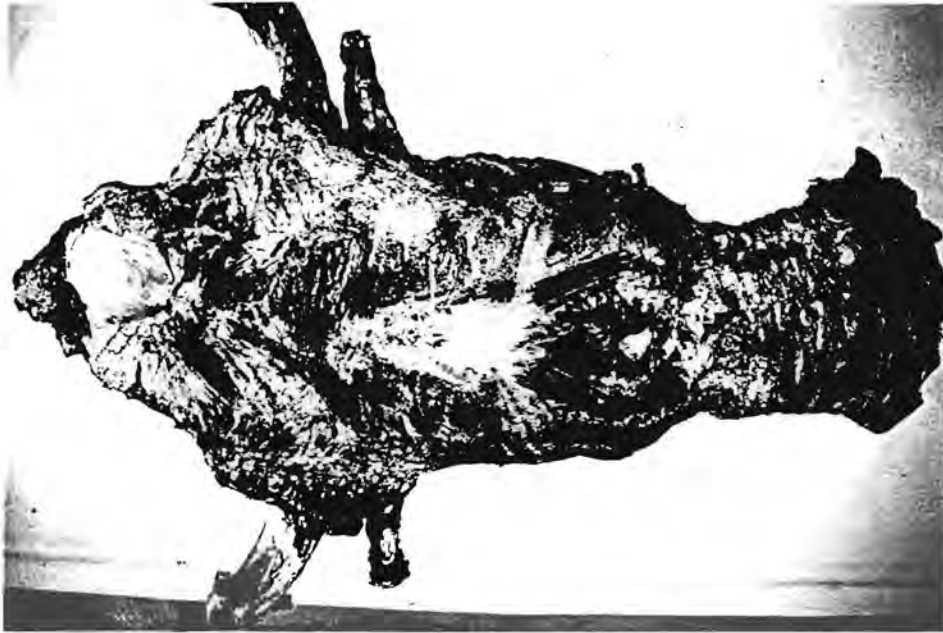


Plate 3: Dorsal view of the laryngeal apparatus of an adult female (# 15) *B. acutorostrata*.

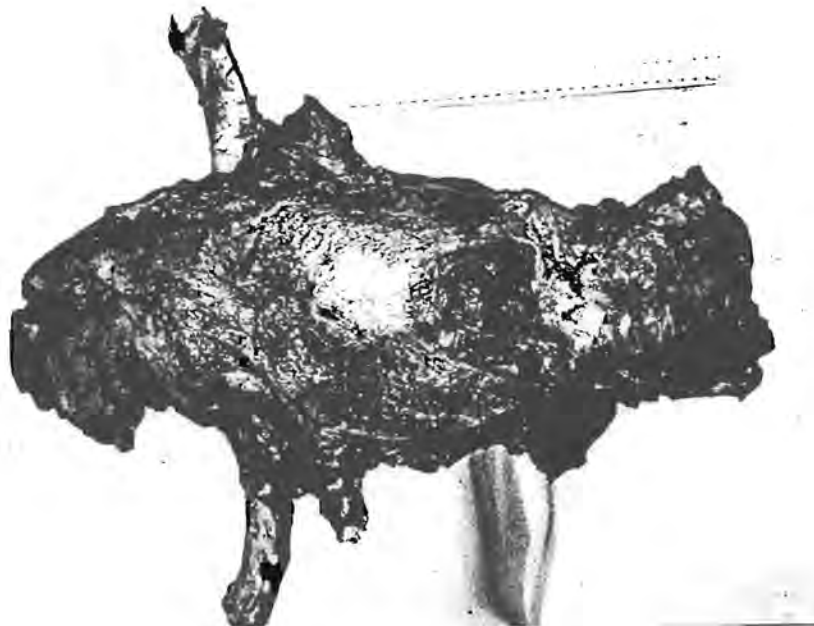


Plate 4: Dorsal view of the laryngeal apparatus of a juvenile female (# 44) *B. acutorostrata*.

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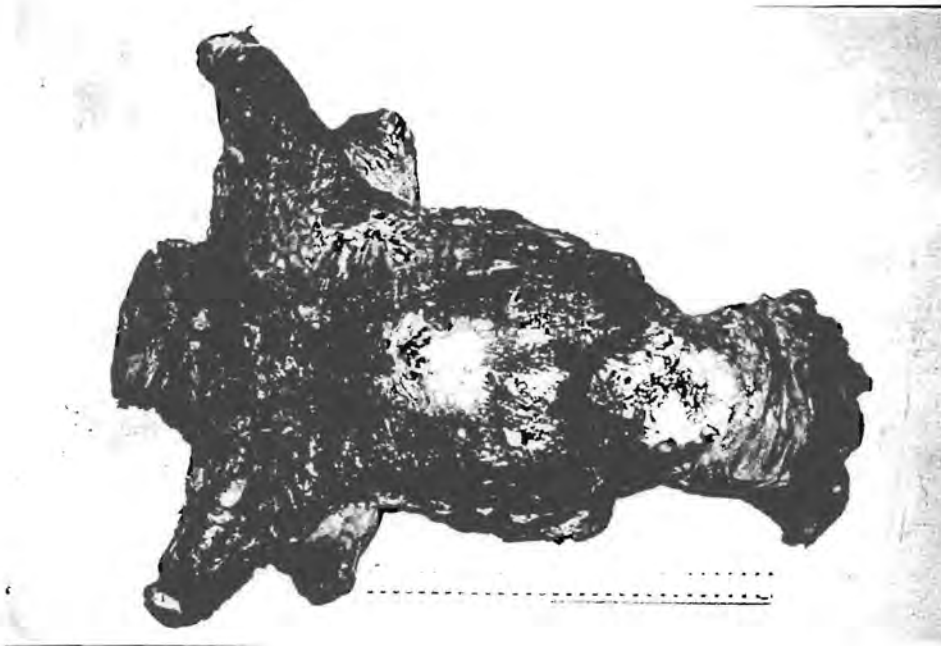


Plate 5: Dorsal view of the laryngeal apparatus of a juvenile male (# 13) *B. acutorostrata*.



Plate 6: Dorsal view of the laryngeal apparatus of an adult male (# 159) *B. acutorostrata*.

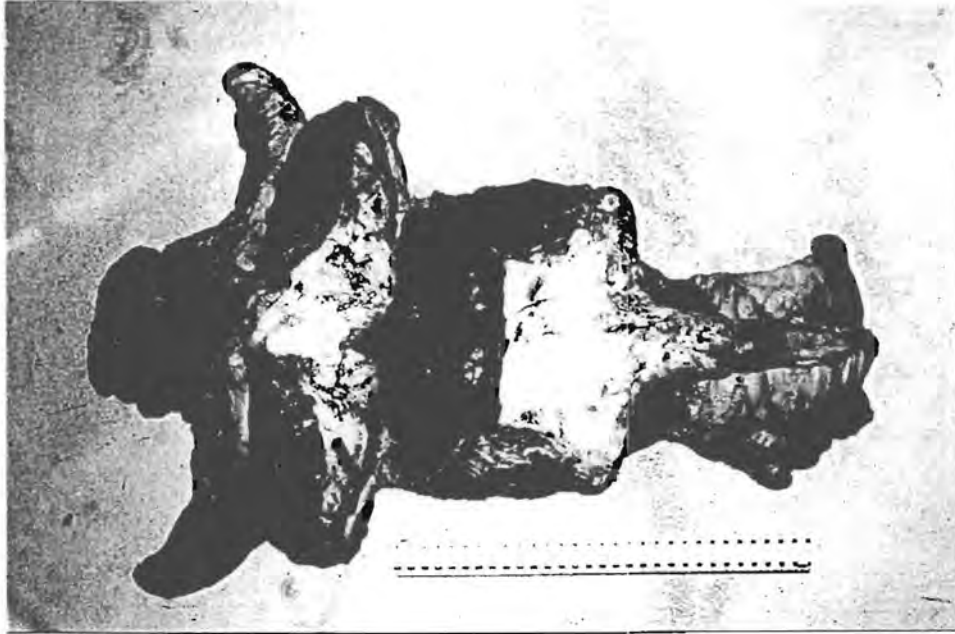


Plate 7: Ventral view of the laryngeal apparatus of a juvenile male *B. acutorostrata* showing the anteriorly situated hyoid bones and the posteriorly occurring sternum bone.

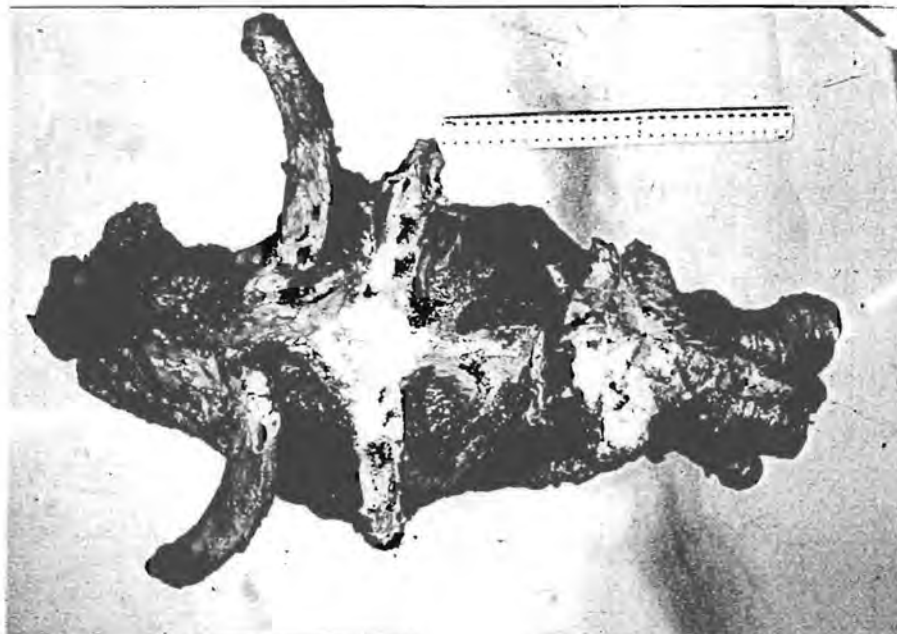


Plate 8: Ventral view of the hyoid bones attached to the laryngeal apparatus of a juvenile female *B. acutorostrata*.

i) *Hyoid bones*

The hyoid, as in all other cetaceans, is composed of three separate bones - the os hyoides and the two styloid bones (Plate 8). The os hyoides can be distinguished as the middle bone, lying anterior to the thyroid cartilage (Plate 9). It extends laterally as two cornua, while its anterior margin bears two anterior projections, separated from each other by a notch in the mesial line. Although the bones and the anterior projections naturally increase in size from the juveniles to the adults, there is much individual variation. In the juvenile male, the posterior margin of the body of the os hyoides is rounded in a posterior direction (Plate 9), whereas in the juvenile female, the posterior margin possesses a slight indentation (Plate 10). The slight notch or indentation seen in the juvenile female is also present in the adult male but is absent in the adult female. Instead, the adult female possesses an even, concave, posterior margin (Plate 11). The os hyoides in all the specimens is curved laterally.

The two styloid bones are found anterior to the cornua of the os hyoides, lying on the ventral surface of the nasopharynx (Plate 12). The bones are attached around their margins, by muscle, to the wall of the nasopharynx. Each bone is of uniform thickness and is essentially convex in shape, though (in the case of the adult male) the posterior margins are not entirely smooth. In the adult female and the juvenile male, the notch on the anterior margin of the os hyoides lies in between the styloid bones whereas in the adult male and juvenile female, the styloid bones are closer together, with the anterior notch of the os hyoides lying beneath the mid-ventral meeting of these bones.

Measurements of the hyoid bones are given in Table 4.

ii) *Sternum bones*

Sternum bones were only available for the juvenile specimens. The sternum is situated on the ventral wall of the trachea and consists of two lateral cornua which join together mesially to form the body. In the juvenile female (Plate 12), the body continues anteriorly in a triangular formation whereas in the male it forms a smooth rectangular plate (Plate 13). The anterior margin of the

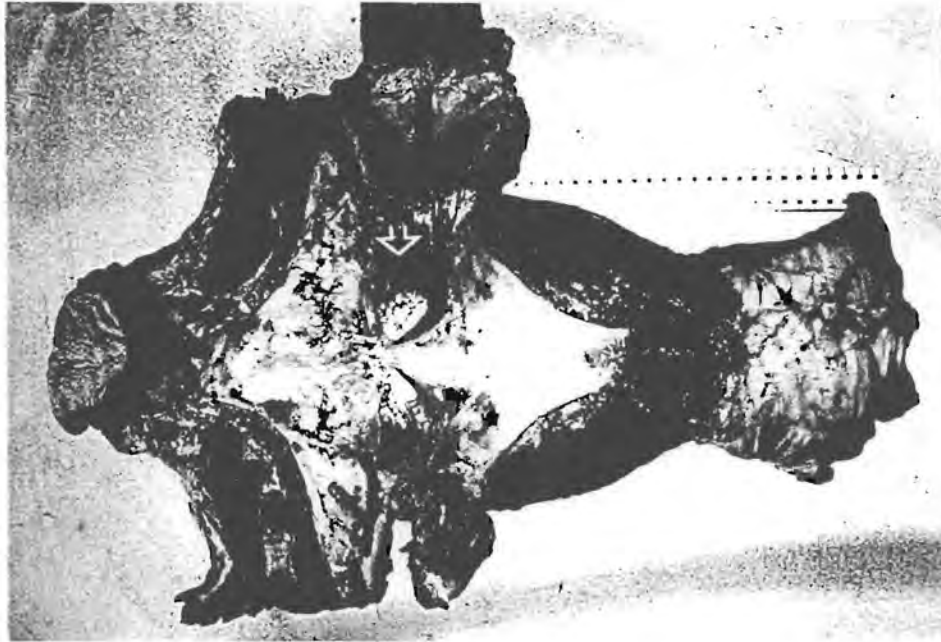


Plate 9

Ventral view of the laryngeal apparatus of a juvenile male *B. acutorostrata* showing the os hyoides (with a rounded posterior margin) lying anterior to the thyroid cartilage. Note the thyro-hyoid muscles anterior to the thyroid cartilage and attached to the posterior margin of the os hyoides (arrow).

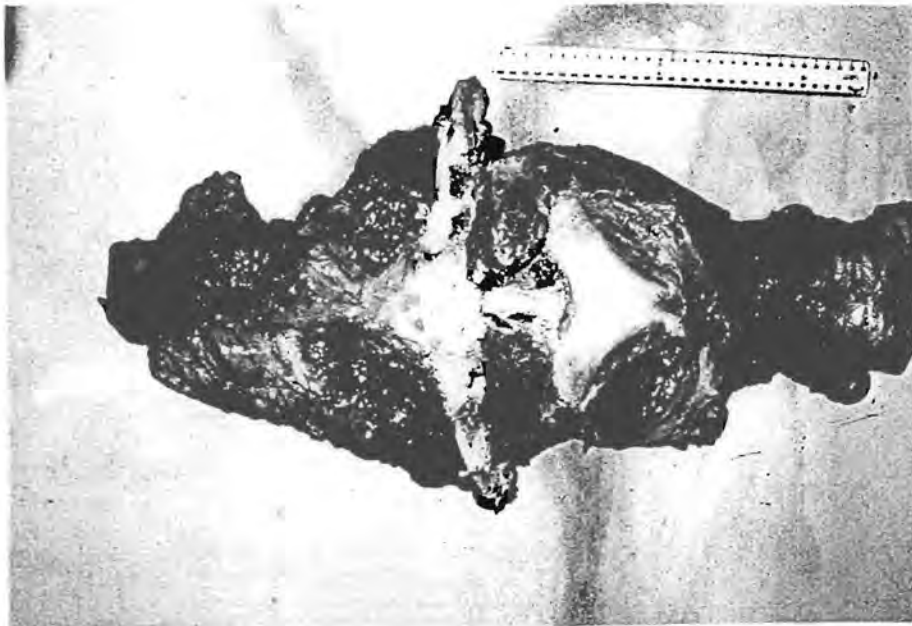


Plate 10:

Ventral view of the laryngeal apparatus of a juvenile female *B. acutorostrata* showing the slight indentation on the posterior margin of the os hyoides, lying anterior to the thyroid cartilage.

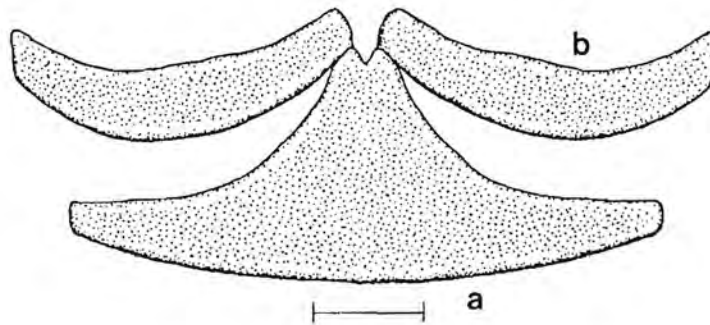


Plate 11: Ventral view of the os hyoides (a) and styloid bones (b) of an adult male *B. acutorostrata* (# 159) showing an even concave posterior margin. Note scale bar = 10 cm.

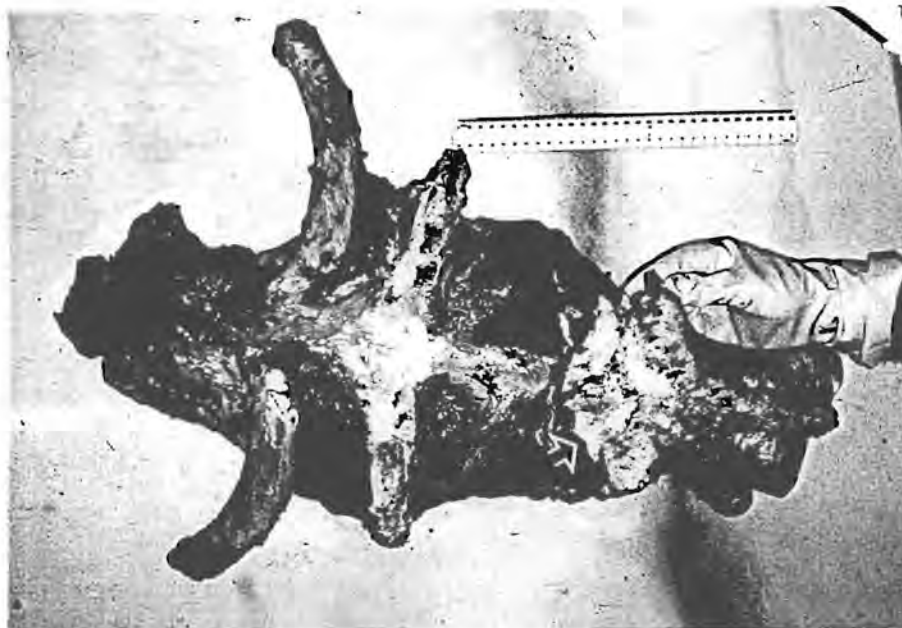


Plate 12: Ventral view of the styloid and sternum bones of a juvenile female *B. acutorostrata*. The styloid bones are found anterior to the cornua of the os hyoides. The anterior margin of the sternum bone is triangular in shape. Note the muscular attachment on the anterior margin of the sternum (possible sterno-thyroid muscle) (arrow).

Table 4 Measurements associated with the laryngeal apparatus of *B. acutorostrata*.

Cartilage/Bone Measurements (cm) (specimen #)		Juvenile ♂ (13)	Adult ♂ (159)	Juvenile ♀ (44)	Adult ♀ (15)
Entire apparatus	Total length (m)	57.8	85.5	57.7	110.0
Thyroid cartilage	Anterior margin	16.8	22.5	17.3	26.2
	Body width	21.3	29.0	22.5	30.0
	Total length	19.2	28.5	14.3	31.2
Cricoid cartilage	Length	13.6	22.0	14.0	21.2
	Width	13.2	21.5	12.0	27.7
	Length ventral LHS cornu	3.7	2.5	6.0	10.5
	Length dorsal LHS cornu	3.0	2.0	5.0	6.0
Epiglottic cartilage	Total length	15.6	28.5	14.3	24.9
Arytenoid cartilages	Depth of notch (between lips)	0.5	1.8	0.8	0.6
	Ave width of lips (widest area)	7.5	12.0	6.4	10.6
	Height of lips (LHS) - tip of lip to cartilage - mid-dorsal measurement	1.6	4.6	2.6	2.2
	Height of lips (RHS) - tip of lip to cartilage - mid-dorsal measurement	2.0	3.8	2.4	2.2
	Ave total length	19.2	28.5	14.3	31.2
Os hyoides	Length cornua LHS	19.5	23.5	17.5	31.0
	Length cornua RHS	19.5	24.2	17.7	31.0
	Width of body - measured from bottom of "v" notch	9.4	13.1	8.4	16.7
Styloid bones	Total length (LHS)	21.7	34.3	25.1	39.1
	Total length (RHS)	21.0	35.2	24.3	39.1
	Average width - at thickest region	4.3	7.5	4.7	9.0



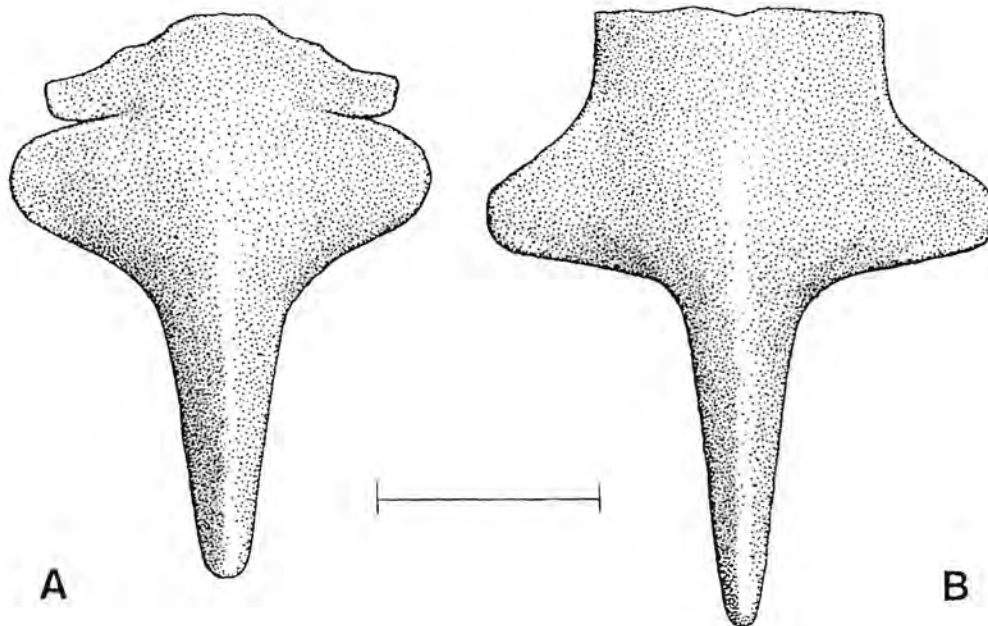


Plate 13: Ventral view of the sternum bone of (A) a juvenile female (# 44) and (B) a juvenile male (# 13) *B. acutorostrata*. Note scale bar = 10 cm.

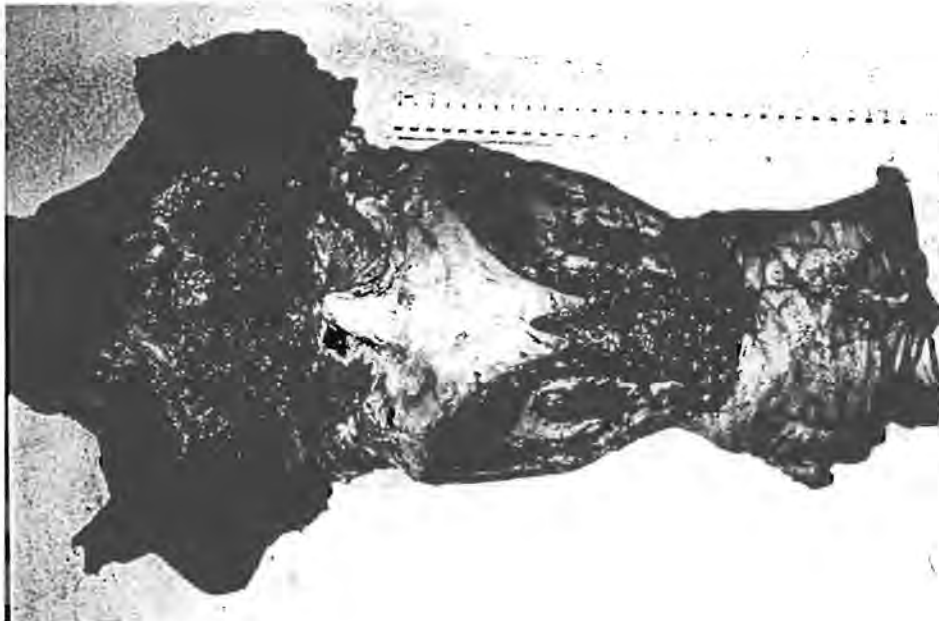


Plate 14: Ventral view of the laryngeal apparatus of a juvenile male *B. acutorostrata* showing the mid-ventral situation of the thyroid cartilage.

sternum is flat and provides a surface for muscle attachment. Posteriorly, the body forms a dagger-like extension narrowing along its anterior-posterior axis, and ending in a pointed tip, which extends as far as the anterior margin of the fifth tracheal ring.

b) Cartilages

The laryngeal cartilages in each specimen are five in number, the single thyroid, cricoid and epiglottic cartilages and the paired arytenoids. The outstanding characteristic of these cartilages is their general flexibility and "softness" which is characteristic of both the juveniles and the adults.

Naturally, the various structures, bones and cartilages increase in size from the juveniles to the adults, but much individual variation exists. Measurements of all the cartilages are given in Table 4.

i) *Thyroid cartilage*

The thyroid cartilage occurs in the mid-ventral region of the laryngeal apparatus (Plate 14). The thyroid cartilage is made up of a horizontal body which gives rise on either side to posterior, vertical cornua. The body of this cartilage is flat with a reduced anterior-posterior diameter (Plate 15). From a posterior aspect, the anterior margin of the body is convex and the posterior margin is concave, the latter possessing a median v-shaped notch (Plate 15). In the adult female the body of the thyroid cartilage possesses a slightly raised ridge along the mid-ventral line. Posterior cornua occur at the left and right extremities of the body and it is at these points that the anterior margin of the body is thickest, forming tubercles (Plate 15). On the outer margins of the tubercles both cornua curve backwards, forming prominent concave arches, resting on either side of the larynx. As each cornu arches concavely, its original band-like character changes to a more rod-like one, showing slight thickening at the posterior tip (Plate 15). It is at these tips that each cornu is articulated with the cricoid cartilage (Plate 16).

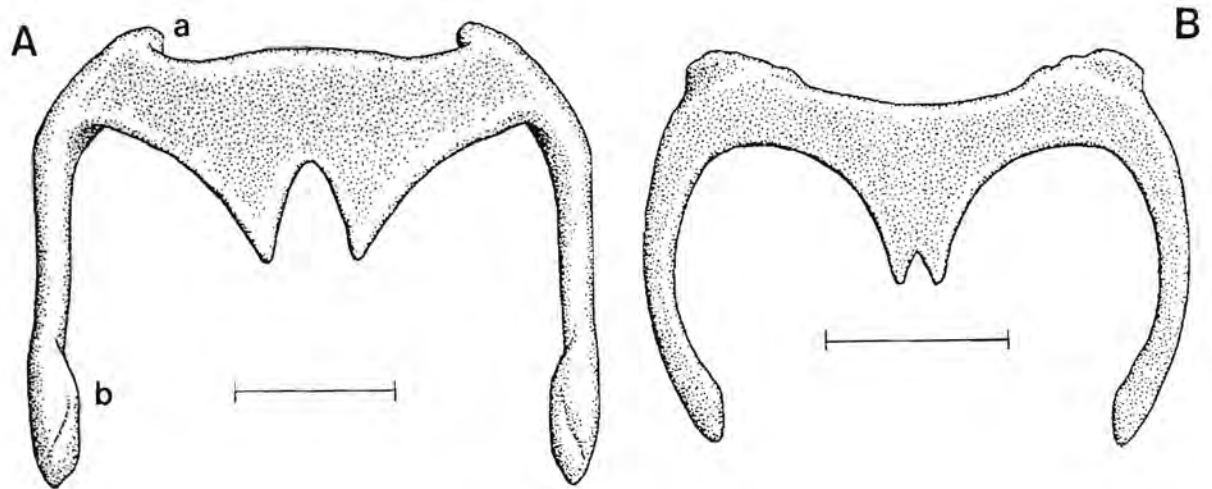


Plate 15: Ventral view of the thyroid cartilage of (A) an adult female (# 15) and (B) a juvenile female *B. acutorostrata*. Note (a) anterior tubercles (well-developed in the adult), notch on posterior margin of the thyroid body and (b) the posterior thickening of the cornua (much thicker in the adult). Note scale bar = 10 cm.



Plate 16: Lateral view of the right hand side of the laryngeal apparatus of a juvenile female *B. acutorostrata* showing the articulation between the thyroid and cricoid cartilages.

ii) *Cricoid cartilage*

The cricoid cartilage, is incomplete ventrally with a dorsally positioned body which continues laterally and ventrally to form two cornua (Plate 17). The body is a large, almost square plate of cartilage which provides facets of articulation with both the arytenoid and the thyroid cartilages, the joints of which have fibrous capsular membranes. The arytenoidal articular facets occur on either side of the anterior margin of the cricoid body. Each facet forms a convex depression lying at an oblique angle to the longitudinal axis of the body of the animal. In between the arytenoid articular facets, the body of the cricoid cartilage is convex in shape. The posterior margin of the body of the cricoid forms a rounded prominence which is continuous with the upper tracheal rings (Plates 18 and 19) - the number of which seems to vary with the size of the animal. The cricoid prominence is continuous with the first tracheal ring in the juvenile female, it borders on the anterior margin of the first tracheal ring in the juvenile male, is continuous between the first and second tracheal ring in the adult male and is continuous with the first three tracheal rings in the adult female. The middle of the lateral margins of the body of the cricoid tend to move inward towards each other, causing their posterior ends to point away from the body. It is at these ends that the facets for articulation with the thyroid cornua are found (Plate 17). Posterior to each facet, the body of the cricoid proceeds ventrally to form its cornua. The part of the cartilage which joins the body of the cricoid to its cornua is more scallop-shaped in the males and the cornua are shorter compared to those of the females (Table 4). The cornua extend to the first tracheal ring in the juvenile male and are in line with the second tracheal ring in the adult male. In the females, however, the cornua lie in line with the fourth and third tracheal rings in the juvenile and adult, respectively. From the dorsal perspective (Plate 19), the cricoid body is slightly concave in the middle. Along the mid-dorsal line of the body, small indentations occur. These indentations range from 0.5 mm in diameter to approximately 1 cm in diameter in the juvenile female and the adults and are possibly neuro-vascular foramina (R Alexander, S A Museum 1997, pers. comm.). However, these indentations were not detected in the juvenile male.

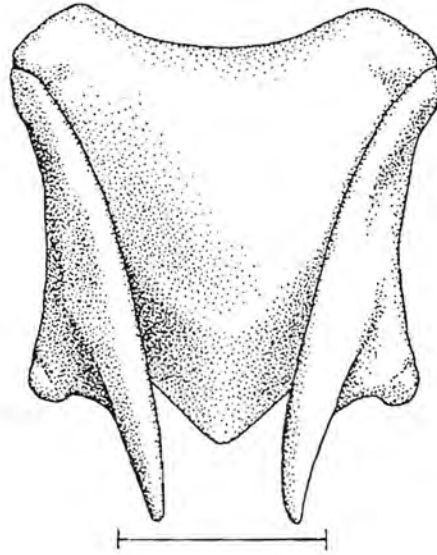


Plate 17: Ventral view of the cricoid cartilage of a juvenile female *B. acutorostrata* (# 44). Note that the cartilage is incomplete ventrally and the facets for articulation occur on the four “corners” of the cartilage. Note scale bar = 10 cm.



Plate 18: Dorsal view of the rounded prominence of the posterior margin of the body of the cricoid cartilage (arrow), of a juvenile female *B. acutorostrata*, which is continuous with the tracheal rings.

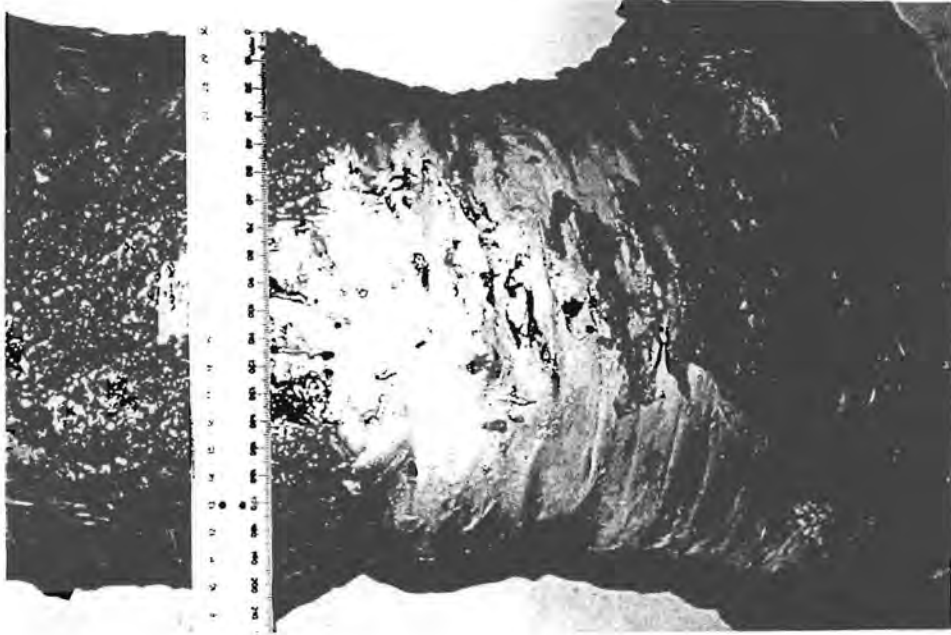


Plate 19: Dorsal view of the body of the cricoid cartilage of an adult female *B. acutorostrata*, being slightly concave along the mid-line. Note foramina.

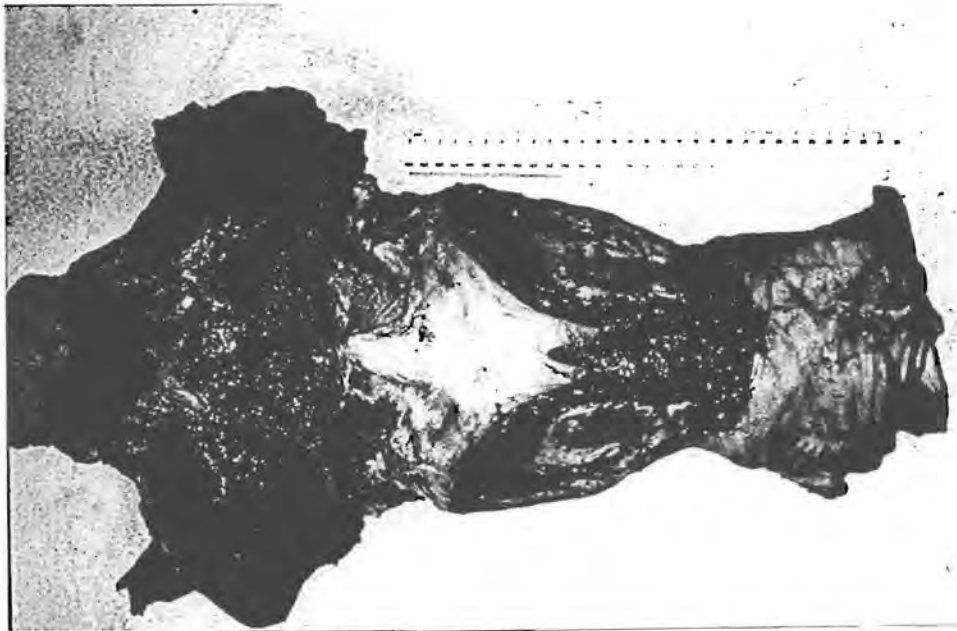


Plate 20a: Ventral view of the laryngeal apparatus of a juvenile male *B. acutorostrata* showing the epiglottic projection occurring anterior to the thyroid cartilage.

iii) *Epiglottic cartilage*

The first indication of the epiglottic cartilage in this species is a small region that projects through the ventral muscular surface, anterior to the thyroid cartilage (Plates 20a and 20b). This region is continuous with the bulk of the cartilage as it appears ventrally above the arytenoid bodies (Plate 21). This cartilage, together with the epiglottic folds extends over the tips of the arytenoid bodies to form a hood-like arrangement (Plate 22). Once removed, the shape of the cartilage is that of a shoe-horn, consisting of a very thin anterior plate surrounding a wide shallow groove, with a thickened extension at its posterior end (Plates 23a and 23b). Table 4 shows the measurements of the epiglottic cartilage in each specimen.

iv) *Arytenoid cartilages*

The arytenoid cartilages consist of antero-ventrally situated, crescentic "wing-like" plates which terminate anteriorly as horn-like processes (arytenoid bodies). Dorsally these bodies continue to form the processi musculares and, posterior to this, they become thinner and taper to form the processi vocales (Plate 24a). The "wing-like" plates are connected to the other two processes by thick basal regions (Plate 24b). The left and right wings approach one another ventrally, at their extremities, so that the arytenoid bodies point dorsally towards the nasopharynx. The arytenoid bodies project beneath the root of the epiglottis forming the ventral margin of the entrance of the larynx (Plate 25). In the juveniles, the arytenoid bodies project an average of 3,6 cm from the floor of the pharynx, and in the adults an average of 6,5 cm. The processi musculares are somewhat "bell-shaped", with the base of the "bells" being incorporated into the processi vocales (Plate 24a). The anterior margins of the processi musculares are slightly rounded so as to accommodate the convexity of the articular facets on the cricoid body (Plate 26). The processi vocales are conical in shape, with their long axes being directed backwards, and lie parallel to each other along the ventral wall of the larynx, forming the dorsal wall of the laryngeal sac (Plate 26). The distal ends are connected by connective tissue. A wide aperture occurs between the processi vocales through which the sac communicates with the trachea (Plate 26). The arytenoid bodies are connected by connective tissue which is continuous with the laryngeal mucosa and which



Plate 20b:

Ventral view of (a) the epiglottic protrusion, occurring posterior to the nasopharynx. Note knob-like structures which occur randomly between the pits and below the anterior end of the nasopharynx (arrow).



Plate 21:

Dorsal view of the epiglottis (lifted) showing (a) the epiglottic ridge of a juvenile male *B. acutorostrata*, which lies over the arytenoid cartilages (ventral view). Note arytenoid lips (arrow).



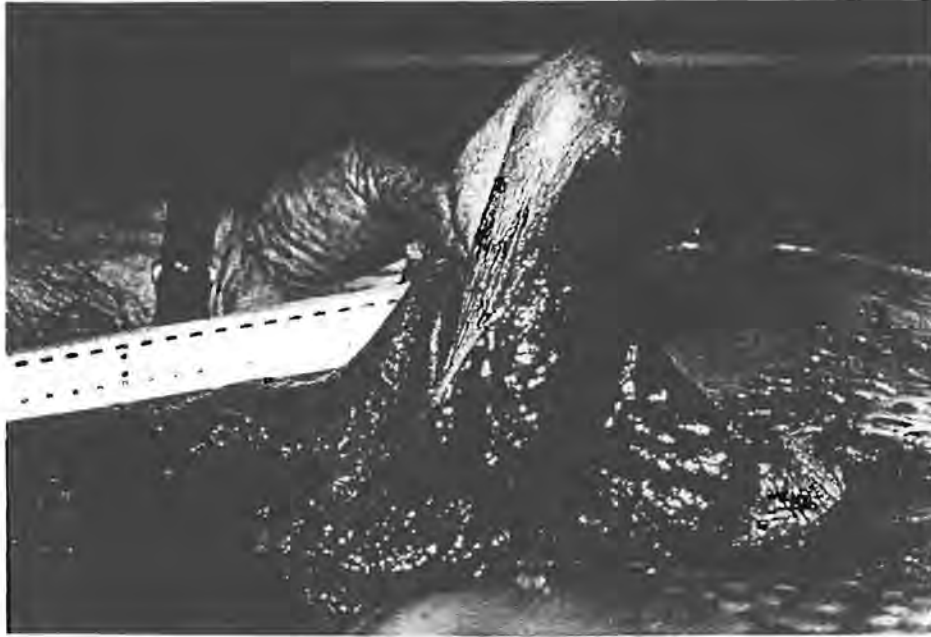


Plate 22: Lateral view of the hood-like arrangement of the epiglottic cartilage of an adult female *B. acutorostrata*. Epiglottic folds occur on either side of the “hood”, supported by the hyo-epiglottic muscles.

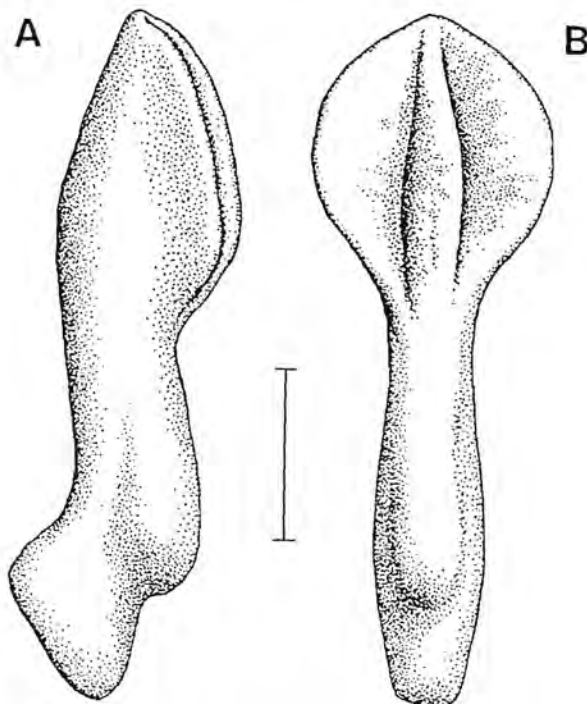


Plate 23: (A) Latero-dorsal view of the epiglottic cartilage of an adult male *B. acutorostrata* (# 159) showing its shoe-horn shape. The posterior region forms the epiglottic protrusion. (B) Dorsal view of the epiglottic cartilage of an adult male *B. acutorostrata* (# 159). The anterior “lips” of the cartilage are parted to reveal the epiglottic ridge. Note scale bar = 5 cm.

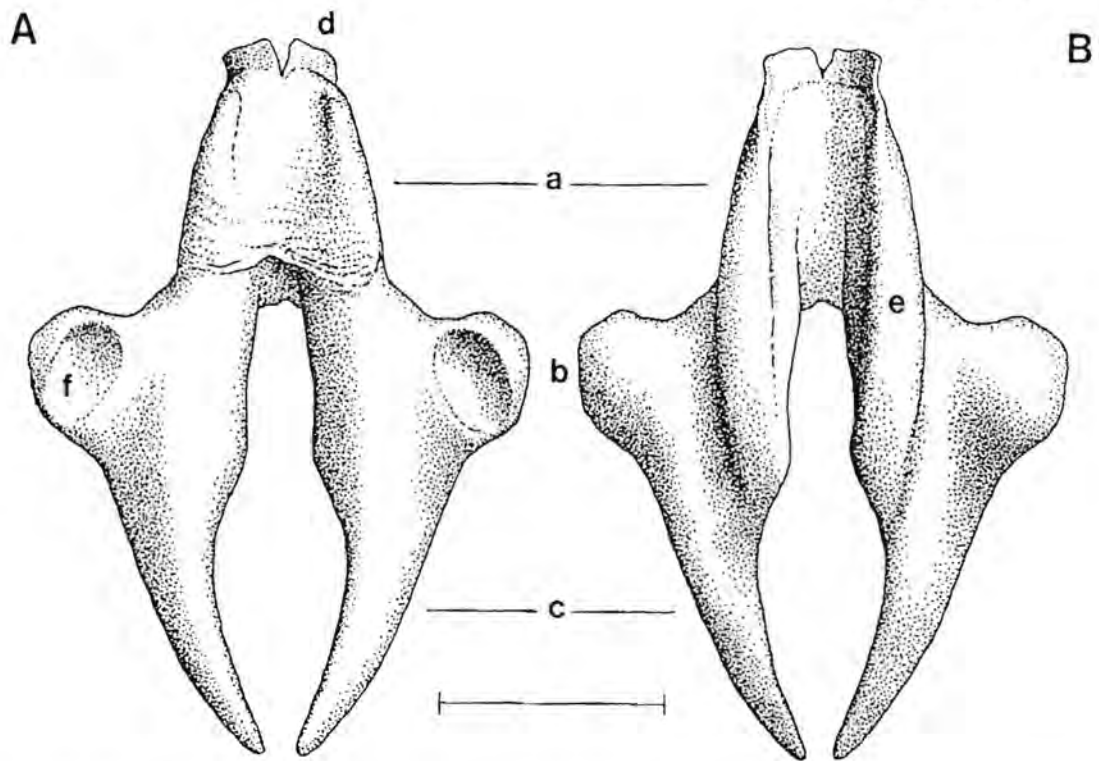


Plate 24:

(A) Dorsal view and (B) ventral view of the arytenoid cartilages of an adult male *B. acutorostrata* (# 159). Labels are as follows: a = arytenoid bodies; b = processi musculares; c = processi vocales; d = arytenoid lips; e = ridges of the arytenoid bodies; f = crico-arytenoid facets. Note scale bar = 10 cm.

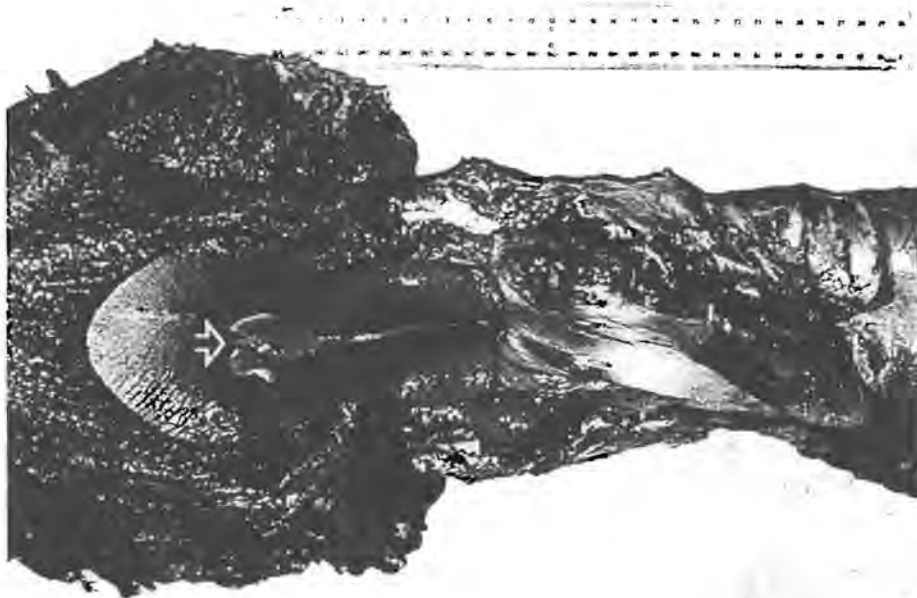


Plate 25:

Ventral view showing the arytenoid bodies projecting beneath the root of the epiglottis (pulled back) of a juvenile female *B. acutorostrata*, forming the ventral margin of the entrance into the larynx. Note the arytenoid lips (arrow).

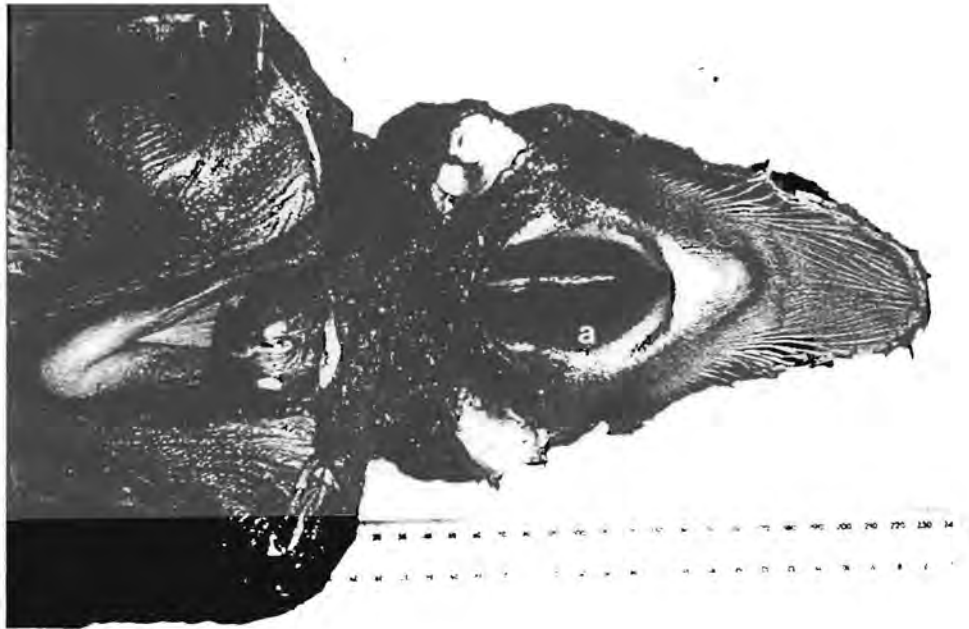


Plate 26: Dorsal view of (a) the arytenoid cartilages and the glottis forming the dorsal wall of the laryngeal sac of a juvenile male *B. acutorostrata*. Note rounded nature of the processi musculares and the folds of the laryngeal sac mucosa.

extends past the bodies forming rounded "lips" (Plates 24a, 24b and 25). These "lips" join together, forming the shape of the letter "m".

c) Myology of the laryngeal apparatus

The musculature of the laryngeal apparatus of *B. acutorostrata* was similar to that described by Benham (1901), so the terminology used by this author for the major muscles of the laryngeal apparatus is applied to this description (Plates 27a and 27b). The various extrinsic and intrinsic muscles of the laryngeal apparatus are composed of highly vascularised, skeletal muscle tissue.

i) *Extrinsic muscles*

On the posterior margins of the styloid bones, bordered by the cornua of the os hyoides, lies a long rectangular muscle, which could possibly be the **sterno-hyoid** (Plate 28). The raised anterior margin of the os hyoides seems to separate this muscle into 2 sections. In the juvenile male, this muscle takes its posterior origin from the anterior, flat region of the sternum, and passes upwards, being inserted into the posterior margin of the os hyoides. This muscle forms two quadrilateral masses, rather than one long one. This muscle was not observed in the other specimens, presumably being removed during initial dissection.

Arising from the anterior border of the thyroid cartilage, the triangular **thyro-hyoid** muscles stretch forward and attach to the posterior margins of the cornua of the os hyoides (Plate 9). The **sterno-thyroid** muscle was not clearly discernible, if at all present, but the juvenile female specimen did display some muscular attachment on the anterior margin of the sternum, which seemed to stretch anteriorly and cover the ventral face of the thyroid cartilage (Plate 12).

ii) *Intrinsic muscles*

Upon the removal of the sternum bones, posterior to the thyro-hyoid muscles and anterior to the tracheal rings, the **thyro-cricoid** muscle can be seen lying in line with the mid-line of the thyroid cartilage. Anteriorly this muscle reaches the epiglottic cartilage (Plate 29) while posteriorly it

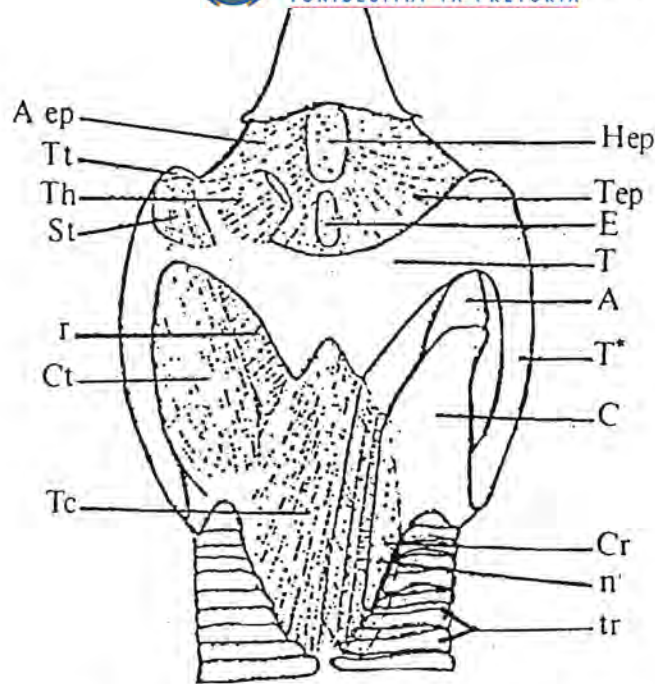


Plate 27a:

Ventral view of entire larynx of *B. acutorostrata*, as seen after the removal of the hyoid bones and the wall of the pharynx. Some of the muscles have been removed from the right side of the figure, so as to show the shape and relations of the cartilages. The right longitudinal muscle (thyro-cricoid) of the sublaryngeal pouch has been cut away so as to exhibit the deeper circular muscles. Letters have the following significance: A: arytenoid cartilage; A.ep: aryteno-epiglottid muscle; C: cricoid cartilage; C.c: Vento-posterior cornu of cricoid cartilage; C.t: Crico-thyroid muscle; E: epiglottid cartilage; Ep: epiglottis; H.ep: Hyo-epiglottid muscle; n: Transverse and circular muscles of the sublaryngeal pouch; r: accessory crico-thyroid muscle; S.t: sterno-thyroid muscle; T: thyroid cartilage; T\*: posterior cornu of thyroid cartilage; T.c: thyro-cricoid muscle; t.ep: thyro-epiglottid muscle; T.h: thyro-hyoid muscle; tr: tracheal rings; T.t: tubercle or ridge on the anterior margin of the thyroid cartilage. (Taken from Benham 1901)

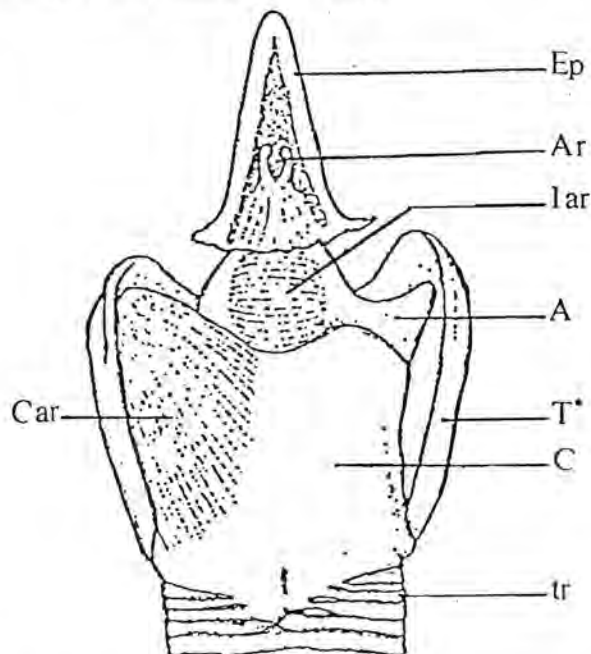


Plate 27b:

Dorsal view of the larynx of *B. acutorostrata*. Some of the muscles have been removed from the right side. Note continuity of the upper tracheal rings with the cricoid cartilage. Labelling as above except for I.ar: inter-arytenoid muscle; C.ar: (posterior) crico-arytenoid muscle. (Taken from Benham 1901).

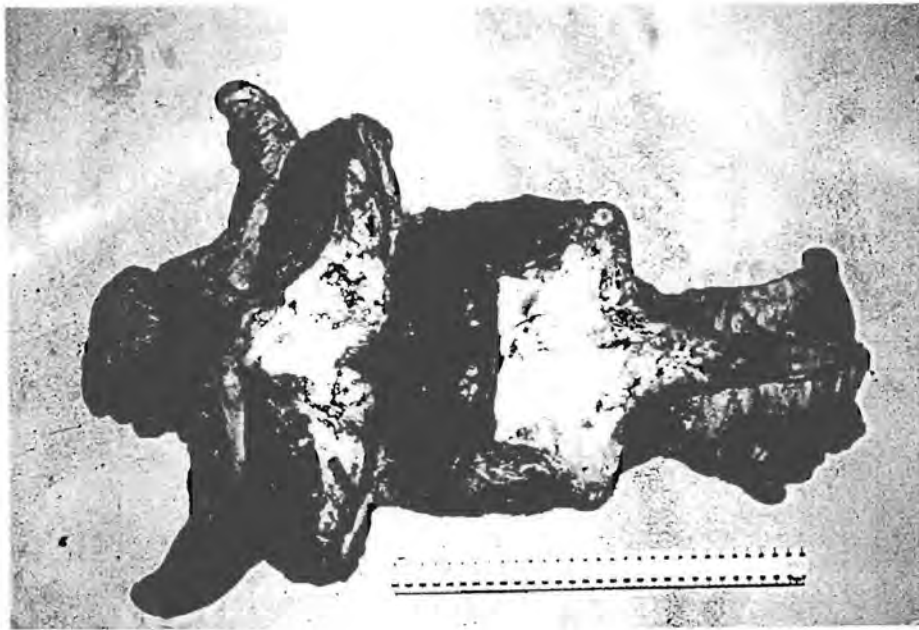


Plate 28: Ventral view of the laryngeal apparatus of a juvenile male *B. acutorostrata* showing the hyoid and sternum bones. Note the association of the rectangular sterno-hyoid muscle with the anterior margin of the sternum bone.

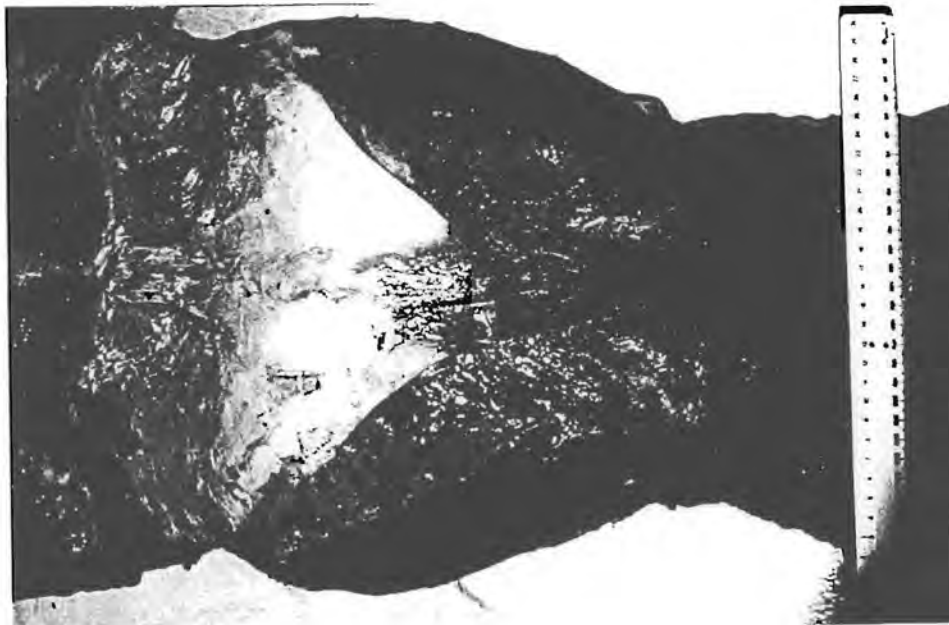


Plate 29: Ventral view of the thyro-cricoid muscle (in line with the mid-line of the thyroid cartilage) of an adult female *B. acutorostrata*.

stretches as far as the tracheal rings, forming part of the outer wall of a blind-ending sac which terminates at the anterior margin of the tracheal rings (Plate 30).

The epiglottis and thyroid cartilages lie posterior to the os hyoides. Only a small part of the epiglottic cartilage protrudes through the **thyro-epiglottic, aryteno-epiglottic** and **hyo-epiglottic** muscles and is situated in line with the middle of the convex anterior margin of the thyroid cartilage (Plate 31). The thyro-epiglottic muscle begins on the inner, lateral side of the body of the thyroid cartilage and passes anteriorly to join the aryteno- and hyo-epiglottic muscles which, together with the epiglottic cartilage, form the epiglottis. The outer margin of the wing and the posterior processus vocales of the arytenoid cartilage provide attachment for the aryteno-epiglottic muscle. This muscle extends to the epiglottic cartilage and penetrates the thyro- and hyo-epiglottic muscles in which it is embedded. The hyo-epiglottic muscle is inserted in the antero-ventral region of the epiglottic cartilage and passes along the sides of the epiglottis (Plate 22). The **thyro-arytenoid** muscle is not very conspicuous and lies across the aryteno-epiglottic muscle. The origin of the thyro-arytenoid muscle is not clearly defined, but it seems to arise beneath the crico-arytenoid muscle from the thyroid cartilage region and continues towards the bodies of the arytenoid cartilages.

Within the arches of the body of the thyroid cartilage, originating from the latero-ventral face of the cricoid body, the **crico-thyroid** muscle fibres extend to the inner surface of the posterior cornu of the thyroid cartilage (Plate 32). Once removed, the **accessory crico-thyroids** are visible, while the lateral part of the cricoid body is also exposed (Plate 33).

The dorsal surface of the laryngeal apparatus is also very muscular in character (Plate 34), although here, only two muscles are distinguishable, namely, the crico-arytenoid and the inter-arytenoid muscles. The **crico-arytenoid** muscle covers most of the dorsal body and lateral surfaces of the cricoid cartilage, with the lateral portion extending beneath the crico-thyroid muscle. The lateral and dorsal portions of the crico-arytenoid cannot be distinguished from one another and together form one muscle mass (Plate 34). This muscle mass extends to the processus muscularis of the arytenoid cartilage. The second muscle found on the dorsal surface of the laryngeal apparatus is the **inter-arytenoid**, and its position is (as its name suggests)

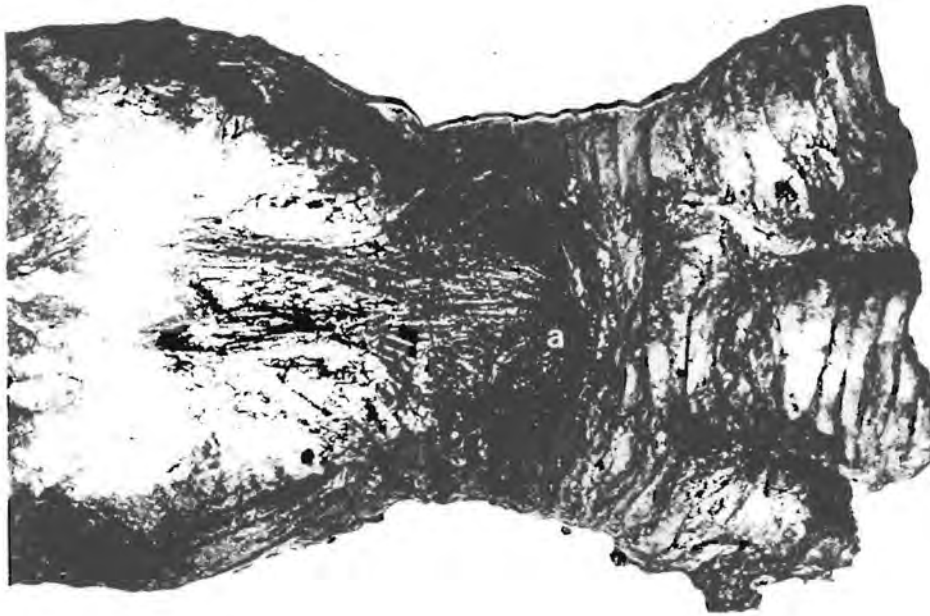


Plate 30: Ventral view of (a) the posterior margin of the thyro-cricoid muscle of an adult female *B. acutorostrata* forming part of the outer wall of the laryngeal sac.

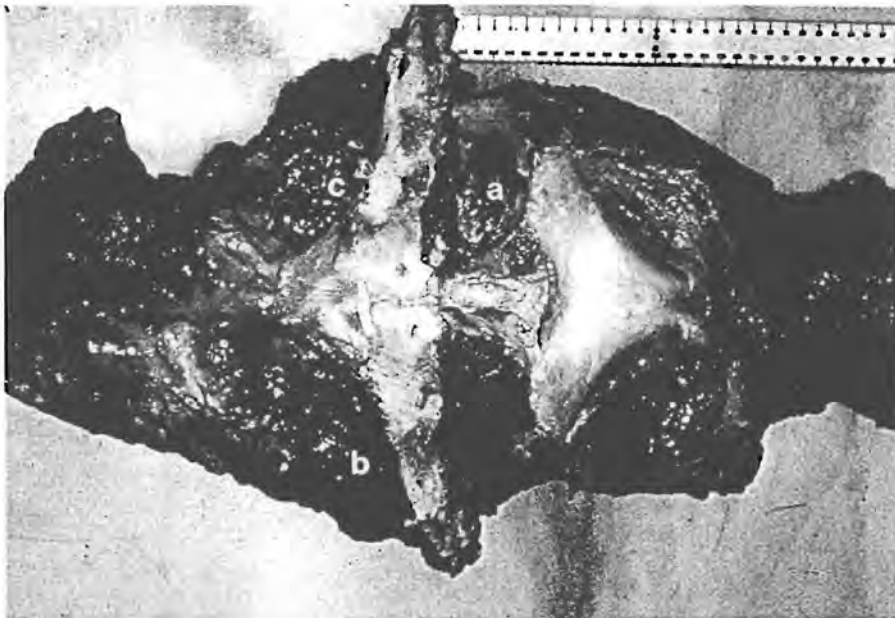


Plate 31: Ventral view of the (a) thyro-epiglottic, (b) aryteno-epiglottic and (c) hyo-epiglottic muscles of a juvenile female *B. acutorostrata*





Plate 32: Lateral view of the right portion of the crico-thyroid muscle and the thyroid cartilage of an adult female *B. acutorostrata*.

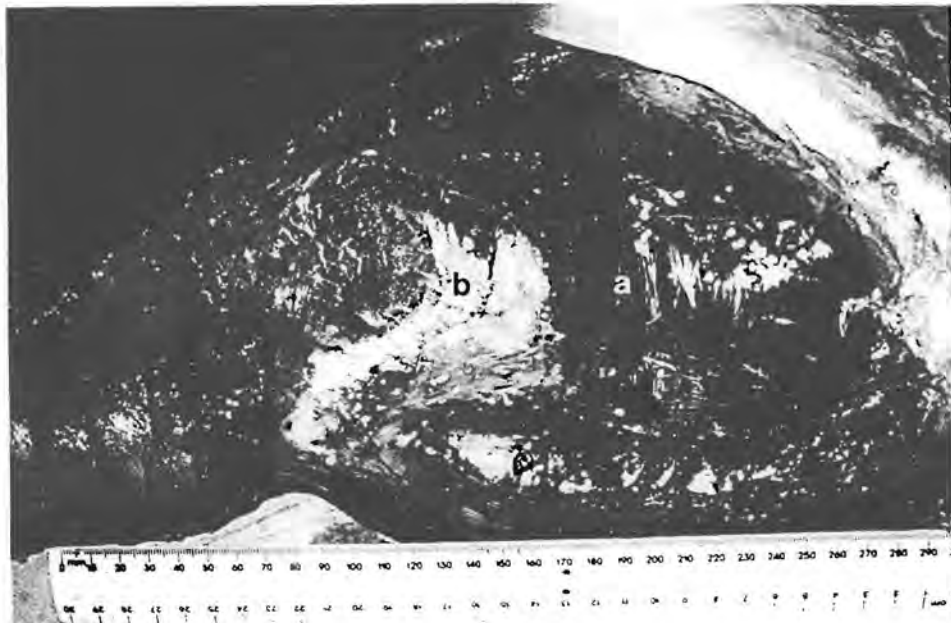


Plate 33: Lateral view of the left portion of the (a) accessory crico-thyroid muscle of an adult female *B. acutorostrata*, with (b) the lateral part of the cricoid cartilage exposed.



Plate 34: Dorsal view of the muscular nature of the laryngeal apparatus of an adult female *B. acutorostrata*. Note the oesophageal opening (arrow) just above the tracheal rings.



Plate 35: Ventral view of the nasopharynx of an adult female *B. acutorostrata* showing cuboidal and rectangularly shaped tissue on the surface of the mucosa.

between the paired arytenoid cartilages, arising from the arytenoid "wings". The posterior opening of the oesophagus lies between the arytenoid "wings" and in the midline of the cricoid body on the dorsal surface (Plate 34).

### 3.2 Histology of the laryngeal apparatus of *B. acutorostrata*

Beginning at the anterior end of the apparatus and proceeding in a posterior direction, the nasopharynx, lying on the ventral side of the animal, is lined by a mucosal layer which on inspection consists of cuboidal and rectangularly-shaped units (being cuboidal close to the epiglottis and becoming rectangular anteriorly) (Plate 35). Histologically, the mucosa consists of a thick layer of stratified squamous epithelium which covers unusually dense concentrations of connective (collagenous) tissue. Muco-serous glands and ducts lie loosely in the connective tissue, which also divides them into distinct lobules. A finger-like dermis reaches into the epidermis (Plate 36). The "fingers" are made up of connective tissue and arise from the lamina propria. Besides these tissue formations, the surface of the mucosal layer is pitted. Tiny pin-holes also penetrate the mucosa throughout the length of the nasopharynx. The mucosa originating in the nasopharynx is dark grey but becomes light pink in colour in the pharynx, with infusions of grey throughout. The grey mucosal tissue is more pronounced in the females particularly in the juvenile, where most of the nasopharynx is dark grey (Plate 37). This grey coloration is due to the presence of melanocytes in the epidermal layer (Plate 38). In the juvenile male, a few small knob-like structures are found to occur randomly between the pits and below the anterior end of the nasopharynx (Plate 20b). In the adults, the muscular tissue around the nasopharynx seems to be penetrated by a network of thin, white-coloured deposits, forming a pattern much like that of the cells of a bee-hive. Upon visual inspection, this network seemed to be made up of adipose tissue, indicating the possible presence of smooth muscle. But histological analysis revealed only small amounts of adipose tissue interspersed between the muscle tissue, which was identified as skeletal muscle. The nasopharynx ends at the posterior narial opening.

The mucosal layer of the nasopharynx is continuous with the narial opening, but adopts a distinctive "elasticated" or "gathered" appearance at the edges of the opening (Plates 20b and 25). The epithelium in this region is not as thick as that found in the nasopharynx (Plate 39). Many



Plate 36: Transverse section of the nasopharyngeal mucosa of an adult male *B. acutorostrata*. Note the finger-like dermis reaching into the epidermis (arrow) as well as large amounts of adipocytes. (Mag. 50x, Masson's Trichrome (MT) stain).

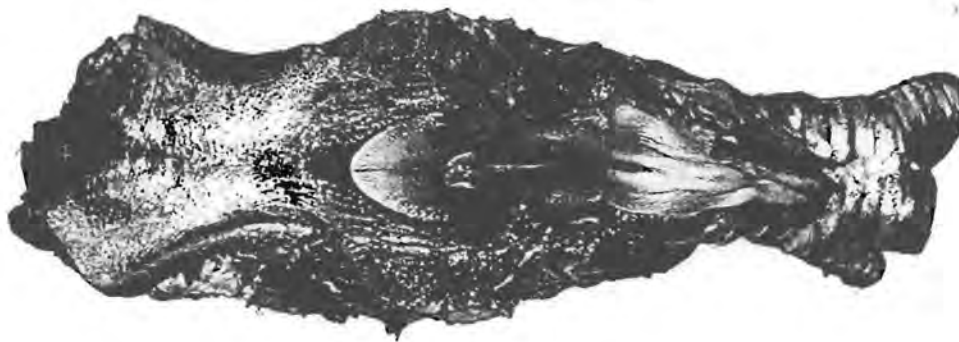


Plate 37: Ventral view of the laryngeal apparatus of a juvenile female *B. acutorostrata* showing the grey mucosal tissue (epiglottis is pulled back).



Plate 38: Transverse section of the nasopharyngeal mucosa of a juvenile female *B. acutorostrata* indicating collections of melanocytes at the base of the epidermal layer (arrow). (Mag. 100x, Haemotoxylin & Eosin (H/E) stain).

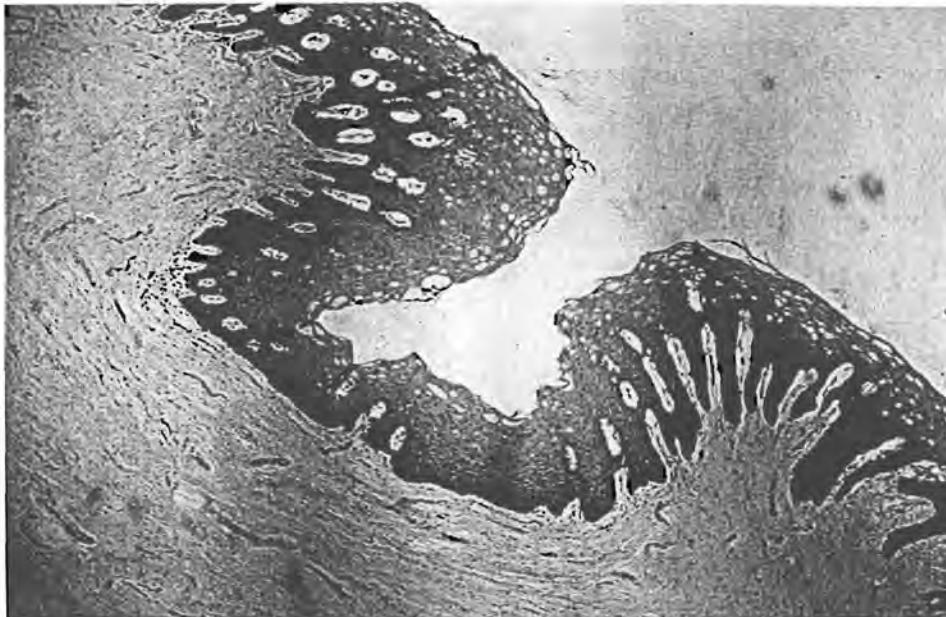


Plate 39: Transverse section of the mucosa of the narial opening of an adult male *B. acutorostrata* indicating undulations of the mucosa. (Mag. 50x, Victoria Blue (VB) stain).

muco-serous glands are present, with most of the glands being mucosal. Skeletal muscle as well as a small amount of connective tissue occurs between the epithelium and the glands. Huge ducts are present along with many blood vessels and capillaries. Lymphocytes are also present in this region and, as in the nasopharynx, collagenous "fingers" protrude into the epidermal layers.

The epiglottis originates from the floor of the pharynx. It is conical in shape, narrowing anteriorly, ending in a somewhat rounded tip, providing a seemingly hood-like appearance (Plate 40). From the dorsal perspective, the margins of the epiglottis are rounded and eventually pass into the aryteno-epiglottic folds. The dorsal surface is grooved, possessing a distinct ridge down the middle (Plate 41). A simple squamosal epithelium lines the epiglottic ridge, which consists entirely of adipose tissue (Plate 42). The ridge is thickest at its middle point and extends downwards into the laryngeal sac. The anterior portion of the epiglottis lies in a furrow on the posterior portion of the nasopharynx; this is accomplished by its free end being inserted into the posterior narial opening (Plate 43).

Simple squamosal epithelial cells characterise the epidermal layer of the pharynx, and due, once again, to the presence of melanin in the basal layer of the epidermis, the anterior region of the pharynx in the juveniles is distinctly grey in colour (Plate 43). In the adults, however, the grey coloration is not as marked, as is the case for the nasopharynx (Plate 44). A longitudinal incision along the sagittal plane of the pharynx reveals the epiglottis, and two clear groups of crypts on the left and right sides of the epiglottis (Plate 45). The crypts along the pharynx begin just below the anterior opening and continue until approximately 5 cm from the posterior tip of the epiglottis (Plate 45). Each group of crypts has, on its side closest to the epiglottis, a "crypt passage/pocket", i.e. the lining of the pharynx "invaginates" (Plate 45). These "invaginations" are also continuous with crypts (Plate 46). Thereafter, there are a few smaller crypts leading into the laryngeal area. The crypts gradually diminish in size until they disappear entirely towards the middle of the pharynx, where the mucosa becomes smooth and continues in this manner until it becomes continuous with the oesophageal mucosa.

The oesophageal mucosa is folded and, once again, distinct left and right groups of crypts occur on each side (Plate 47). The oesophagus is lined with a notably thick stratified-squamous

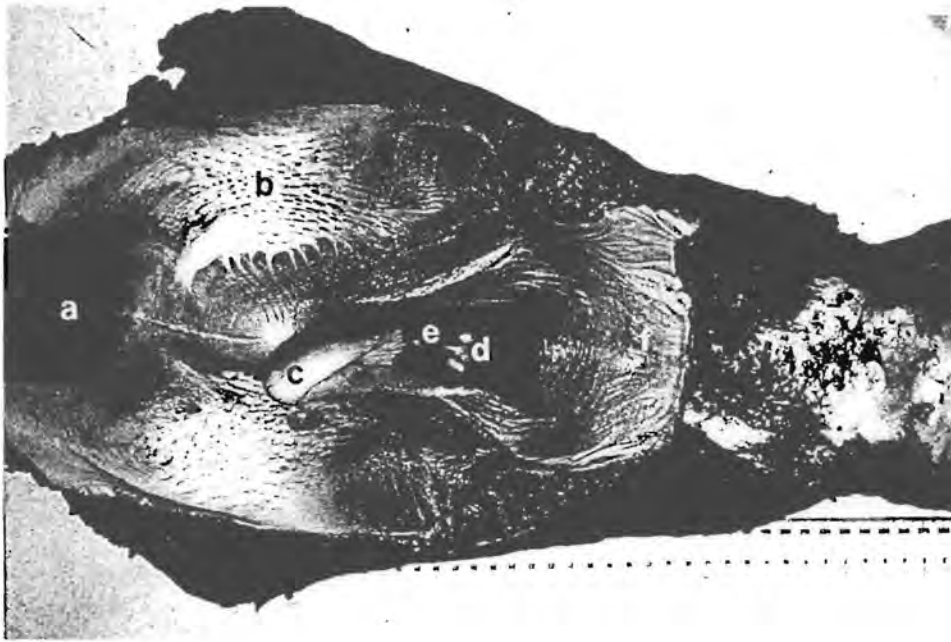


Plate 40: Sagittal section along the dorsal side of the laryngeal apparatus of a juvenile male *B. acutorostrata* exposing the (a) nasopharynx, (b) pharynx, (c) epiglottis, (d) arytenoid bodies, (e) arytenoid lips and (f) the oesophagus. Note the shape and origin of the epiglottis.

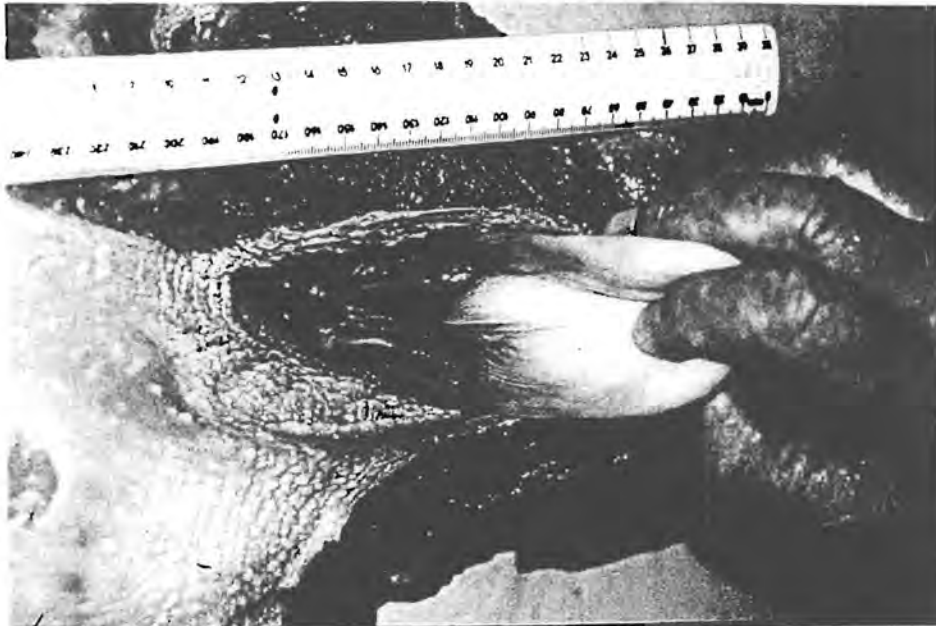


Plate 41: Ventral view of the epiglottis (pulled back) exposing the epiglottic ridge of a juvenile male *B. acutorostrata*.

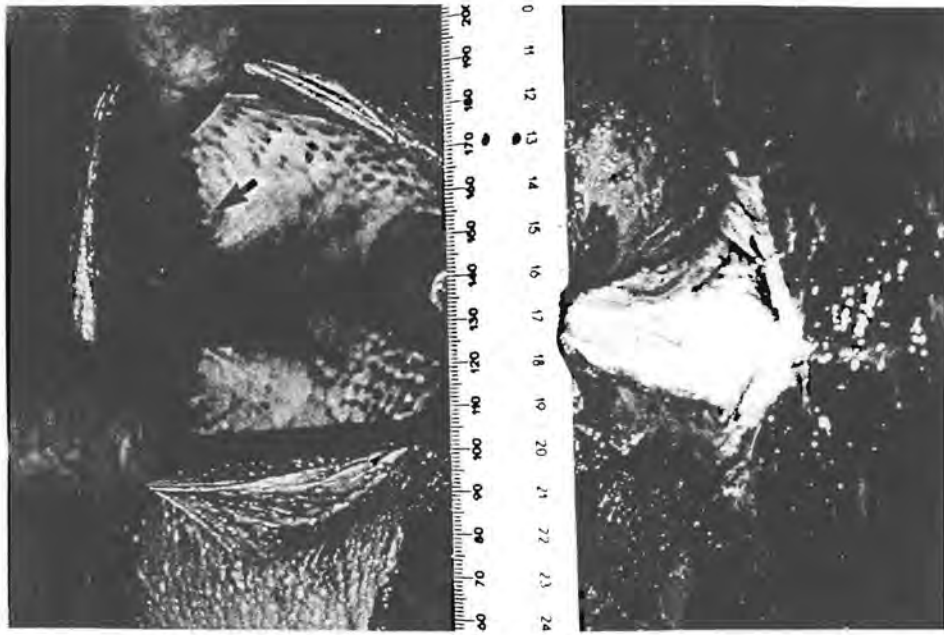


Plate 46: Ventral view of the epiglottic protrusion of a juvenile male *B. acutorostrata* (posterior nare pulled back). Note the presence of crypts in the crypt passages (arrow).

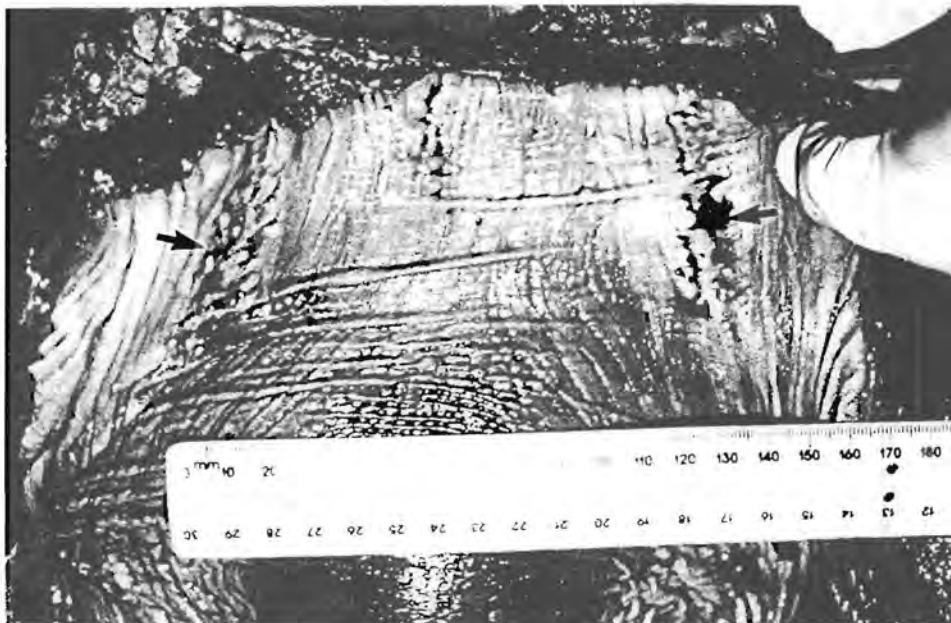


Plate 47: Dorsal view of the oesophagus of an adult female *B. acutorostrata* (exposed by a sagittal incision) showing distinct groups of crypts (arrows).



epithelial layer and mucous glands are present in great numbers (Plate 48). The base of each crypt has a duct opening into it and they are surrounded by lymphocytes. Enormous lymph nodes (resembling tonsils) are present amongst the many glands (Plate 49).

As previously mentioned, the arytenoid bodies project beneath the root of the epiglottis. The lips which join the anterior tips of the arytenoid bodies possess a stratified squamous epithelial layer which covers mainly connective tissue intermingled with collagen fibres (Plate 50). This region forms the posterior margin of the entrance into the laryngeal area, leading into the trachea. The tracheal mucosa lines the ventral surface of the body of the cricoid cartilage and the dorsal wall of the laryngeal sac (Plate 51). The lining of the trachea is brown in colour and is characterised (on the dorsal wall of the laryngeal sac) by tasselled folds (Plates 26 and 52) which are covered by a thick stratified columnar epithelium (Plate 53). The epithelium is thicker in the depressions compared to the edges of the protrusions (Plate 54). This epithelium is not typical stratified columnar epithelium as the top-most cells are not squamous but columnar in nature. On inspection, the cells merge from thick stratified squamous cells to less thick cells, to stratified columnar cells which merge with very thin pseudo-stratified columnar cells. Small aggregations of lymphocytes are present as well as goblet cells. Mucous glands are present, but are restricted to regions of the epidermis (Plate 55).

The trachea continues posteriorly where it is surrounded and supported by cartilagenous (tracheal) rings and eventually splits to form the bronchi (Plates 18 and 56). The tracheal rings are incomplete ventrally and terminate with rounded ends. Dorsally, preceding rings are fused with succeeding rings making the definition of individual rings quite difficult.

The upper tracheal rings are continuous dorsally with the cricoid cartilage (Plates 19 and 57) and ventrally they provide attachment for the laryngeal sac (Plate 58).

The laryngeal sac lies on the ventral aspect of the larynx, below the thyroid cartilage and between the cricoid cornua (Plate 58). The ventral wall of the sac is formed by a thick skeletal muscular layer (Plate 59). The mucosa of the laryngeal sac is smooth with two distinct rows of crypts on either side of the sac which diminish in size at the posterior end of the sac and meet up to form a group of smaller crypts around the rounded end of the sac (Plate 60). Pseudo-stratified



Plate 48: Transverse section of the oesophageal mucosa of an adult male *B. acutorostrata* showing the thick stratified squamous epithelial layer and large mucous glands (arrow). (Mag. 50x, H/E).



Plate 49: Transverse section of the oesophageal mucosa of an adult female *B. acutorostrata* showing (a) enormous lymph nodes occurring below the epidermis and above large glands. (Mag. 50x, H/E).

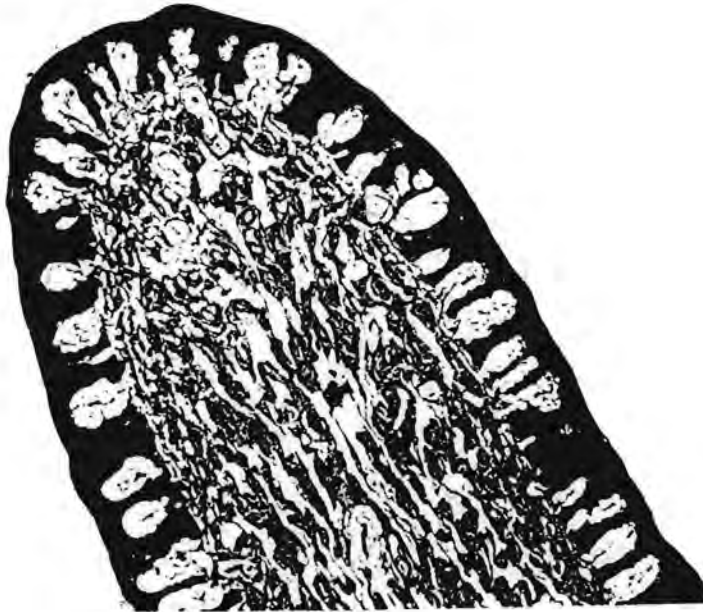


Plate 50: Transverse section of the right hand side arytenoid lip of an adult female *B. acutorostrata*. Note the large amounts of connective tissue (blue/green). (Mag. 50x, VB).



Plate 51: Lateral view of (a) the laryngeal sac and the tracheal rings of an adult female *B. acutorostrata* showing that the tracheal mucosa is continuous with the ventral surface of the body of the cricoid cartilage and the the dorsal wall of the laryngeal sac.

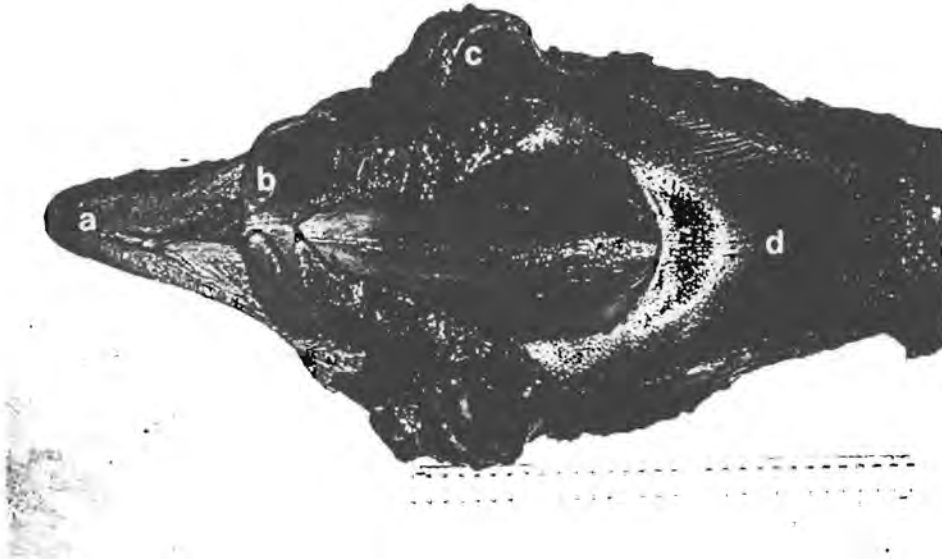


Plate 52: Dorsal view of the (a) epiglottis, (b) tips of the arytenoid bodies, (c) processus musculares and the (d) laryngeal sac of an adult female *B. acutorostrata*. Note the folded nature of the tracheal/external laryngeal sac mucosa.



Plate 53: Transverse section of the tracheal mucosa of an adult male *B. acutorostrata* showing the folded nature of the mucosa. (Mag. 50x, H/E).



Plate 54: Transverse section of the tracheal mucosa of an adult male *B. acutorostrata* showing the thicker epithelium in the depressions of the mucosa. (Mag. 50x, H/E).



Plate 55: Transverse section of the tracheal mucosa of an adult male *B. acutorostrata* showing the restriction of mucous glands to the epidermal region. Note the atypical epithelial structure and ducts which pierce the epithelium. (Mag. 50x, H/E).

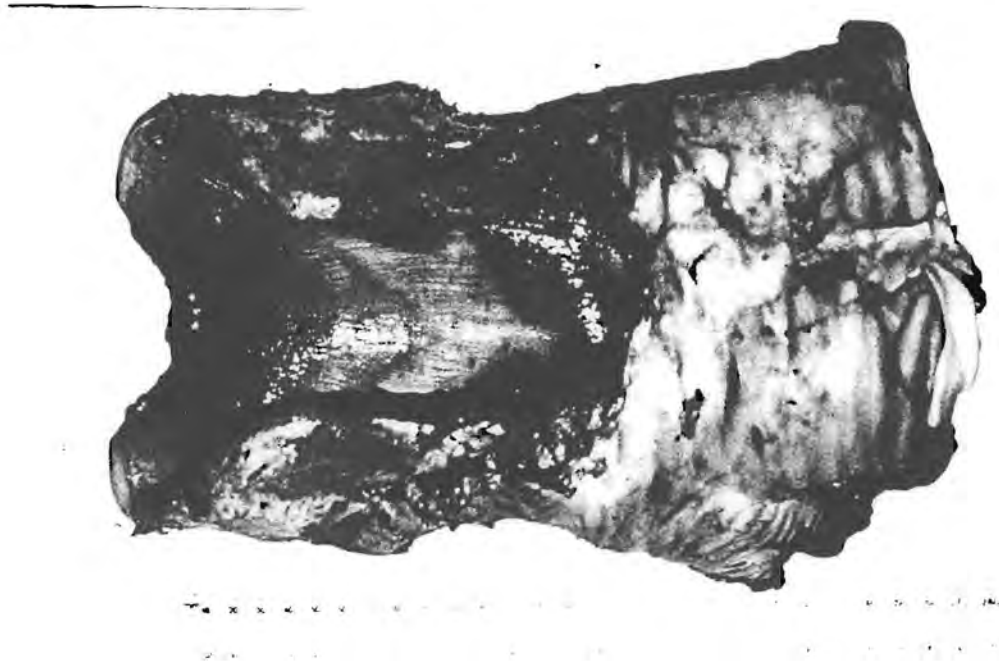


Plate 56: Ventral view of the cricoid cartilage continuous with the tracheal rings of a juvenile male *B. acutorostrata*, which split to form the bronchi.

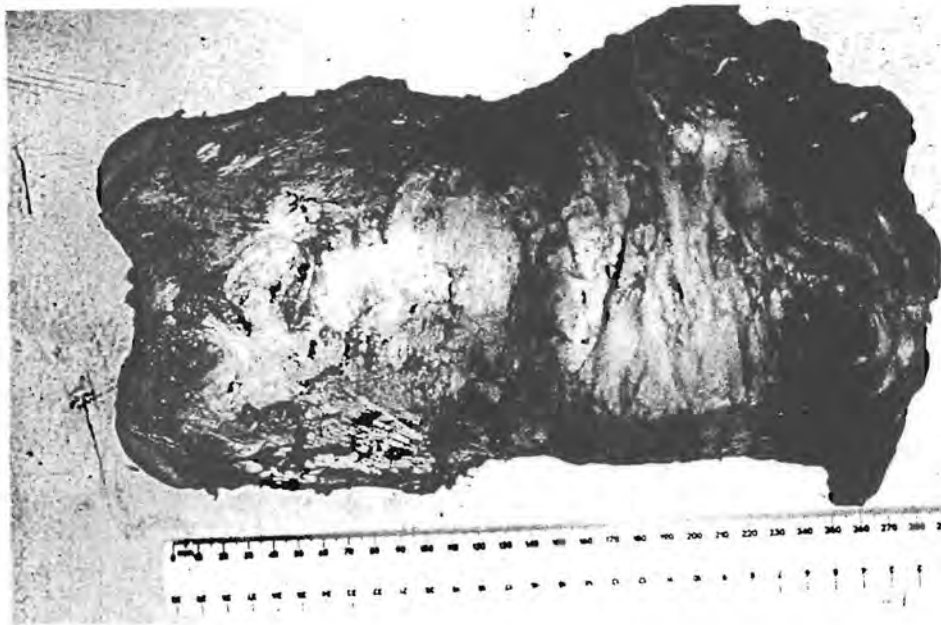


Plate 57: Dorsal view of the body of the cricoid cartilage of a juvenile male *B. acutorostrata* which is continuous with the tracheal rings.

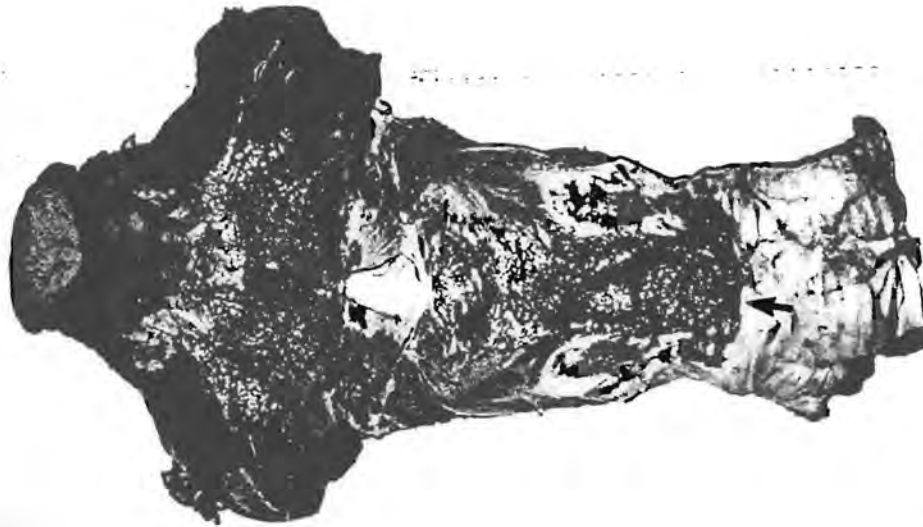


Plate 58: Ventral view of the laryngeal apparatus of a juvenile male *B. acutorostrata*. Note the posterior attachment of the laryngeal sac with the tracheal rings (arrow).

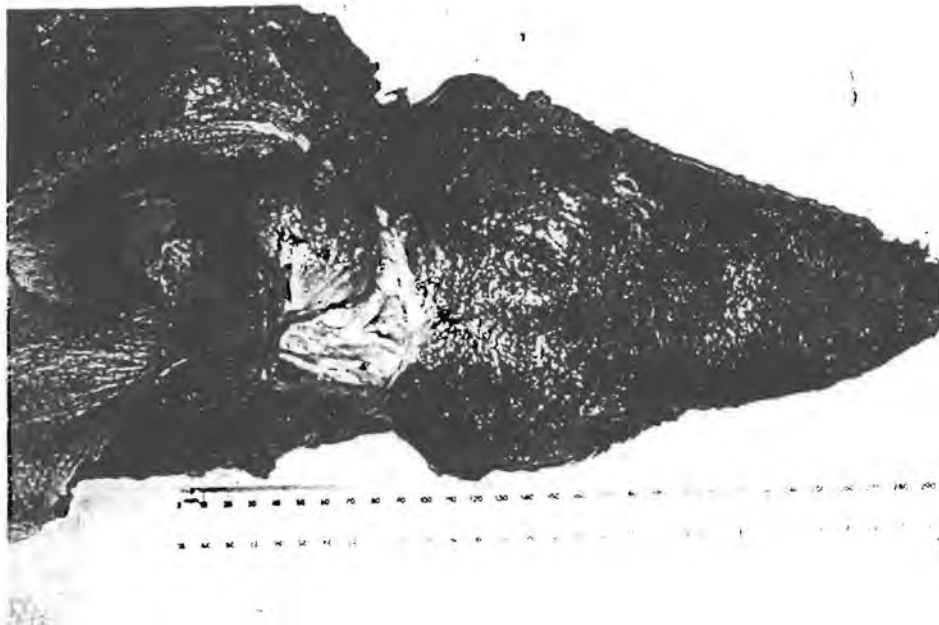


Plate 59: Ventral view of the muscular wall of the laryngeal sac of a juvenile male *B. acutorostrata*.

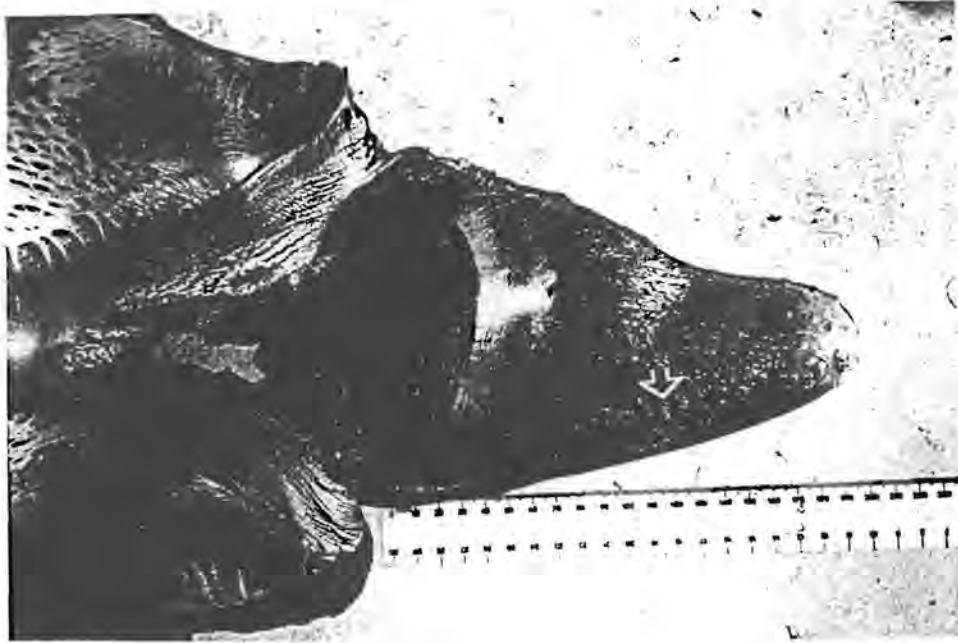


Plate 60: Dorsal view of the mucosa of the laryngeal sac of a juvenile male *B. acutorostrata*. Note organisation of crypts (arrow) (sac turned inside out).



Plate 61: Transverse section of the mucosa of the laryngeal sac of an adult male *B. acutorostrata*. Note lymphoid tissue in depression. (Mag. 100x, VB).



columnar epithelium lines the inside of the laryngeal sac (Plate 61). Beneath the epidermis there are three layers of dense connective tissue with extremely large scattered serous glands, adipose tissue interspersed with connective tissue, and skeletal muscle, respectively (Plate 62).

Skeletal muscle is present in all the layers, but increases in abundance towards the exterior of the sac. This whole region is infiltrated with lymphocytes and lymphoid tissue is found in the depressions occurring along the epidermis (Plate 61). Deep ducts leading from the many glands are lined with pseudo-stratified cuboidal epithelial cells, which are unusually elongated (Plate 63). These ducts appear to pierce the epithelium of the laryngeal sac (Plate 63). The whole structure is innervated and very well vascularised, having adipose tissue, elastin and collagen fibres dispersed throughout (Plate 64). Measurements taken from the bottom of the notch of the thyroid cartilage to the end of the sac reveal its length to be 11 cm in the juvenile male (Plate 60), 11.3 cm in the juvenile female (Plate 65), 22.5 cm in the adult male (Plate 66) and 28.8 cm in the adult female (Plate 67). The width of the sac decreases posteriorly to give the sac a triangular shape (Plates 59 and 65-67). Measured at their widest points, in the same order as above, the sacs measured, 8.3 cm, 12.2 cm, 15.4 cm and 20.9 cm, respectively.



Plate 62: Transverse section of the dorsal mucosa of the laryngeal sac of an adult male *B. acutorostrata*. Note muscle interspersed between glands, adipose tissue and blood vessels. (Mag. 100x, VB).



Plate 63: Transverse section of the ventral mucosa of the laryngeal sac of an adult female *B. acutorostrata* showing ducts leading from glands which are lined with elongated, cuboidal epithelial cells and lymphatic tissue below the epidermis (arrow). (Mag. 100x, H/E).



Plate 64: Transverse section of the ventral wall of the laryngeal sac of an adult male *B. acutorostrata* showing (a) large nerves and (b) blood vessels. (Mag. 100x, H/E).

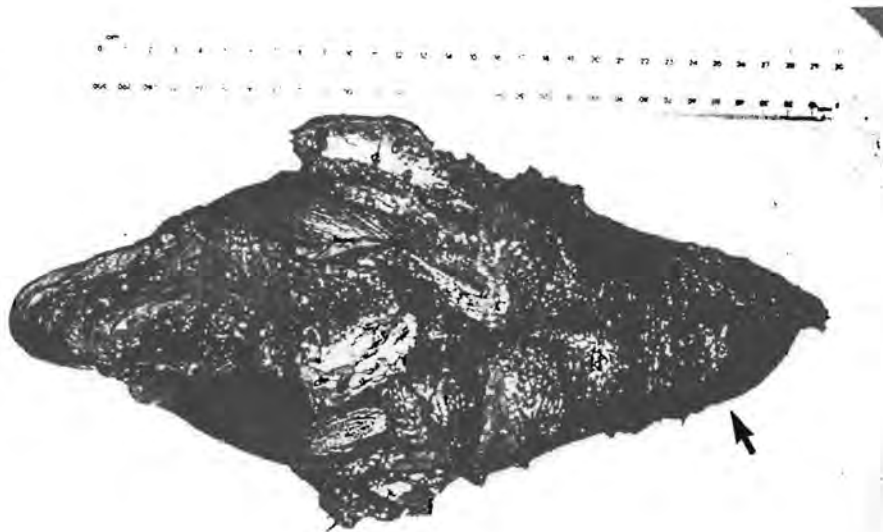


Plate 65: Ventral view of the laryngeal sac (arrow) of a juvenile female *B. acutorostrata*.

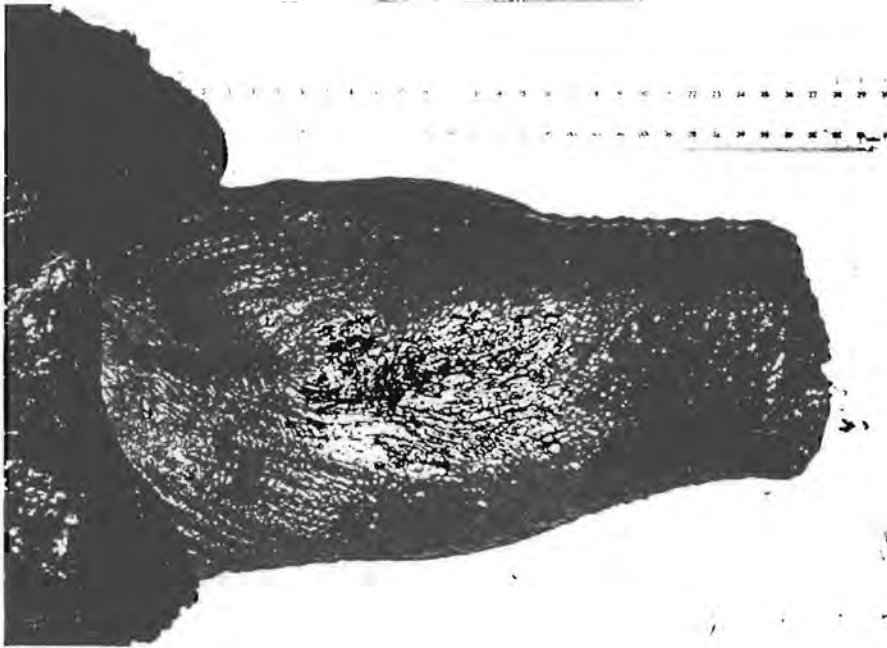


Plate 66: Ventral view of the laryngeal sac of an adult male *B. acutorostrata* (sac turned inside out).

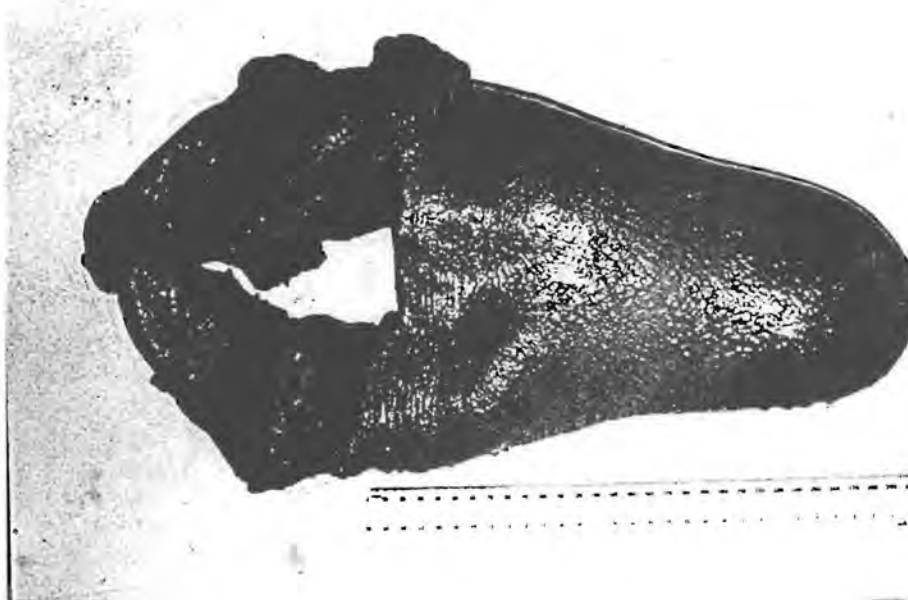


Plate 67: Dorsal view of the laryngeal sac of an adult female *B. acutorostrata* (sac turned inside out).

### 3.3 Gross anatomy of *Caperea marginata*

The overall organisation of the laryngeal apparatus of *C. marginata* conforms with that of *B. acutorostrata*, but structural differences do occur, and these are discussed below.

Lengths of the laryngeal apparatus' were measured from the nasopharynx to end of tracheal rings (when present), and ranged from 23.4 cm in the juvenile male (91/27) (Plate 68), 29.2 (Plate 69) to 37.2 cm (Plate 70) in the juvenile females (90/12 and 89/3, respectively) and 60.9 cm in the adult male (93/07) (Plate 71). These measurements are as accurate as possible, bearing in mind that the nasopharynges and tracheal rings were not complete in most of the specimens. However, the complete viscera of the last-mentioned juvenile female (89/3) was available, so that all the tracheal rings remained intact (Plate 70).

The most outstanding character, evident on the ventral wall of the laryngeal apparatus of the juvenile female (90/12), was the presence of part of the aorta (which moves from the left hand to the right hand side of the apparatus) and the ducti arteriosus and ligamentum (Plate 73).

The only adult specimen was procured after the process of autolysis had already begun and unfortunately, when preserved, the apparatus underwent considerable distortion during subsequent fixation in a large drum. Consequently, even though some assumptions could be made with reference to the juvenile specimens, the gross morphological character of the adult larynx of this species was difficult to determine from this specimen.

#### a) Bones

Unfortunately none of the specimens of *C. marginata* possessed sternum bones, and hyoid bones were only preserved in one of the juvenile females (89/3) (Plate 72).

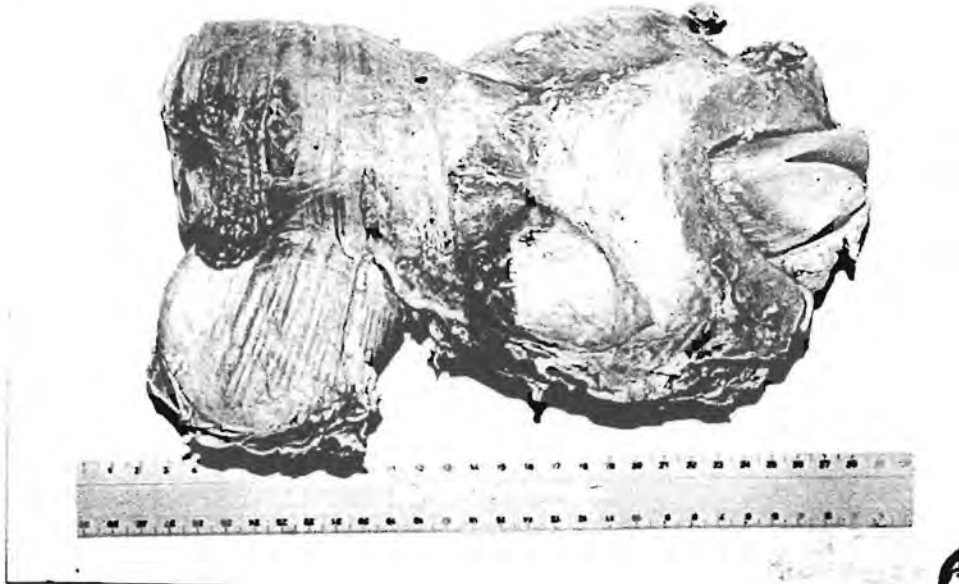


Plate 68: Dorsal view of the laryngeal apparatus of a juvenile male *C. marginata*.

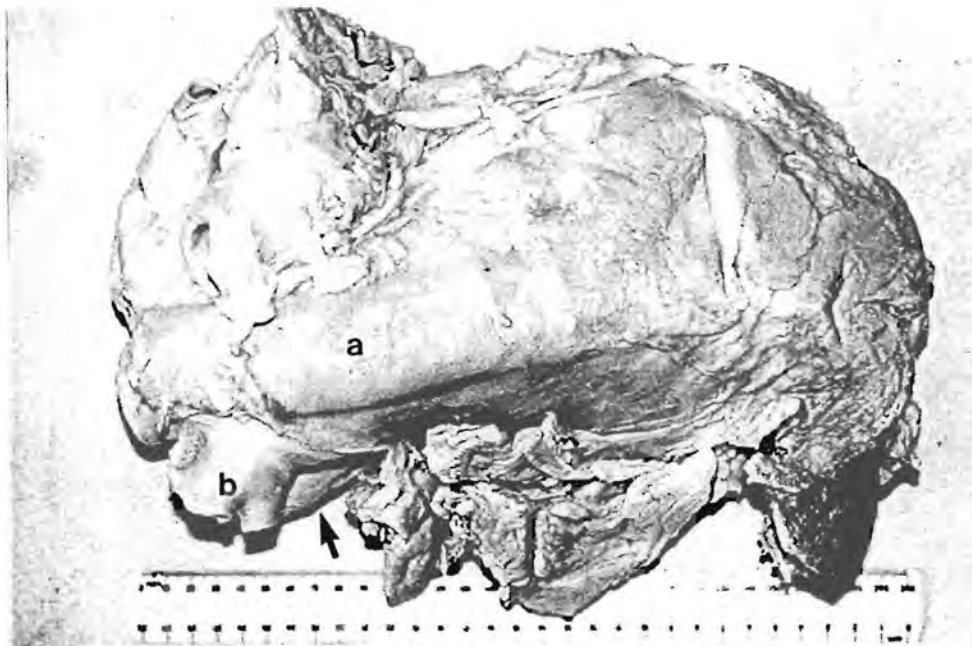


Plate 69: Dorsal view of the laryngeal apparatus of a juvenile female *C. marginata* (# 90/12). Note (a) oesophagus, (b) tracheal rings, (arrow) laryngeal sac.

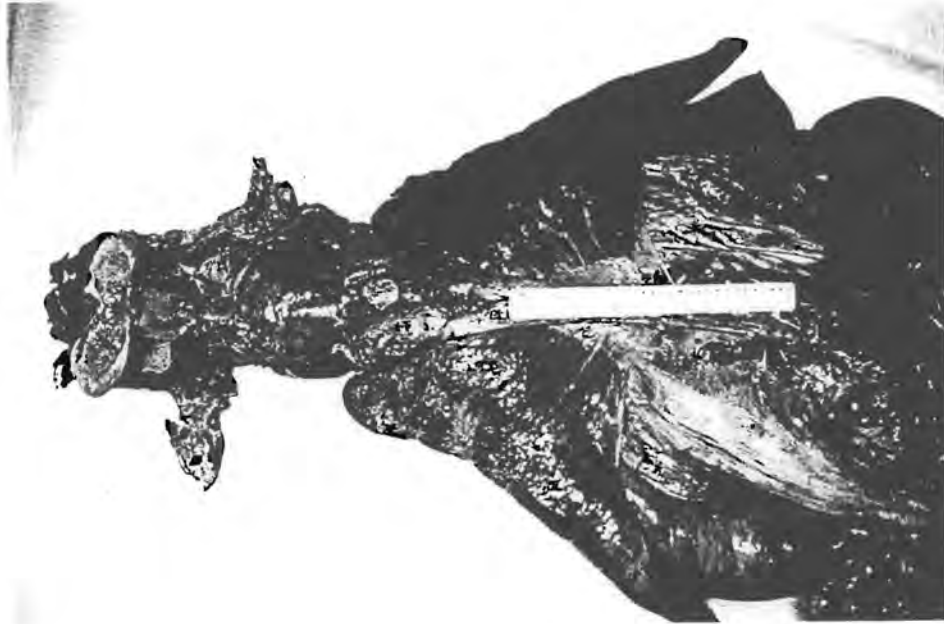


Plate 70: Dorsal view of the laryngeal apparatus of a juvenile female *C. marginata* (# 89/3).

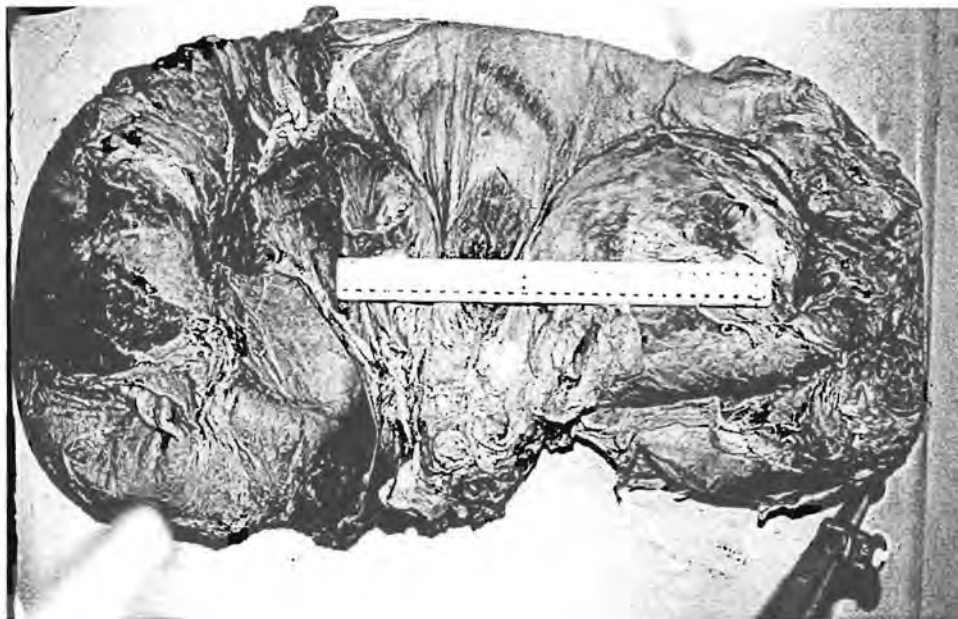


Plate 71: Lateral view of the laryngeal apparatus of an adult male *C. marginata* (ventral surface facing upwards).



Plate 72: Ventral view of the hyoid bones attached to the laryngeal apparatus of a juvenile female *C. marginata* (# 89/3).

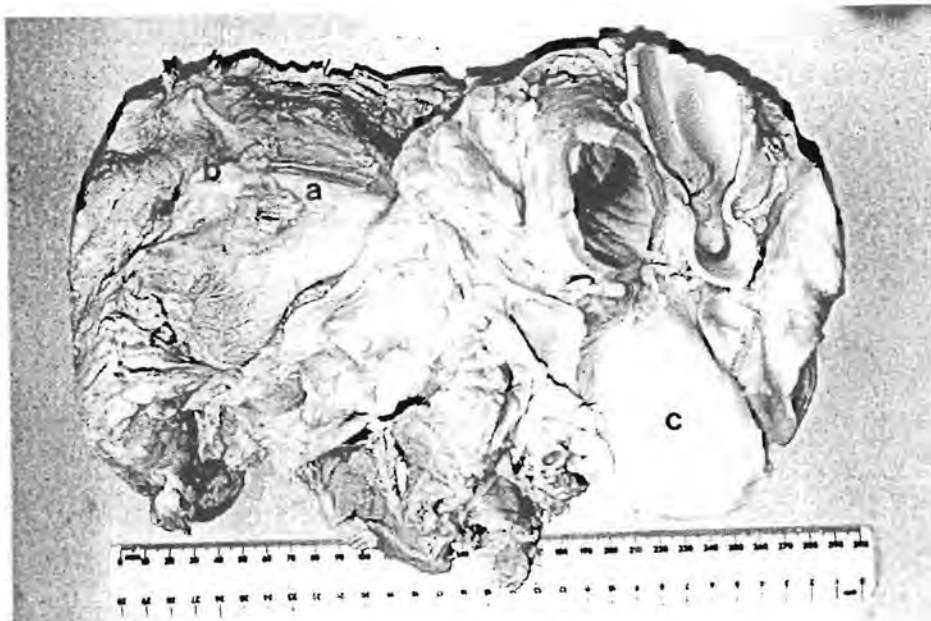


Plate 73: Ventral view of the laryngeal apparatus of a juvenile female *C. marginata* (# 90/12) showing the ducti arteriosus and ligamentum. Note (a) thyroid cartilage, (b) epiglottic protrusion, (c) laryngeal sac.



i) *Hyoid bones*

The styloid bones of the juvenile female (89/3) are articulated with the os hyoides via small interconnecting pieces of cartilage, which are attached on each side of the posterior "v" of the os hyoides (Plate 74). The cartilage pieces themselves are not contiguous with either the os hyoides or the styloid bones and are attached to both only by small clumps of soft connective tissue, measuring approximately 3 cm in length.

The styloid bones are curved and lie attached to the apparatus in the form of horizontal "s"-shapes. The measurements of the various bones are given in Table 5.

b) *Cartilages*

The single thyroid, cricoid, epiglottic and the paired arytenoid cartilages are present in *C. marginata* and the positioning of these cartilages in the laryngeal apparatus of this species correlates with the positioning of these cartilages in *B. acutorostrata*. As in *B. acutorostrata*, the softness and flexibility of the various cartilages is a notable characteristic. The measurements of the various cartilages are given in Table 5.

i) *Thyroid cartilage*

The thyroid cartilage itself is soft, but is much sturdier compared to the extremely flexible thyroid cartilages found in *B. acutorostrata*. Distinct tubercles are present and in one of the juvenile females (89/3), form a distinctive shape (Plate 75). An anterior view of this specimen's cartilage shows that the tubercles possess dorsal cartilaginous peaks, which continue basally as two forward/ventral facing protrusions (Plate 75). All the specimens of this species possess a distinct ridge on the mid-ventral line of the thyroid cartilage which seems to provide attachment for the epiglottal protrusion (Plate 76).

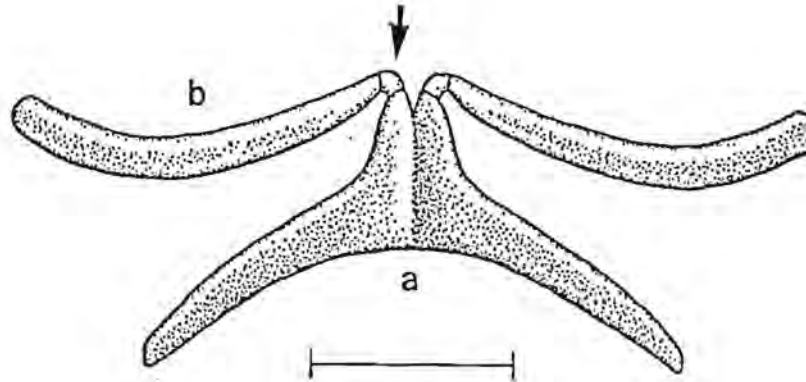


Plate 74: Ventral view of (a) the os hyoides and (b) the styloid bones of a juvenile female *C. marginata* (# 89/3) showing the cartilaginous pieces connecting the os hyoides to the styloid bones (arrow). Note scale bar = 10 cm.

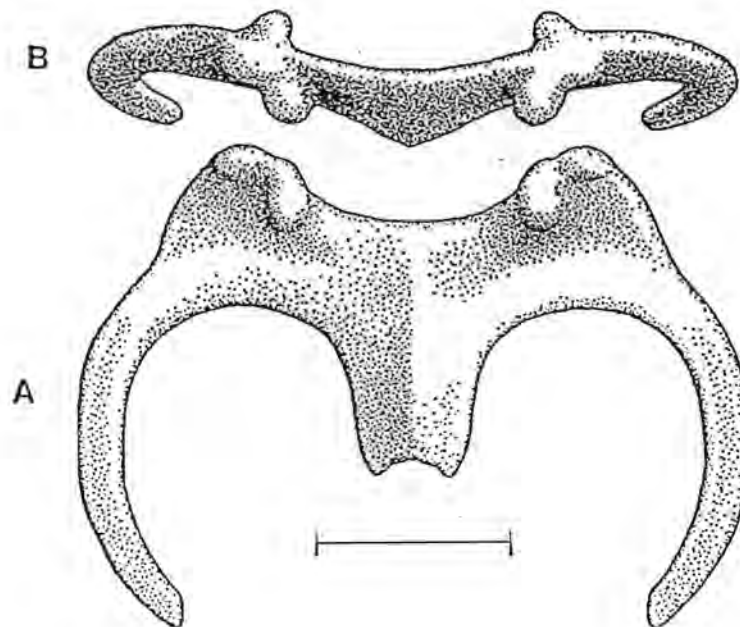


Plate 75: (A) Ventral view and (B) top view of the thyroid cartilage of a juvenile female *C. marginata* (# 89/3) showing distinct tubercles. Note the distinctive shape of the tubercles. Note scale bar = 5 cm.

Table 5 Measurements associated with the laryngeal apparatus of *C. marginata*.

Cartilage/Bone Measurements (cm) (specimen #)		Juvenile ♀ (89/3)	Juvenile ♀ (90/12)	Juvenile ♂ (91/27)	*Adult ♂ (93/07)
Entire apparatus	Total length	37.2	29.2	23.4	60.9
Thyroid cartilage	Total length	11.7	13.7	12.5	25.0
	Body width	12.4	14.1	11.0	30.0
Cricoid cartilage	Length	10.4	11.3	9.9	18.2
	Width	9.4	9.5	9.5	21.3
Epiglottic cartilage	Total length	8.5	7.9	4.4	15.2
Arytenoid cartilages	Ave total length	15.2	14.5	15.2	28.2
Os hyoides	Length cornua LHS	22.6	-	-	-
	Length cornua RHS	tip cut	-	-	-
	Width of body - measured from bottom of "v" notch	3.7	-	-	-
Styloid bones	Total length (LHS)	19.5	-	-	-
	Total length (RHS)	21.0	-	-	-
	Average width - at thickest region	2.1	-	-	-

\* Deformed character of specimen resulted in measurements differing from one side of a cartilage/bone to another, therefore, where applicable, averages are quoted.

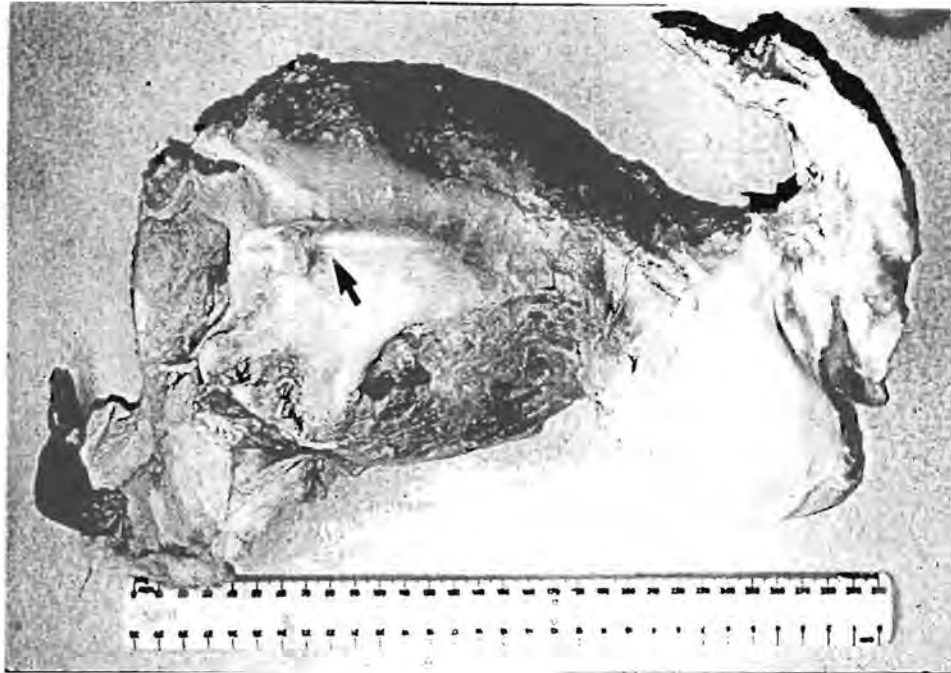


Plate 76:

Ventral view of the thyroid cartilage on the ventral surface of the laryngeal apparatus of a juvenile female *C. marginata* (# 90/12). Note distinct ridge along the mid-line of the thyroid cartilage being attached to the epiglottic protrusion (arrow).

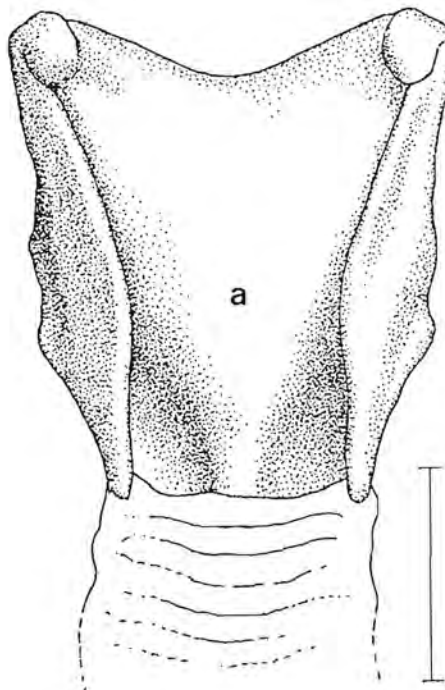


Plate 77:

Ventral view of the cricoid cartilage of a juvenile female *C. marginata* (# 90/12) attached to the tracheal rings. Note (a) the distinct cushion on the anterior ventral surface of the cricoid body. Note scale bar = 5 cm.

ii) *Cricoid cartilage*

The general structure and situation of the cricoid cartilage in *B. acutorostrata* is reflected in *C. marginata*, forming a cartilaginous plate dorsally and being incomplete ventrally (Plate 77). The major difference in the cricoid cartilage of *C. marginata* is that although the body does continue laterally and ventrally (forming raised arches) no distinct cornua are present (Plate 78). The "cushion" on the inside, anterior region of the body is well developed, continuing posteriorly as a ridge towards the tracheal rings (Plate 77). In this species, the middle region of the dorsal surface of the cricoid plate is indented (Plate 79). Foramina are also present in the posterior region. In the juvenile male, the cricoid cartilage is continuous with the first tracheal ring, while in the two juvenile females the cricoid is continuous with the third (90/12) and fourth (89/3) tracheal rings, respectively. Unfortunately in the adult male, the tracheal rings as well as the cricoid cartilage's association with them was indeterminable.

iii) *Epiglottic cartilage*

As in *B. acutorostrata*, a portion of the epiglottic cartilage protrudes through the ventral, muscular surface of the laryngeal apparatus, anterior to the thyroid cartilage (Plate 80). This protrusion was initially thought to be an extension of the thyroid cartilage, forming a "peak" between the tubercles. On closer inspection it was evident that this "peak" is in fact the epiglottic protrusion which is attached by connective tissue to the mid-ventral ridge of the thyroid cartilage (Plate 76). However, in the adult male it is evident that the thyroid and the epiglottic cartilage are continuous with each other, a union which presumably occurs as the animals age (Plate 81).

The epiglottic cartilage is reduced compared to that of *B. acutorostrata*. The comparable hood, which is tightly associated with the arytenoid bodies, only extends to the top of these bodies and is not as conspicuous as that of *B. acutorostrata* (Plate 82). A middle ridge and aryteno-epiglottic folds are barely discernible (Plate 83). The shape of the cartilage can be compared to a spoon, i.e. anteriorly it is convex, from a ventral perspective, continuing posteriorly into a broad rod

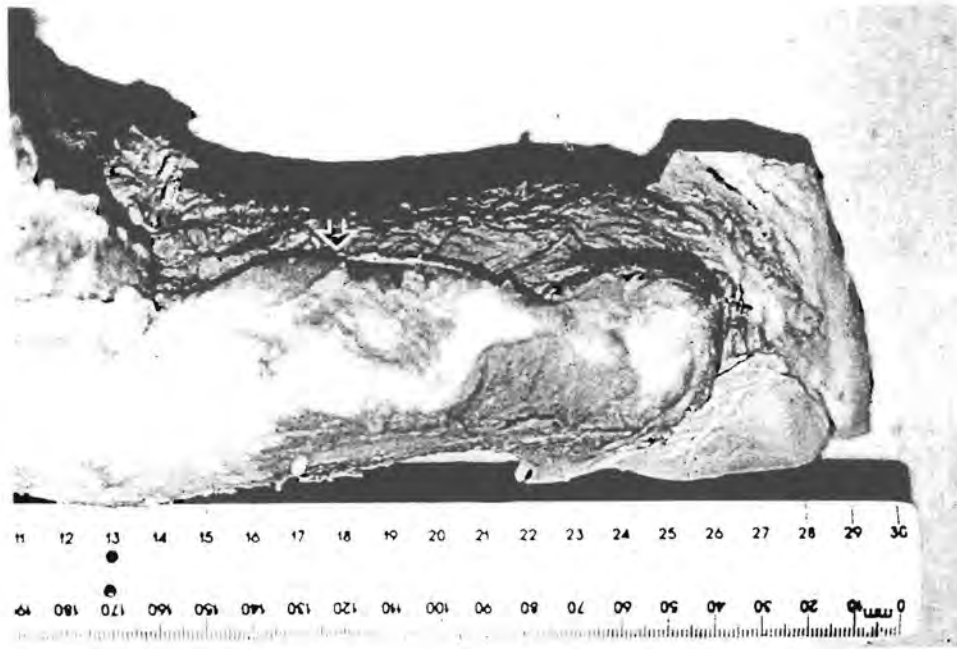


Plate 78: Lateral view of the cricoid cartilage of a juvenile female *C. marginata* (# 90/12) showing the lack of distinct ventral cornua (arrow).



Plate 79: Dorsal view of the cricoid cartilage attached to the tracheal rings of a juvenile female *C. marginata* (# 89/3) indicating the indented nature of the middle region of the cricoid cartilage (arrow).

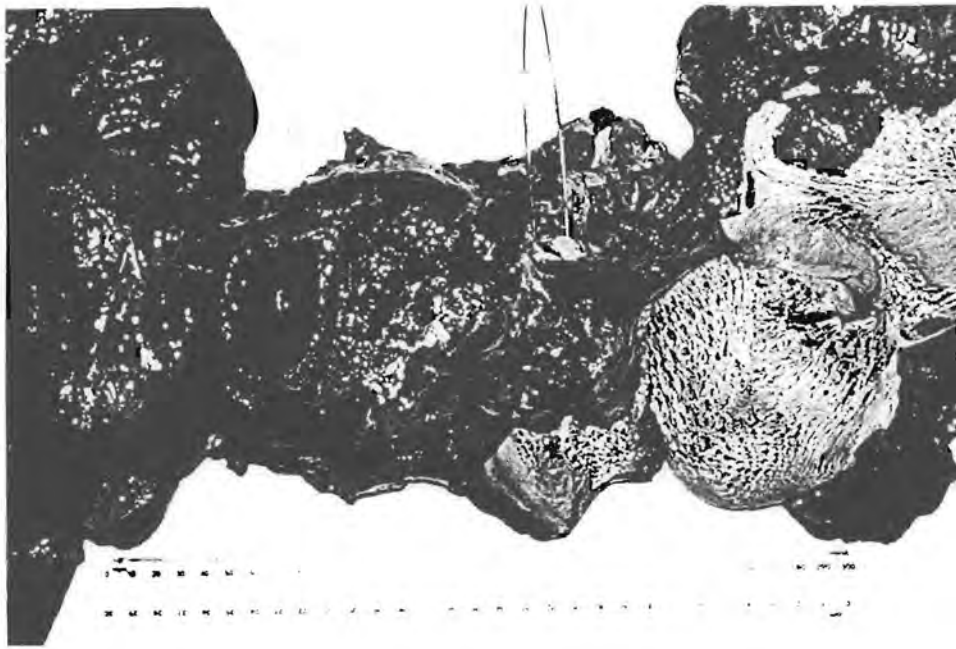


Plate 80: Ventral view of the laryngeal apparatus of a juvenile female *C. marginata* (# 89/3) with the epiglottic protrusion being indicated by the forceps.

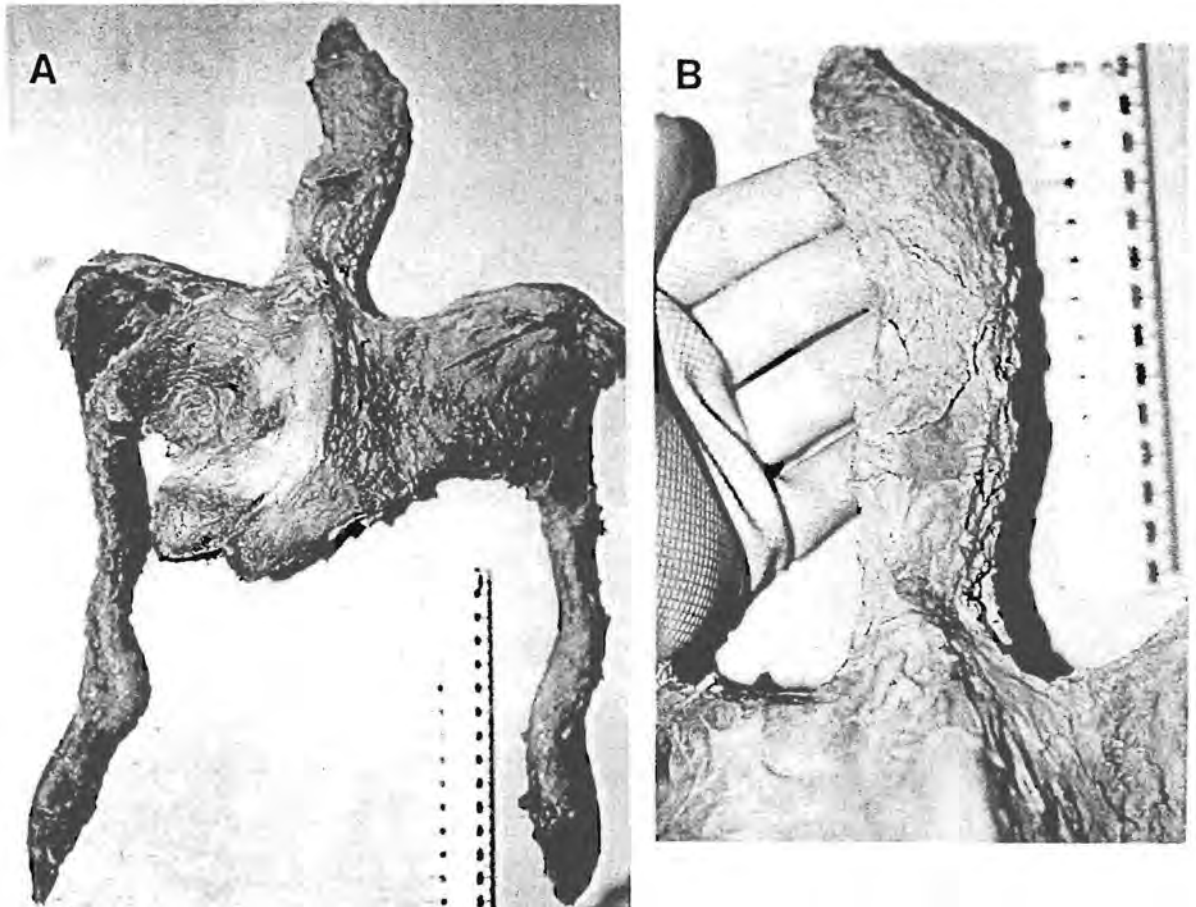


Plate 81: (A + B) Ventral view of a thyroid and epiglottic cartilage of an adult *C. marginata* (distorted during preservation). Note the continuation of the thyroid cartilage with the epiglottic cartilage (tip of the epiglottic protrusion has been cut off).

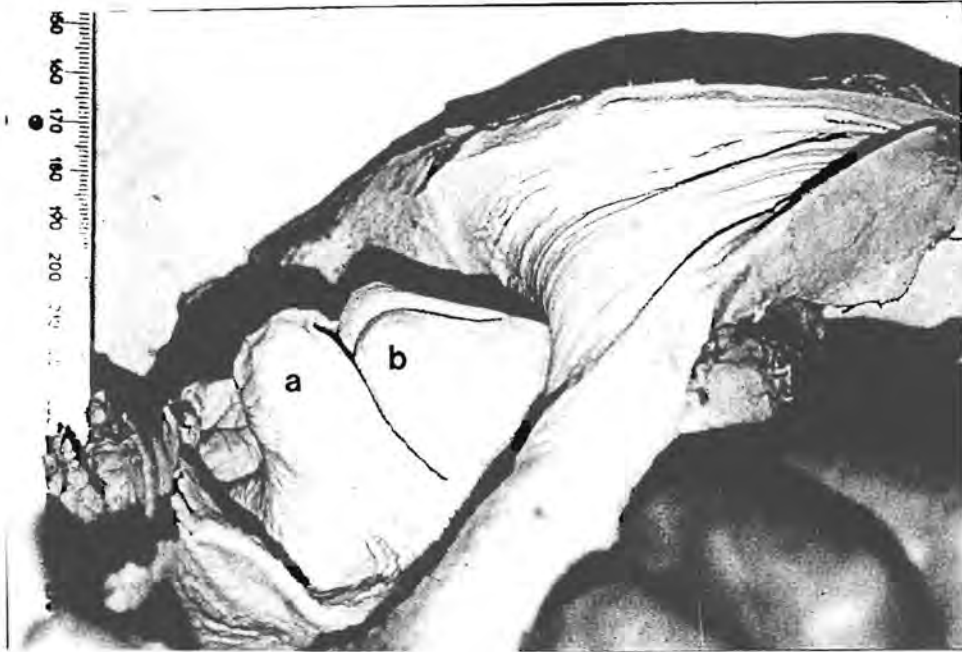


Plate 82: Lateral view of (a) the anterior region of the epiglottic cartilage and (b) the arytenoid bodies of a juvenile female *C. marginata* (# 90/12). Note reduced size of the epiglottic "hood".

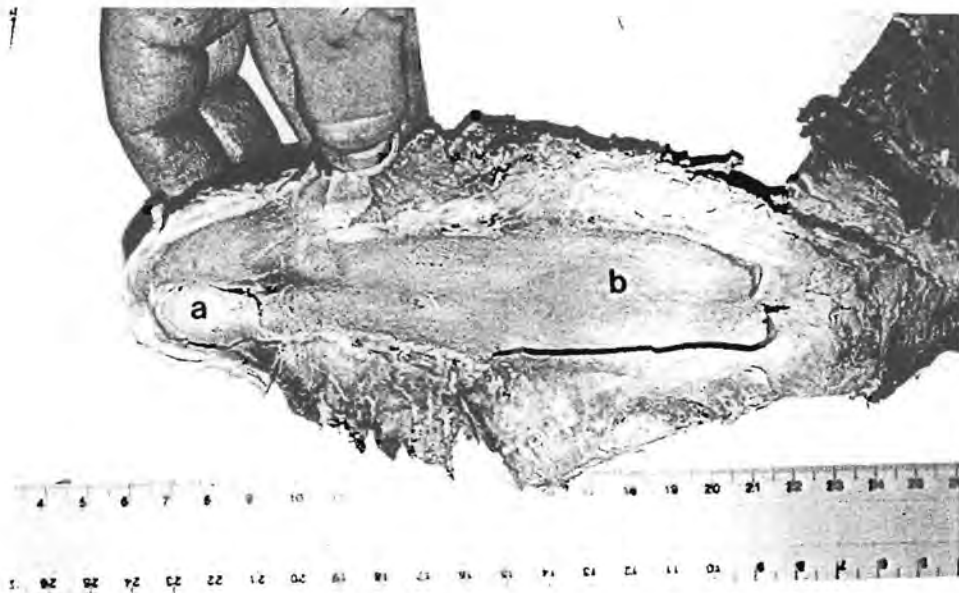


Plate 83: Dorsal view of (a) the epiglottis and (b) the trachea (arytenoid cartilages have been removed) of a juvenile male *C. marginata*. Note the lack of a middle ridge and of distinct aryteno-epiglottic folds of the epiglottis.



(which is slightly convex) (Plate 84), which eventually becomes continuous with the thyroid cartilage in the adult male. The anterior and posterior margins of the cartilage are slightly extended, forming small wings (Plate 84).

iv) *Arytenoid cartilages*

The arytenoid cartilages of *C. marginata* are more compact in structure than those of *B. acutorostrata* i.e. the arytenoid bodies are continuous posteriorly with the processi vocales so that on first inspection there is no clear point of separation between the two aforementioned components of these cartilages (Plate 85). The tips of the arytenoid bodies are broad and are laterally flattened. In the juveniles, the right hand side tip generally projects 0.6 cm further than the left hand side tip (Plate 82) and in the adult, the left hand side tip projects 2.2 cm further than the right hand side tip. The crescentic "wings" are reduced in size and no connective tissue "lips" are present (Plates 82 and 85). The anterior tips of the arytenoids are firmer compared to those found in *B. acutorostrata* and the inner surface of the arytenoid bodies are pitted and have a rough texture, reminiscent of the tongue of a cat (Plate 86). This coarse epithelium is covered with crypts and joins the bodies on their interior, medial sides. The processi vocales are joined posteriorly by connective tissue and they are not continuous with the dorsal wall of the laryngeal sac, but they do provide the connection between the laryngeal sac and the rest of the apparatus (Plate 87). Approximately three-quarters of the way down the ventral side of the processi vocales, there is a small opening (approximately 1 cm in length) which leads into the laryngeal sac, thus making the opening between the arytenoid wings the connection between the trachea and the laryngeal sac (Plate 88).

- Once dissected out, each arytenoid cartilage seemed to consist of two components which merge to form the arytenoid bodies i.e. the ventral margins of the arytenoid bodies continue posteriorly as narrow rods which are closely associated, but separate, to the interior margin of the processi vocales. The processi vocales and processi musculares continue anteriorly along their interior margins to form the dorsal margins of the arytenoid bodies (Plate 89).

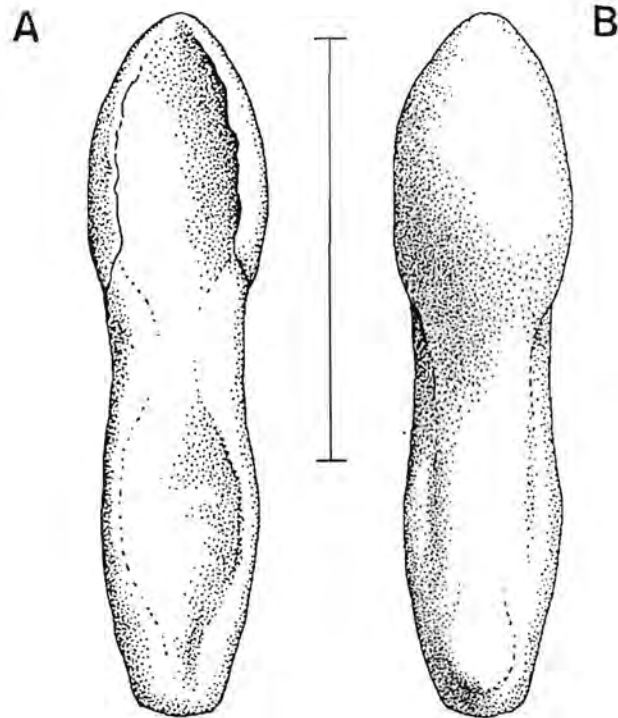


Plate 84: Dorsal (A) and ventral (B) view of the epiglottic cartilage of a juvenile female *C. marginata* (# 89/3). Note scale bar = 5 cm.

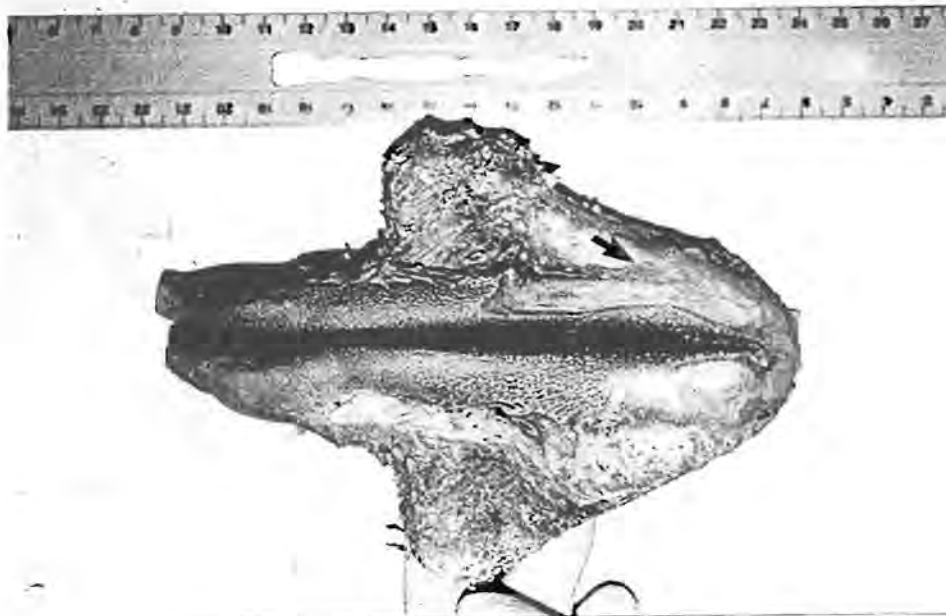


Plate 85: Ventral view of the arytenoid cartilages of a juvenile male *C. marginata*. On first inspection there is no clear point of separation between the arytenoid bodies and the processus vocales (arrow).

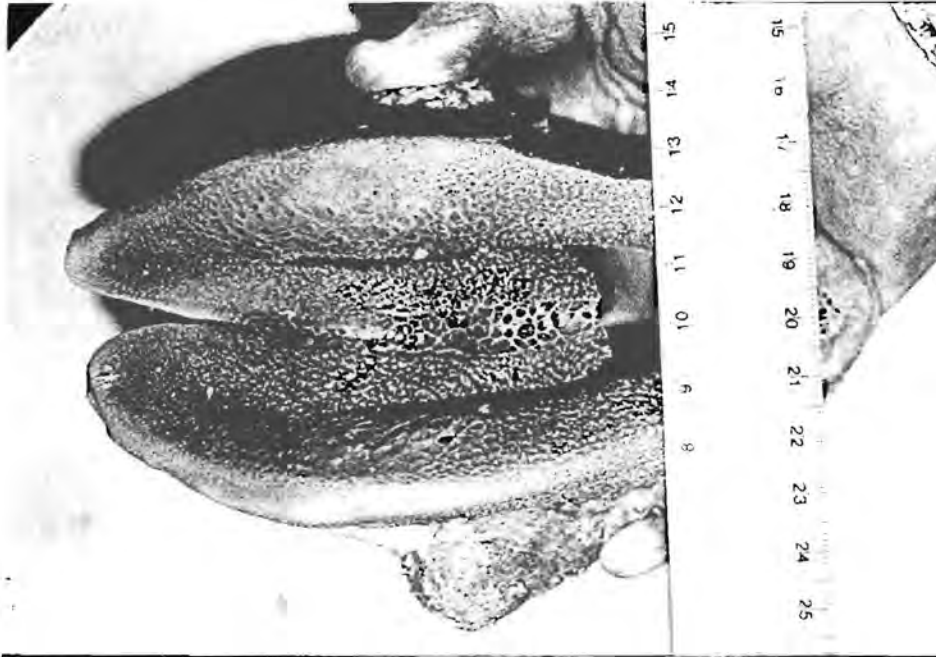


Plate 86: Ventral view of the arytenoid cartilages of a juvenile male *C. marginata*. Cartilages have been parted to expose the pitted, rough texture of the inner surface of the mucosa.

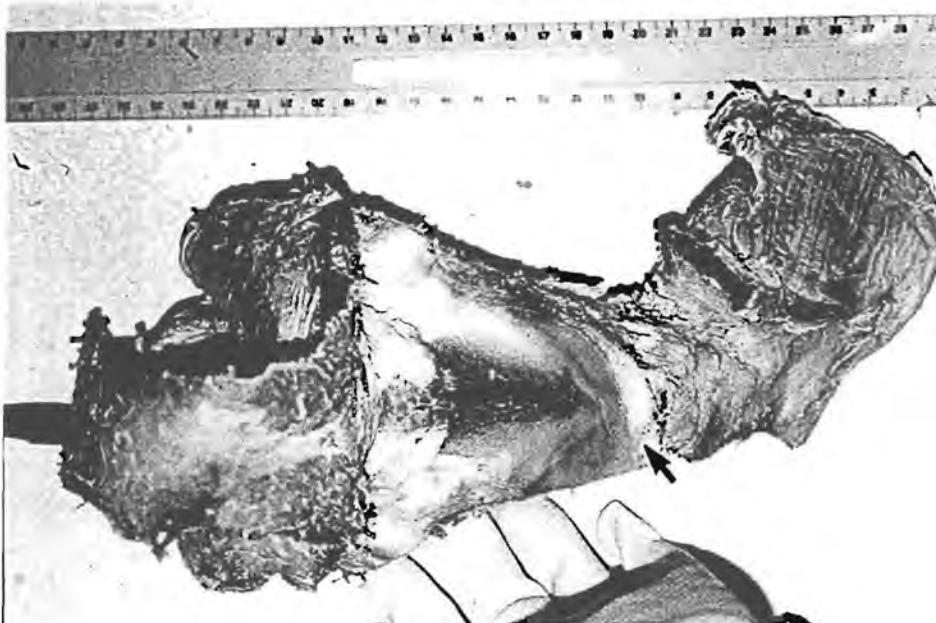


Plate 87: Dorsal view of the laryngeal apparatus of a juvenile male *C. marginata*. The oesophagus has been lifted to expose the arytenoid cartilages which are not continuous with the dorsal wall of the laryngeal sac, but act as a connection between the laryngeal sac and the rest of the apparatus (arrow).



Plate 88: Ventral view of the arytenoid cartilage of a juvenile female *C. marginata* (# 90/12) indicating the opening to the laryngeal sac (arrow).

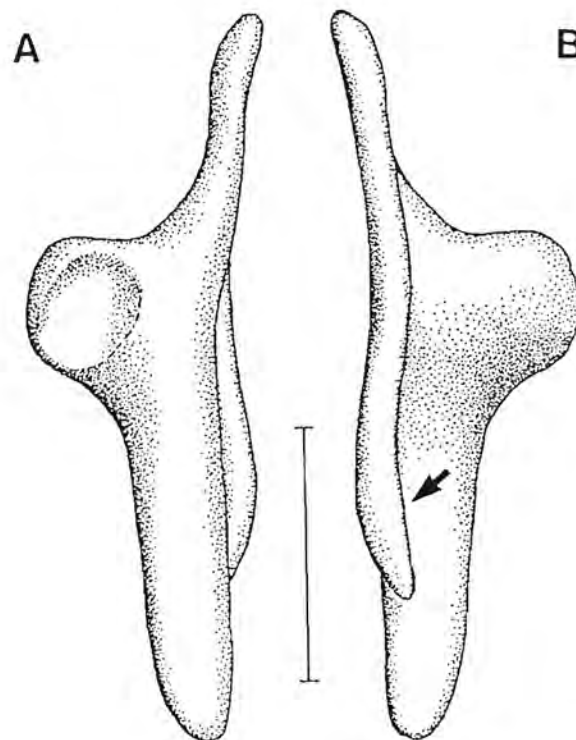


Plate 89: Dorsal (A) and ventral (B) views of the arytenoid cartilage of an adult *C. marginata* showing the separation of the cartilage into two components (arrows) which fuse to form the arytenoid bodies. Note scale bar = 10 cm.

c) Myology of the laryngeal apparatus

The musculature of the laryngeal apparatus of *C. marginata* is similar to that described for *B. acutorostrata* by Benham (1901), so the terminology used by this author for the major muscles of the laryngeal apparatus is applied to this description (Plates 27a and 27b).

As already mentioned, sternum bones, complete nasopharynges and, consequently, their surrounding musculature were not recorded in any of the *C. marginata* specimens. Also, the condition of the specimens was such that the insertions/terminations of the various extrinsic and intrinsic muscles were not clearly defined.

i) *Extrinsic muscles*

The only extrinsic muscle identified was found in the adult male. The **sterno-thyroid** muscle was found on the right hand side body of the thyroid cartilage, situated approximately 2 cm from the interior, right hand side arch of the thyroid cartilage (Plate 90).

ii) *Intrinsic muscles*

The thyro-cricoid, the crico-thyroid, the accessory crico-thyroid (Plate 91) and the crico-arytenoid muscles (Plate 92), being the only discernible muscles, seemed to be present in the same aspect as in *B. acutorostrata*. The accessory crico-thyroid muscles seemed to continue to form the muscular base of the epiglottis. All of the identified muscles were skeletal muscles, being well vascularised and innervated (Plates 93 and 94).

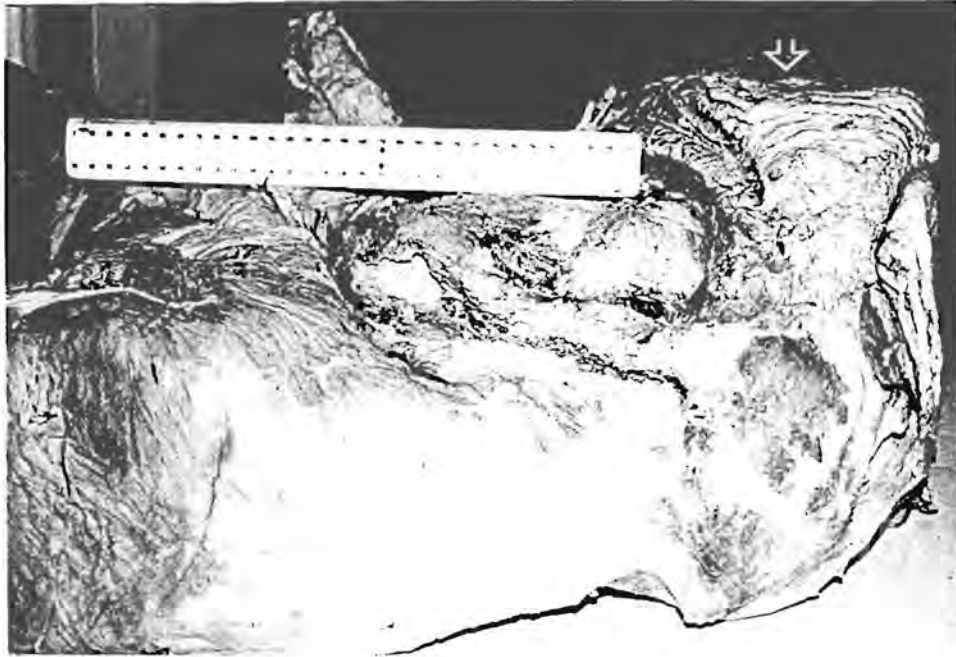


Plate 90: Lateral view of the laryngeal apparatus of an adult male *C. marginata*. Note the sterno-thyroid muscle above the thyroid cartilage (arrow).

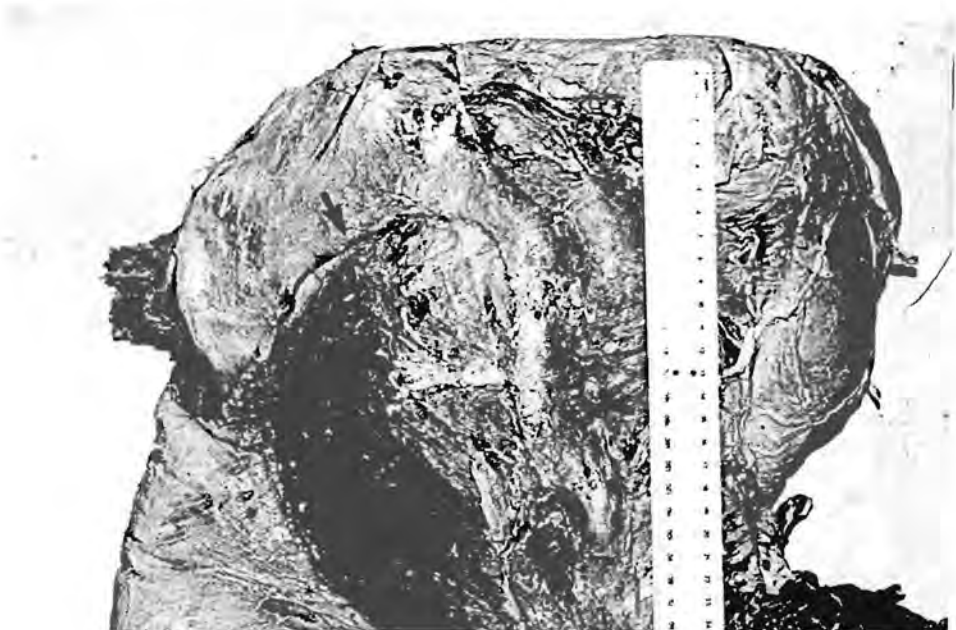


Plate 91: Lateral view of the laryngeal apparatus of an adult male *C. marginata* exposing the accessory crico-thyroid muscle between the thyroid cornu arch (arrow) (ventral surface of the laryngeal apparatus is on the left hand side of the Plate).

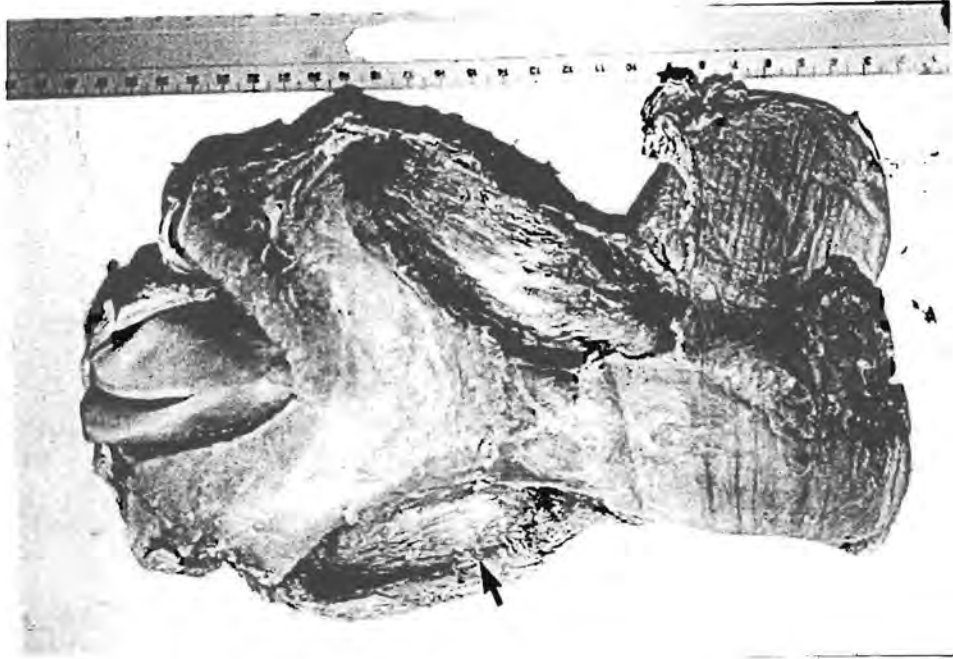


Plate 92: Dorsal view of the laryngeal apparatus of a juvenile male *C. marginata* indicating the position of the crico-arytenoid muscles (arrows) (muscles have been removed).

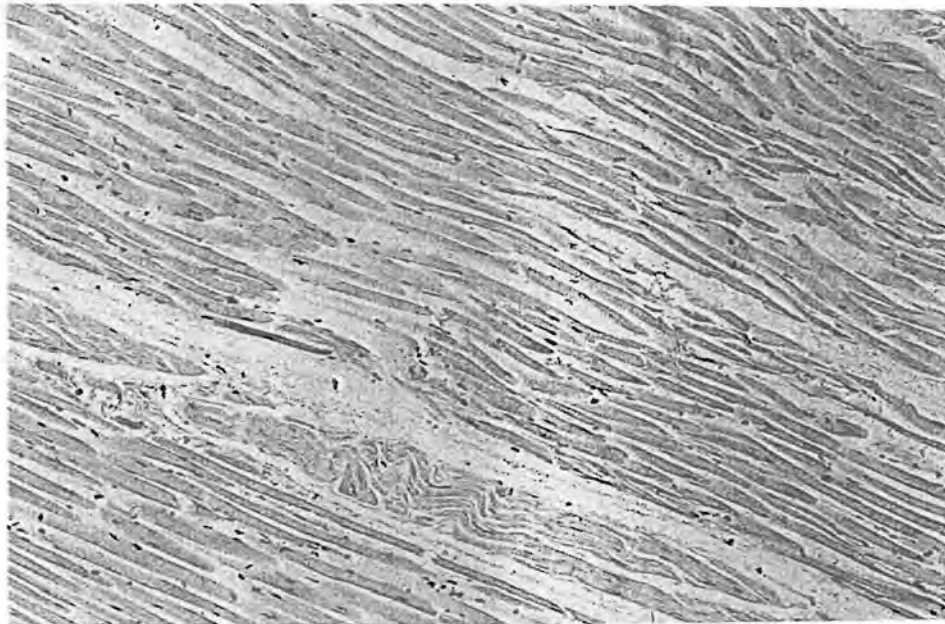


Plate 93: Longitudinal section of the crico-arytenoid muscle of a juvenile female *C. marginata* (# 89/3) showing typical skeletal muscle as well as the presence of nerves. (Mag. 100x, H/E).

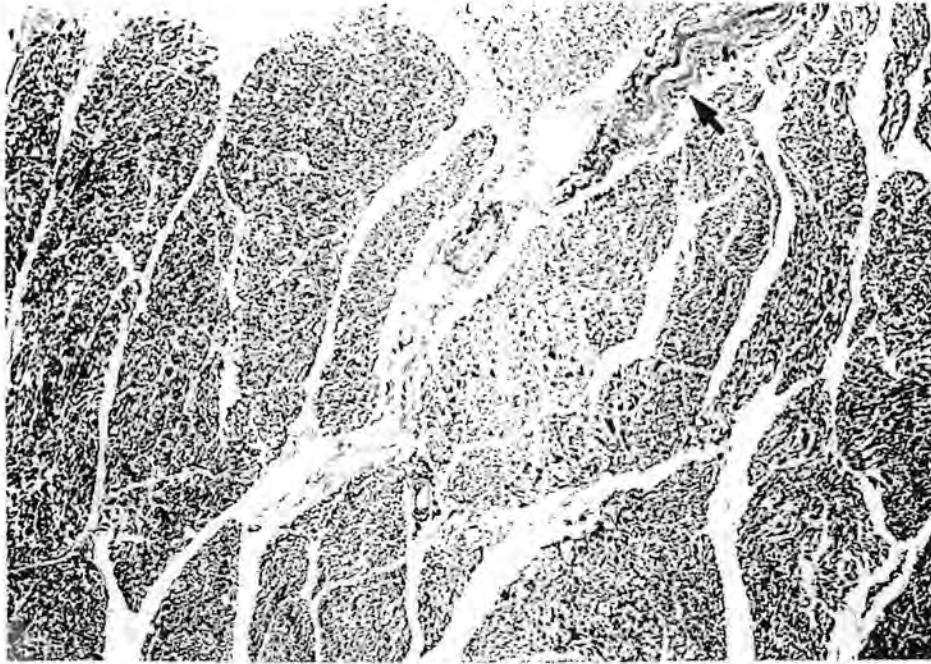


Plate 94: Transverse section of the thyro-cricoid muscle of a juvenile female *C. marginata* (# 89/3) showing skeletal muscle bundles interwoven with connective tissue and spiralling blood vessels (arrow). (Mag. 25x, MT).

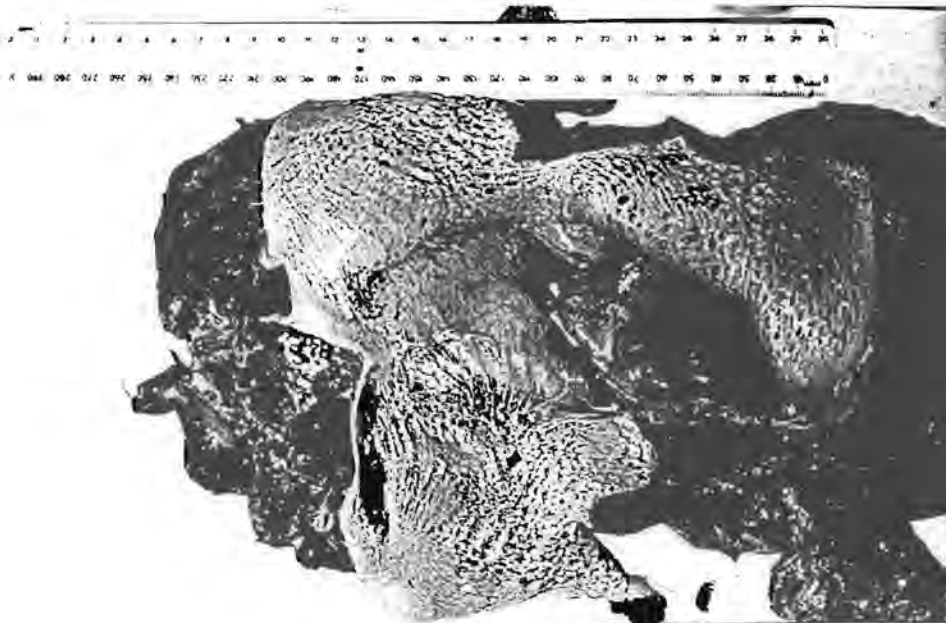


Plate 95: Remnants of the nasopharynx of a juvenile female *C. marginata* (# 89/3). Note the abundance of crypts.



### 3.4 Histology of the laryngeal apparatus of *C. marginata*

Unfortunately, the nasopharynx had been removed from three of the four *C. marginata* specimens during their initial dissection, but one female specimen (89/3) did possess remnants of the nasopharynx, upon which an abundance of crypts occurred on either side (Plate 95). Histological analysis revealed that these crypts open into the nasopharyngeal space, providing avenues for secretions from the many serous glands present. Glands are also scattered throughout the underlying skeletal muscle layer, which is innervated and vascularised (Plate 96). The nasopharyngeal epithelial layer was only discernible by the presence of a basement membrane which was succeeded by a collagenous connective tissue layer. The posterior nare occurs at the posterior end of the nasopharynx, directly anterior to the epiglottis (Plate 97). The lining of the nare is a soft, membranous flap of skin - which, when pulled away (in an anterior direction) from the epiglottis, reveals the narial opening (Plate 97). The lining of the margin of the opening is smooth, having a slightly "gathered" nature with no crypts occurring on its exterior surface. This area is well innervated, glands occur and are surrounded by skeletal muscle bundles (Plate 98).

The epiglottic mucosa is smooth with many tiny holes dispersed throughout. Histologically the epithelium is made up of stratified squamous cells. The tip of the epiglottic "hood" is white in colour and is composed predominantly of adipose tissue (Plate 99). Blood vessels are strangely arranged in coils and richly supply the region, reaching directly beneath the epithelium (Plate 99). The Masson's trichrome stain revealed cytoplasm-filled adipocyte-type cells occurring throughout the mucosa (Plate 100).

The pharyngeal mucosa is of a grey colour, being more pronounced in the juvenile male specimen, although no melanocytes were seen during histological analysis (Plate 101). The pharyngeal epithelium is made up of stratified squamous cells, most of which had pulled away from the rest of the tissue during preparation (Plate 102). In one of the juvenile females, (89/3), besides the peeling away of the epidermal layer being evident, two distinct groups of elongated cells occurred on the left and right hand sides of the pharynx (Plate 103). Masses of dense connective tissue with skeletal muscle occur beneath the epithelium (Plate 104) and very large nerves in close apposition to many blood vessels occur throughout the pharyngeal region. Many crypts line the

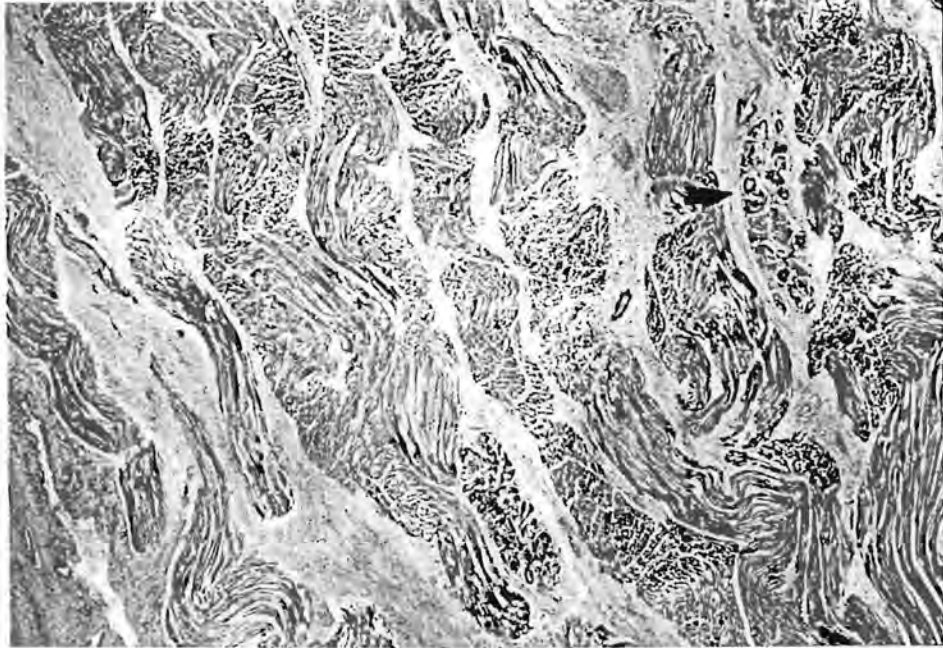


Plate 96: Longitudinal section of the nasopharynx of a juvenile female *C. marginata* (# 89/3). Note scattering of glands throughout skeletal muscle (arrow). (Mag. 25x, H/E)

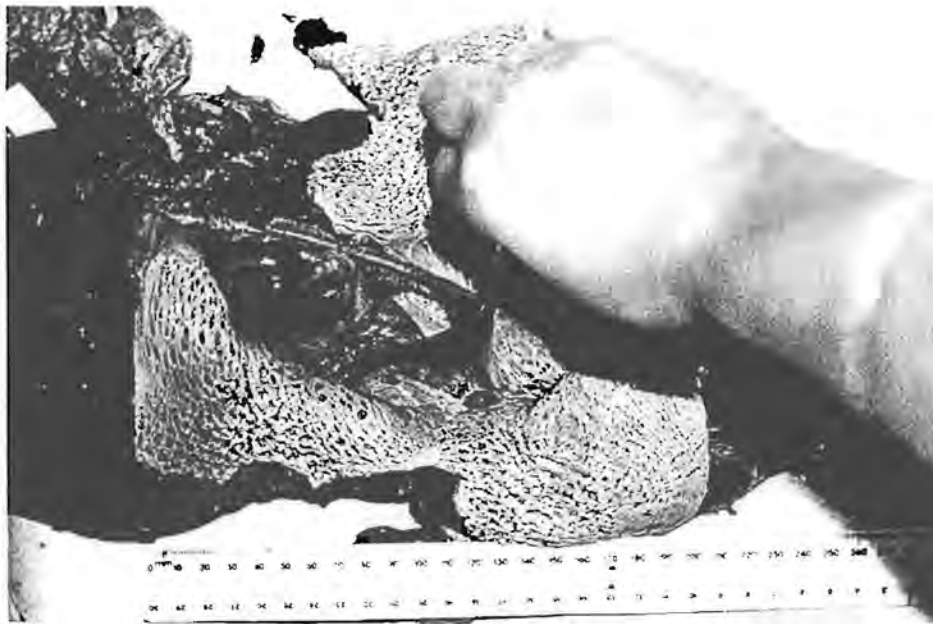


Plate 97: Dorsal view of the laryngeal apparatus of a juvenile female *C. marginata* (# 89/3). Posterior nare is pulled back to reveal the narial opening (anterior to the epiglottis).



Plate 98: Transverse section of the margin of the narial opening of a juvenile female *C. marginata* (# 89/3). Note the muscular layer which surrounds the glands and nerves. (Mag. 50x, MT).

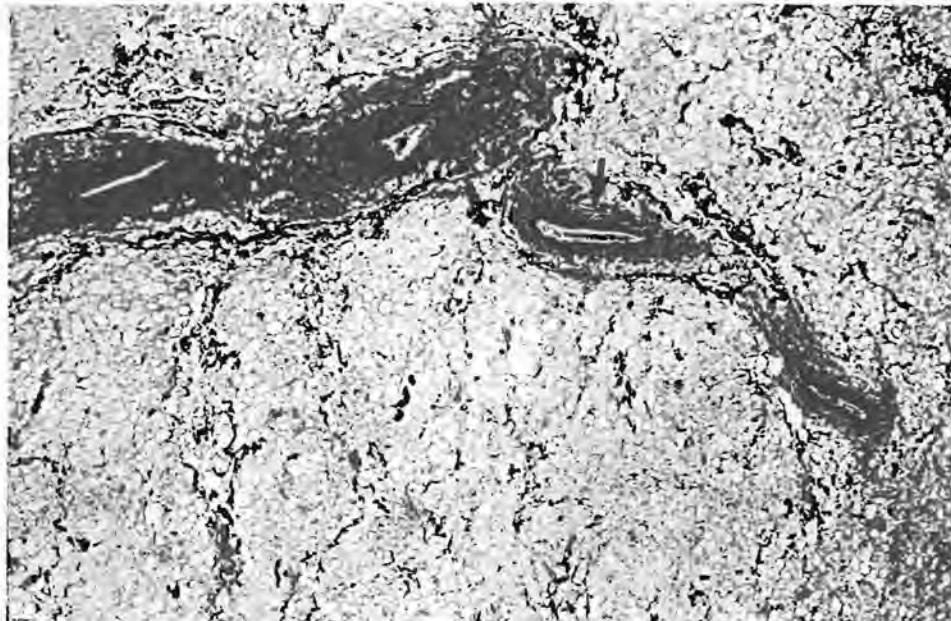


Plate 99: Transverse section of the epiglottic "hood". Note spiralling blood vessels (arrow) coursing through the adipocytes. (Mag. 25x, MT).



Plate 100:

Longitudinal section of the epiglottic "hood" mucosa of a juvenile female *C. marginata* (# 89/3). Cytoplasm-filled adipocyte-type cells (reddish-brown) are scattered throughout the mucosa. (Mag. 100x, MT).

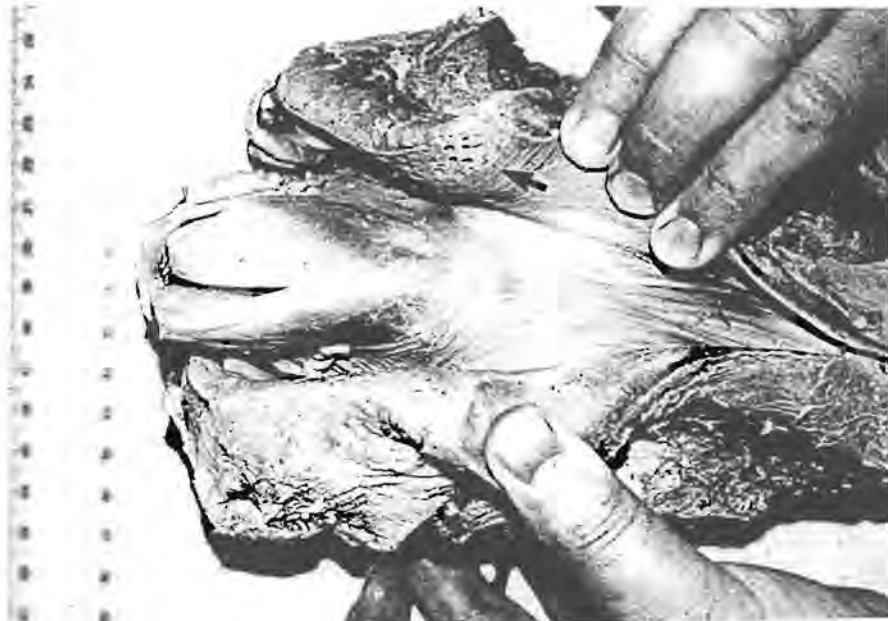


Plate 101:

Dorsal view of the exposed oesophageal mucosa of a juvenile male *C. marginata*. Note that the pharyngeal region around the arytenoid bodies and the oesophageal mucosa is grey in colour and that crypts are present on the dorsal wall of the pharynx (arrow).

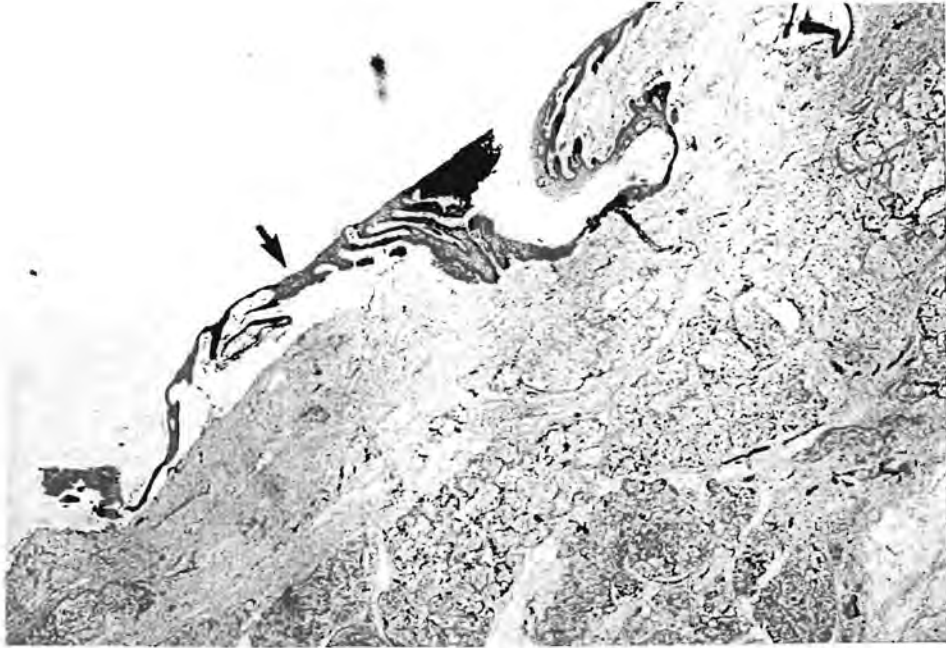


Plate 102: Longitudinal section of the pharyngeal lining of a juvenile female *C. marginata* (# 89/3). Note the epithelium pulling away from the rest of the tissue (arrow), as well as large glands. (Mag. 25x, H/E).

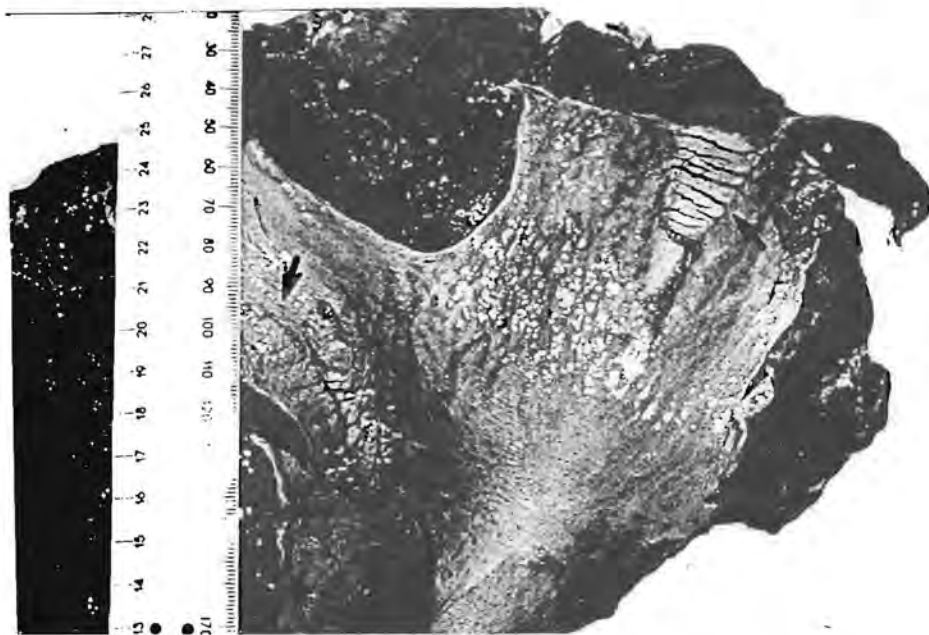


Plate 103: Ventral view of the pharynx of a juvenile female *C. marginata* (# 89/3). Note the two distinctive groups of elongated cells (arrows).

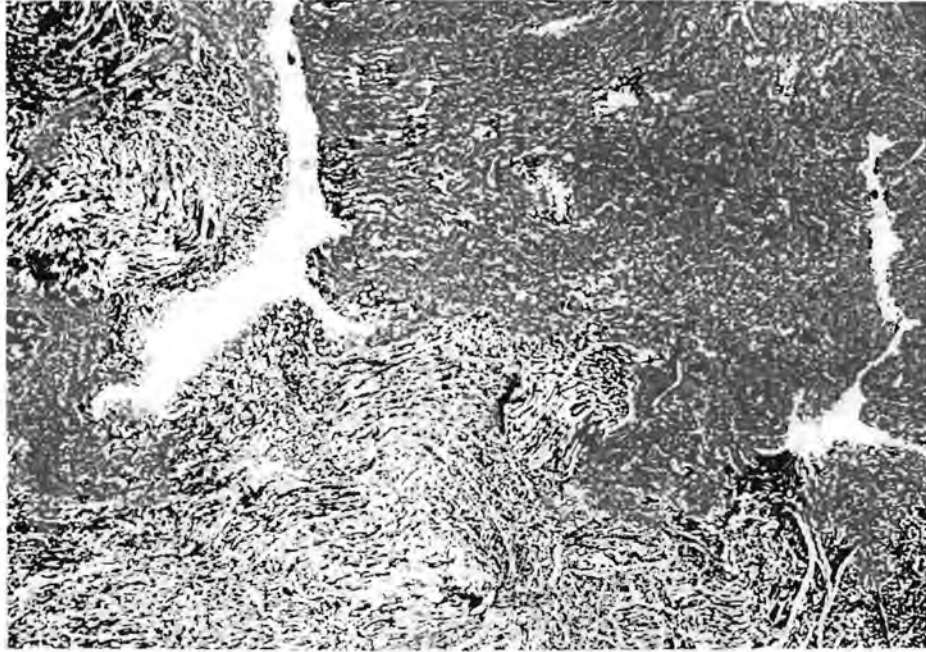


Plate 104. Transverse section of the pharynx of a juvenile female *C. marginata* (# 89/3). Note the mass of connective tissue (blue/green) and muscle. (Mag. 25x, MT).

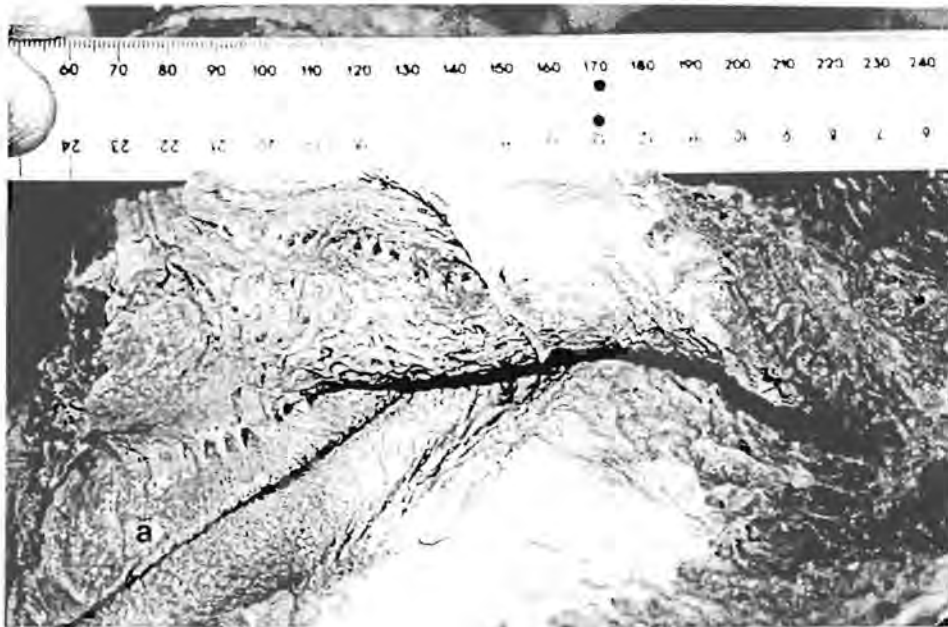


Plate 105. Ventral view of (a) the arytenoid bodies and part of the pharynx of an adult male *C. marginata*. Note crypts.

pharynx, with an isolated group of crypts occurring on the internal, dorsal wall. Large groups of crypts and glands are present on the ventral surface of the pharynx, on the left and right hand sides of, and anterior to, the arytenoid tips (Plates 101 and 105).

The structure of the mucosa of the arytenoid tips is composed mainly of dense connective tissue which is interspersed with serous glands (Plate 106). In longitudinal section, the undulations of the stratified squamous epithelium show the coarse nature of the mucosal surface (Plate 106).

As in *B. acutorostrata*, the arytenoid cartilages form the ventral margin of the entrance to the laryngeal area, which then leads into the trachea, whose margins are made up by the cricoid and arytenoid cartilages. The tracheal mucosa lines the ventral surface of the body of the cricoid cartilage (Plate 107) and continues to the tracheal rings, where it splits to form the bronchi.

Only one juvenile female (89/3) specimen had an uninterrupted set of tracheal rings. From the few available on the other specimens, as well as from the former set, the rings were found to be incomplete ventrally, with no other definable features, besides for the flexible character of the cartilage. The tracheal mucosa consists of stratified columnar epithelium which overlays large amounts of adipose tissue and elastin in conjunction with connective tissue (Plate 108). This region is well vascularised and innervated. Small serous glands and ducts are visible.

From a dorsal perspective, the arytenoid mucosa (the pharyngeal mucosa that is continuous with the arytenoid tips) continues posteriorly into the oesophagus and the number of crypts decreases in this direction (Plate 109).

The oesophageal mucosa is smooth and longitudinally folded (Plate 110). The epithelium is stratified squamous, which overlies dense connective tissue and lower lying skeletal muscle (Plate 111). Lymphocytes are present, dispersed in between the muscle. Two small lines of crypts pass from the pharynx, continuing down either side of the oesophagus and small nodules or knobs protrude from the lining, occurring throughout the oesophagus (Plate 110). Tiny stones were found between the arytenoid bodies and continued to be found in the trachea and the oesophagus. The stones were a mixture of sand grains and small pieces of shell. Most of the stones occurred

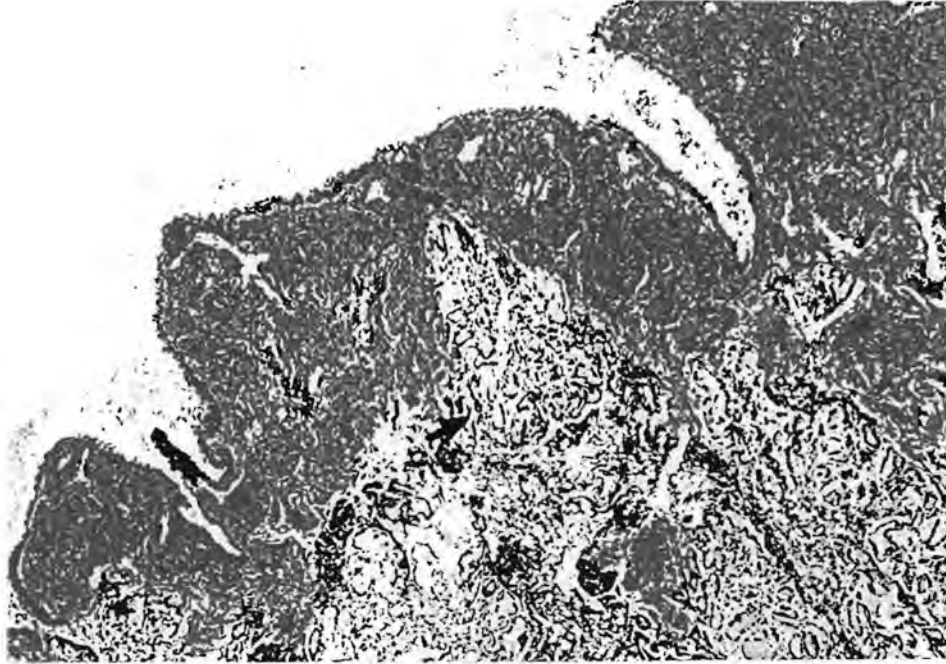


Plate 106: Longitudinal section of the lining of the arytenoid bodies. Note the connective tissue (blue/green) and the serous glands (arrow). (Mag 50x, MT).

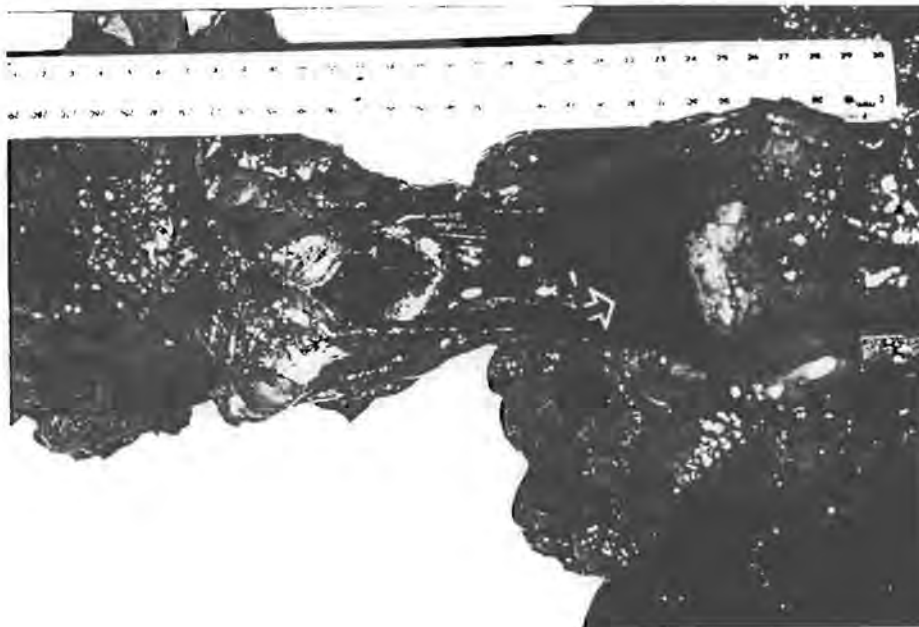


Plate 107: Dorsal view of the laryngeal apparatus of a juvenile female *C. marginata* (# 89/3) with the cricoid cartilage pulled away from the apparatus to reveal its ventral surface. Note that the tracheal mucosa lines the ventral surface of the body of the cricoid cartilage (arrow)





Plate 108: Longitudinal section of the tracheal lining of a juvenile female *C. marginata* (# 89/3). Note elastin (black), adipocytes, connective tissue and blood vessels. (Mag. 25x, VB).

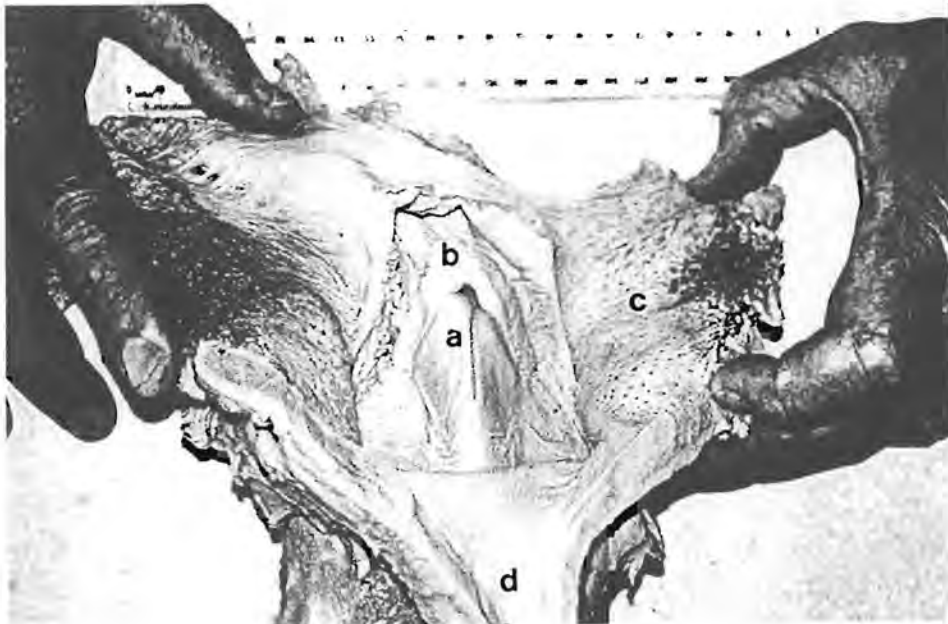


Plate 109: Dorso-lateral view of the (a) arytenoid bodies, (b) epiglottic "hood", (c) parts of the pharynx and (d) the oesophagus of a juvenile female *C. marginata* (# 90/12). Note that the arytenoid mucosa is continuous posteriorly with the oesophagus.

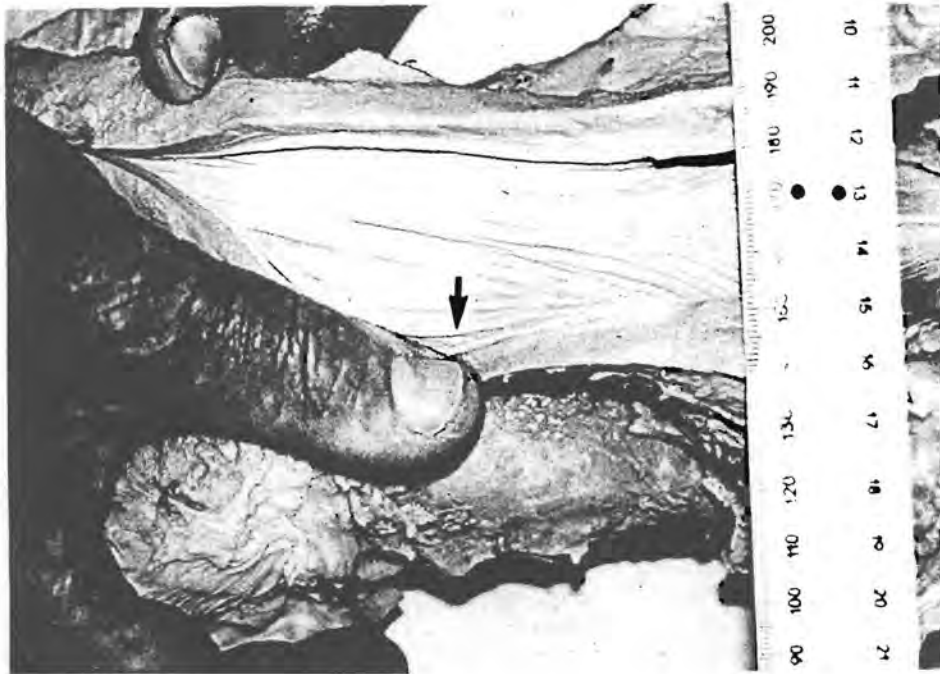


Plate 110: Dorsal view of the oesophagus of a juvenile female *C. marginata* (# 90/12). A sagittal incision reveals the folded oesophageal mucosa. Note knobs/nodules on the mucosa (arrow) (not very clear in Plate).

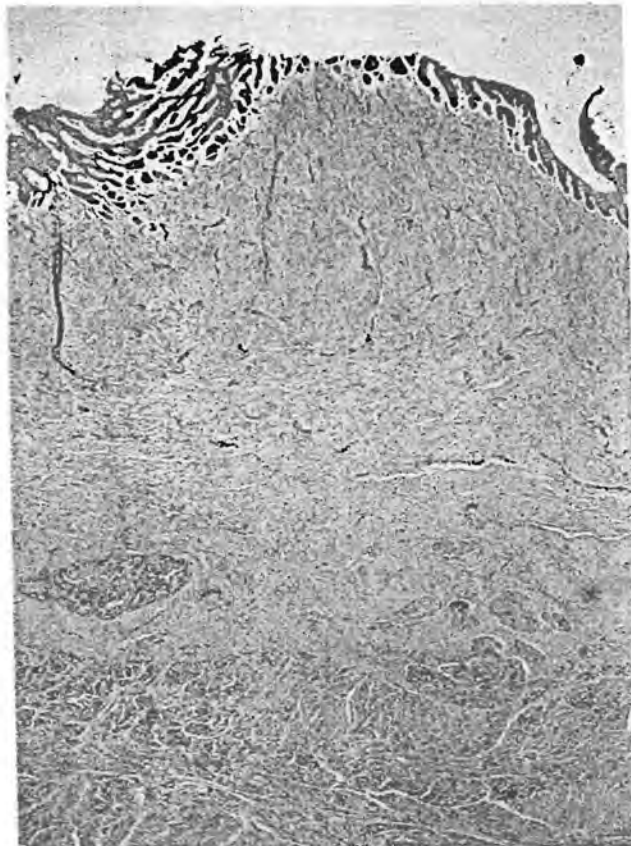


Plate 111: Longitudinal section of the oesophageal mucosa of a juvenile female *C. marginata* (# 89/3) showing epithelial layer, dense connective tissue layer and skeletal muscle layer.

freely, lying on the mucosa, but some stones found in relation to the arytenoid bodies seemed to be fixed in some of the crypts. The stones were probably introduced into the animals during stranding.

Ventrally, the arytenoidal mucosa continues in a posterior direction to form a blind-ending laryngeal sac (Plate 112). This is accomplished through a small opening (approximately 1-1.5 cm wide in the juveniles and approximately 2.5-3 cm in the adult) which occurs on the left hand side of the animal, to the left of the arytenoid bodies (Plates 88 and 113).

On the ventral side of the apparatus, the laryngeal sac protrudes half-way between the "v" notch of the thyroid cartilage and the tracheal rings, in between the cricoid cornua (Plate 114). The sac lies to the right hand side of the apparatus, lateral to the side of the tracheal rings, essentially being separate from the rest of the apparatus (Plate 114).

The wall of the laryngeal sac is very muscular and nerves are clearly visible coursing around the exterior of this structure. Within the mucosa, some nerves and blood vessels seemed to form a distinctive pattern whereby adipose tissue occurs on the outer margins, and moving inwards, blood vessels occur on either side of a nerve (Plate 115). It is not unusual to find nerves and blood vessels in close relation to each other, as blood vessels do tend to shadow the pathways of nerves. The adipose layer may perform an insulating function.

The sac is also well supplied with spiralling blood vessels in conjunction with spiralling nerves (Plate 115). Serous glands together with connective tissue and elastin fibres, underlain by parallel rays of muscle (Plate 116), compose the rest of the upper external layers of the laryngeal sac.

A ventral, longitudinal incision to inspect the internal character of the sac reveals two distinct rows of crypts, which stretch down either side of the laryngeal sac (Plate 117). The crypts diminish in size as they approach the posterior end of the sac. Other smaller crypts are present throughout the sac. The mucosal lining of the interior, in the two preserved juvenile specimens, is grey and yellowish in colour (Plates 117 and 118), whilst the (89/3) frozen female specimen showed no distinctive colouration of the interior laryngeal sac lining (Plate 119).

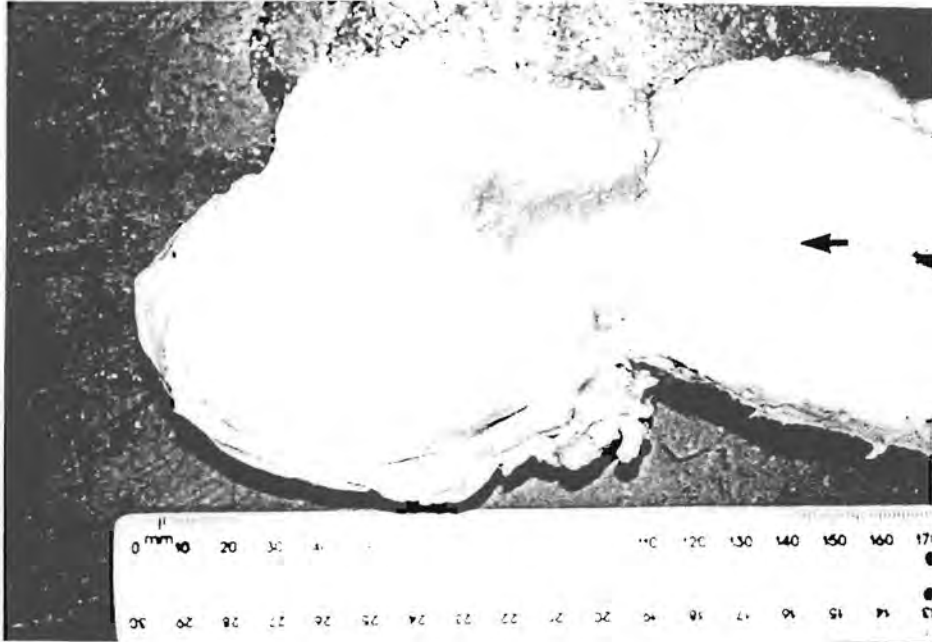


Plate 112: Dorsal view of the posterior tips of the processi vocales of a juvenile female *C. marginata* (# 90/12), providing attachment for the laryngeal sac (arrow). The arytenoid mucosa is continuous with the cavum of the laryngeal sac.

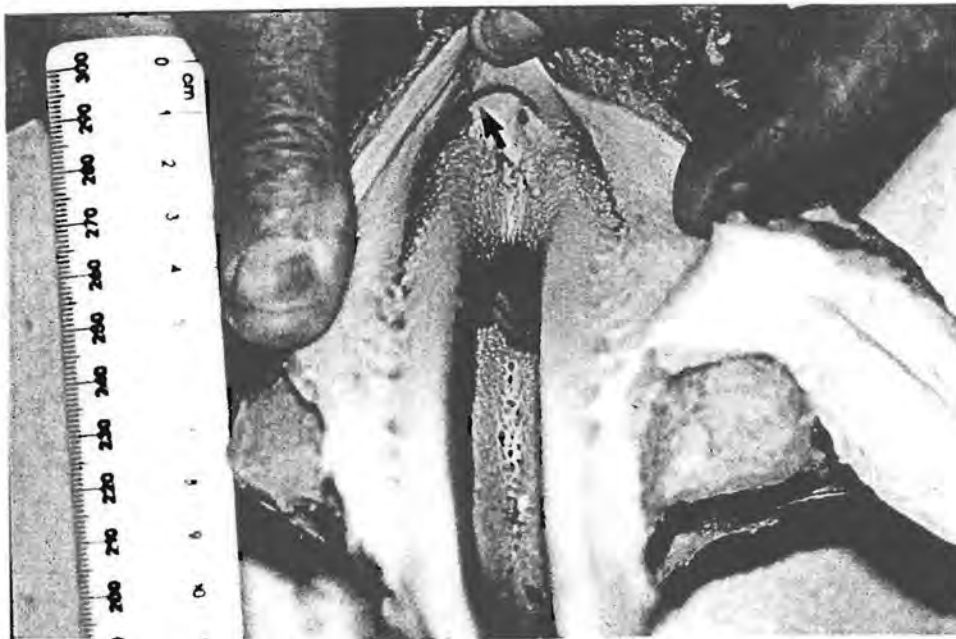


Plate 113: Antero-ventral view of the arytenoid cartilages and the small opening which leads into the laryngeal sac of a juvenile female *C. marginata* (# 90/12) (arrow).

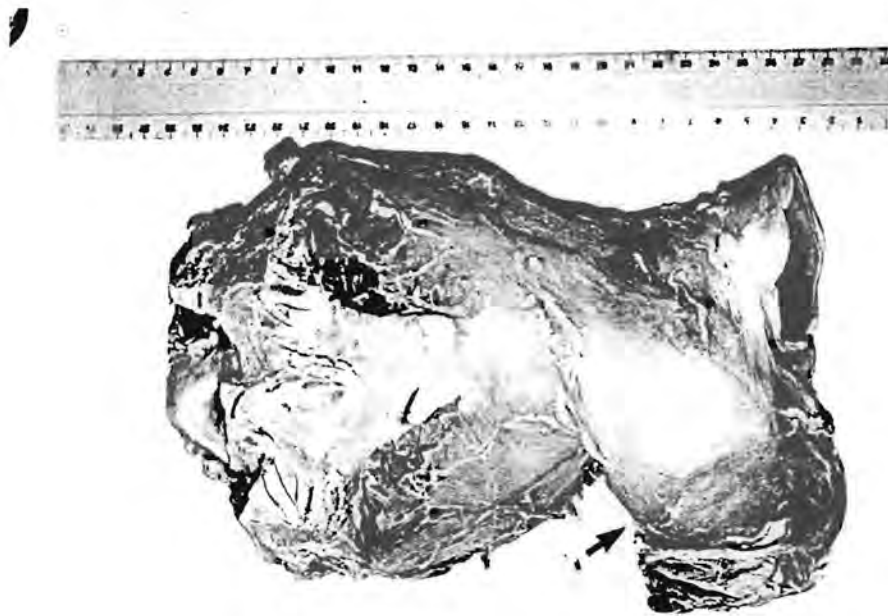


Plate 114: Ventral view of the laryngeal apparatus of a juvenile male *C. marginata* indicating the position of the laryngeal sac (arrow).

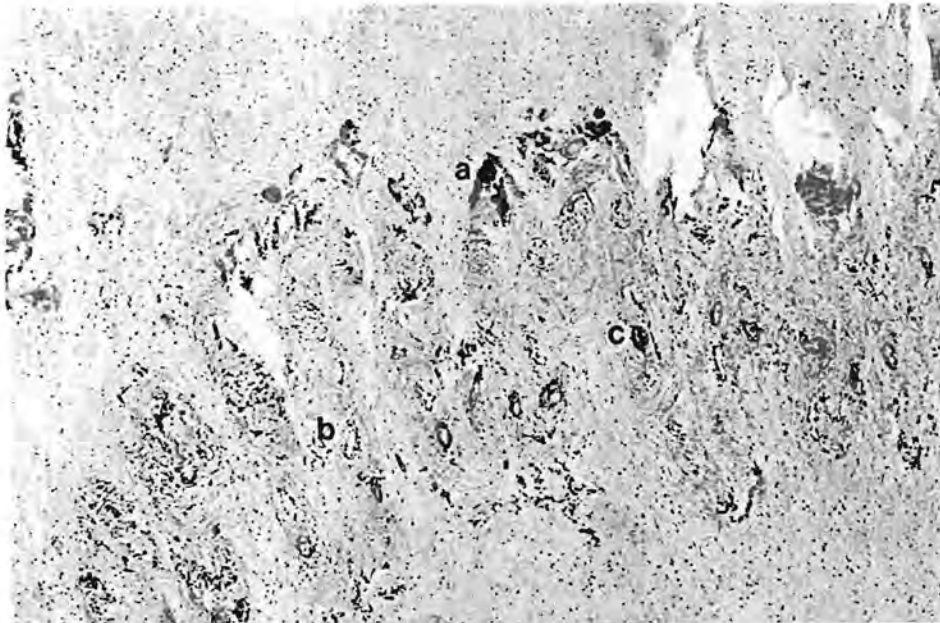


Plate 115: Transverse section of the laryngeal sac of a juvenile female *C. marginata* (# 89/3) showing the distinctive pattern formed by (a) adipose tissue, (b) spiralling blood vessels and (c) nerves. (Mag. 50x, H/E).

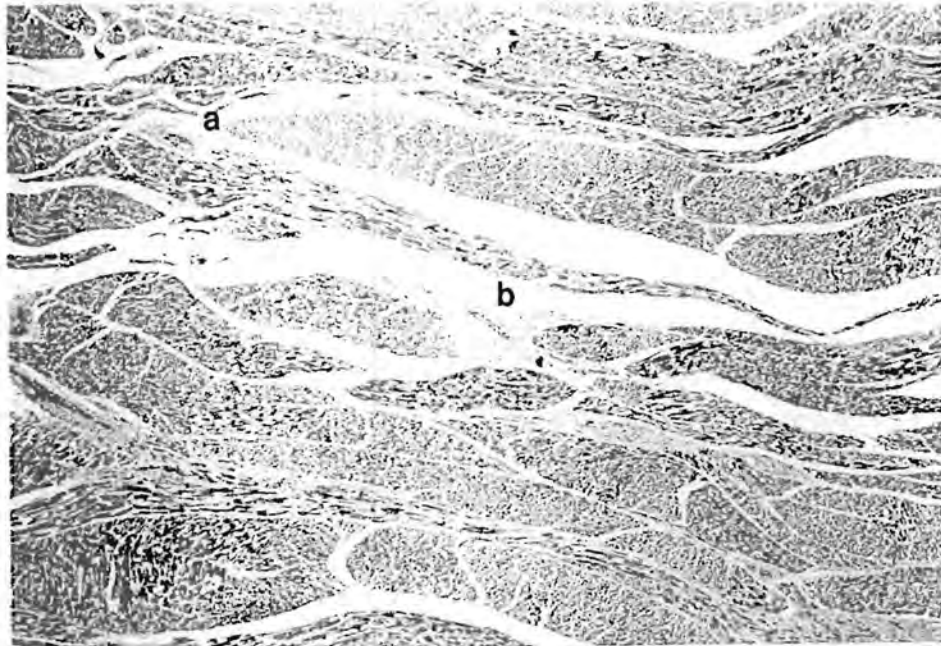


Plate 116: Longitudinal section of the parallel rays of skeletal muscle of the upper external layer of the laryngeal sac of a juvenile female *C. marginata* (# 89/3). Note (a) nerves and (b) blood vessels. (Mag. 25x, H/E).



Plate 117: The laryngeal sac of a juvenile male *C. marginata* (# 91/27). A longitudinal incision reveals two distinct rows of crypts. Note coloration of the mucosa.

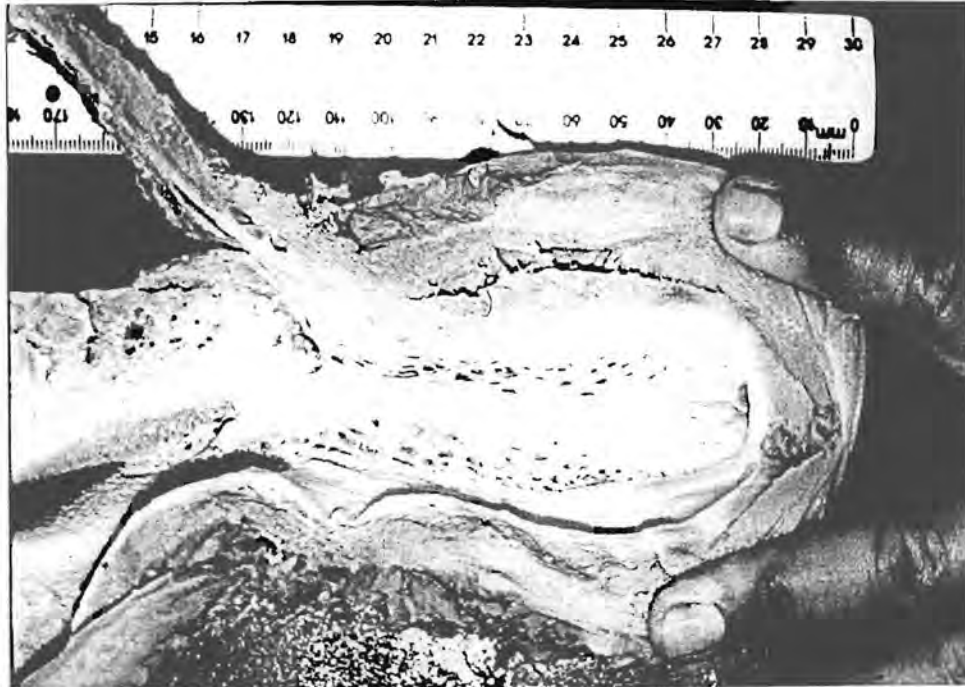


Plate 118: The laryngeal sac of a juvenile female *C. marginata* (# 90/12). A longitudinal incision reveals two distinct rows of crypts. Note coloration of the mucosa.

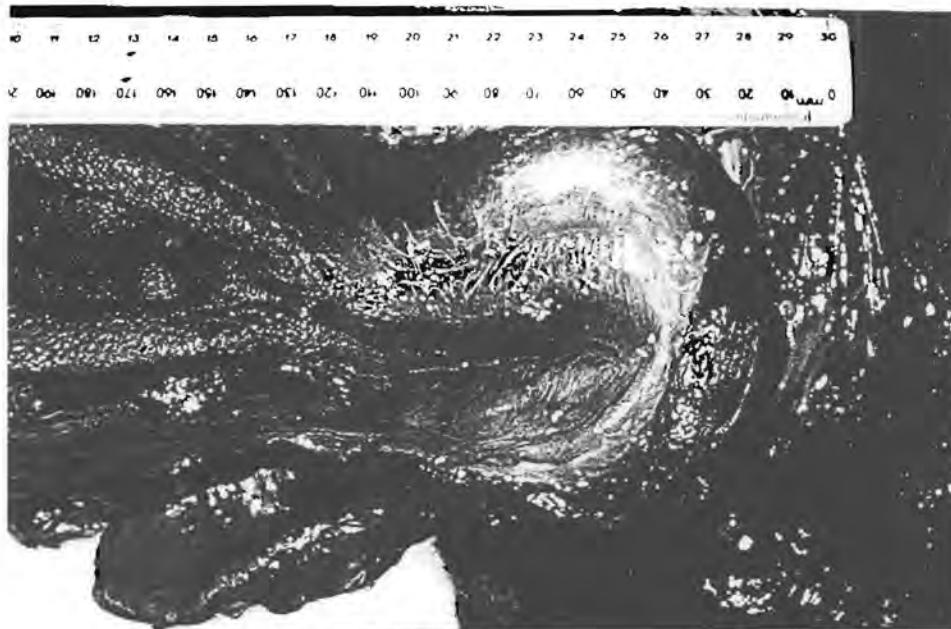


Plate 119: The laryngeal sac of a juvenile female *C. marginata* (# 89/3). A longitudinal incision reveals two distinct rows of crypts. Note lack of grey coloration of mucosa.

These are compared to the definite grey colouration seen in the adult (Plate 120). The colouration of the laryngeal sac mucosa may be the result of preservation. The epithelium itself was not well preserved; in certain areas it seems that the epithelium is two layers thick and in other areas, only basement membranes remained. Lymphatic tissue was detected beneath the epithelial layer (Plate 121). Large serous glands filled with proteinaceous secretions are associated with ducts which visibly pierce the epithelium (Plate 122). Large nerves and large blood vessels, as well as connective tissue, course through the thick, parallel rays of skeletal muscle, which form the wall of the laryngeal sac (Plate 116). Undulating chains of adipocyte-type cells occur near the epidermis (Plate 123).

Measurements of the lengths of the sacs were taken from their opening, near the arytenoids, to their posterior ends, while the widths were measured across their widest points. The sacs of the juvenile females (89/3) and (90/12) were 10 cm long x 5.2 cm wide (Plate 68) and 11.5 cm long x 6.7 cm wide (Plate 69), respectively, and the juvenile male's (91/27) sac measured 12 cm x 8 cm (Plate 70). The adult male's sac measured 51.2 cm in length and 36.1 cm in width (Plate 120).

The introduction of air down the pharynx of the juvenile female (89/3) specimen, which was attached to the viscera, caused the laryngeal sac as well as the lungs to inflate (Plates 124 and 125).





Plate 124: Lateral view of the laryngeal apparatus of a juvenile female *C. marginata* (# 89/3) showing (a) the laryngeal sac and (b) lungs before inflation. Arrow indicates hose insertion.

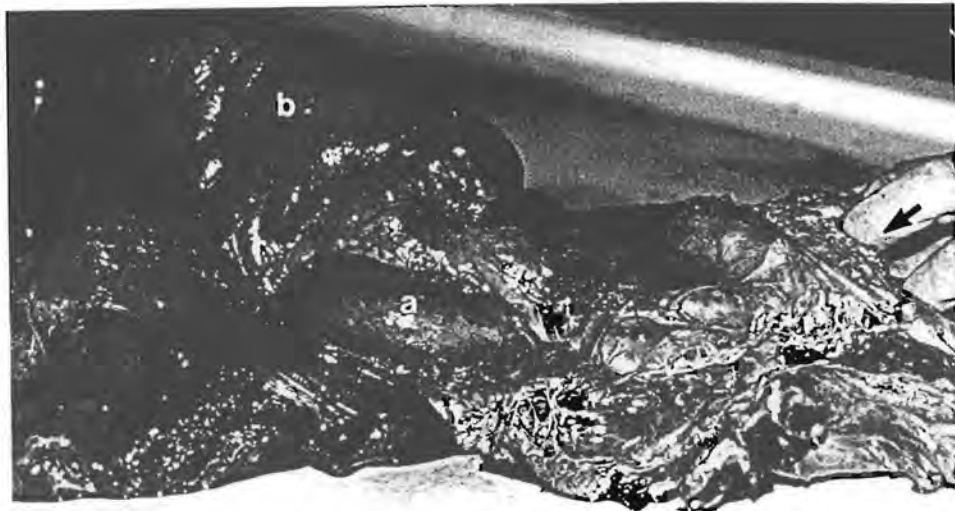


Plate 125: Lateral view of the laryngeal apparatus of a juvenile female *C. marginata* (# 89/3) showing (a) the laryngeal sac and (b) lungs during inflation. Arrow indicates hose insertion.