

Comparative anatomy of the larynx of the minke whale,
Balaenoptera acutorostrata and the pygmy right whale, *Caperea marginata*.

by

Desray Reeb

Submitted in partial fulfilment of the
requirements for the degree of

M.Sc. (Zoology)

in the
Faculty of Agricultural and Biological Sciences
University of Pretoria
Pretoria

May 1997



Comparative anatomy of the larynx of the minke whale,
Balaenoptera acutorostrata and the pygmy right whale, *Caperea marginata*.

by

Desray Reeb

Supervisor: Dr P. B. Best
Mammal Research Institute
Department of Zoology
University of Pretoria
Pretoria

Abstract

The laryngeal apparatus of *C. marginata* is described for the first time and proves to be entirely different from that of any mysticete so far described, especially in the position of the laryngeal sac which is separate from the tracheal rings and lies to the right of the animal. Massive ontogenetic development of the sac in adult males is demonstrated, far greater than that seen in a series of two juvenile and two adult *B. acutorostrata* also examined. Histological analysis of the laryngeal sacs of both *C. marginata* and *B. acutorostrata* shows the walls to be highly muscular, well innervated and vascularised, indicating an active organ. Coiled blood vessels and nerves found in *C. marginata* support the theory that in this species the sac undergoes extensive expansion and contraction, and a possible association with the unique thoracic structure of the species is suggested. The roles of the laryngeal sac and arytenoid cartilages in mysticete sound production are discussed.

ACKNOWLEDGEMENTS

I always thought that once I reached the point when I had to say my “thank yous”, that my thesis would have reached its end. One thing is for certain though, my thesis would definitely not be complete without this section.

My supervisor, Dr Peter B Best, alias “Dr Fluke”, without you the whale wouldn't have had a tale! Thank you so much for all your help enabling the completion of this project. Thank you for taking a chance, putting up with me and providing me with the opportunity and the privilege of working with one of the “last of the whalers”, but a legend in whale research.

My thanks go to Mr Shigetoshi Nishiwaki, the head of the 1993/94 JARPA research cruise, Mr Hajime Ishikawa, Chief of researchers who collected the minke whale material, Ms Ryoko Zenitani who performed the age analysis on the specimens and the rest of the 1993/94 JARPA crew.

Edwina Steenboom at neuropathology for her patience, her guidance on sectioning and for preparing and staining my slides. Thanks also to Annelie Visser who helped with the last batch of slides. I would like to thank Prof Cruse for allowing this co-operation.

Dr Sue Kidson at UCT for helping me with the histological analysis and for the enthusiasm with which it was always done. Bev Seymour for kindly arranging and supervising the photomicroscopy. Prof Sellars for taking the time to listen and for loaning me literature. Dr Paterson and Heiko Schoenfuss for providing me with literature.

Rachel Alexander who kept my chin up, my heart hopeful and who always had a solution to my problems. You're the best! I look forward to OUR champagne. Herschel Mair for his support and for making my photos possible, without emptying the coffers. Cedric Hunter for creating the wonderful drawings contained in this thesis. Cedric Goliath and Manfred for dealing with my many computer gremlins. Dr Barbara Cook for allowing me access to a light microscope and to Leonie Juritz for her support and advice.

Prof Skinner, MRI and the University of Pretoria, without whom this project would not have been possible. FRD for providing me with a 2 year bursary and to Santa De Klerk at the University of Pretoria for administering these funds.

S.A. Museum for providing the Whale Unit with a home and to all my friends at the S.A. Museum who have always gone out of their way to help me smile, no matter what, thank you all so much. The staff at the S.A. Library and the S.A. Museum library for helping me dredge up all the old literature and to Rina Krynauw for translating my summary into Afrikaans.

My "Metboard Family", thank you so much for all your support and for providing the "means to this end".

My family for being patient, supportive and loving as always.

Dov - we did it! I couldn't have done it without you. I don't know where or how to begin to thank you. You truly are the brightest star!

Berny and Gavin - you've never let me give up on my dreams and I'll never let you either! To all my other very special friends - you all make everything possible! Thank you for your support and understanding.

To my Zeider, you had to go, but you never left. I Love you.

Last, but definitely not least thanks must go to the whales.

LIST OF CONTENTS

	Page
ABSTRACT	ii
ACKNOWLEDGEMENTS	iii
LIST OF CONTENTS	v
LIST OF TABLES	vii
LIST OF PLATES	viii
CHAPTER 1: INTRODUCTION	1
1.1 Problems with nomenclature	13
CHAPTER 2: MATERIALS AND METHODS	15
CHAPTER 3: RESULTS	20
3.1 Gross anatomy of <i>Balaenoptera acutorostrata</i>	20
a) Bones	20
<i>i) Hyoid bones</i>	24
<i>ii) Sternum bones</i>	24
b) Cartilages	29
<i>i) Thyroid cartilage</i>	29
<i>ii) Cricoid cartilage</i>	31
<i>iii) Epiglottic cartilage</i>	34
<i>iv) Arytenoid cartilages</i>	34
c) Myology of the laryngeal apparatus	39
<i>i) Extrinsic muscles</i>	39
<i>ii) Intrinsic muscles</i>	39
3.2 Histology of the laryngeal apparatus of <i>Balaenoptera acutorostrata</i>	46
3.3 Gross anatomy of <i>Caperea marginata</i>	66
a) Bones	66
<i>i) Hyoid bones</i>	70

b)	Cartilages	70
i)	<i>Thyroid cartilage</i>	70
ii)	<i>Cricoid cartilage</i>	74
iii)	<i>Epiglottic cartilage</i>	74
iv)	<i>Arylenoid cartilages</i>	78
c)	Myology of the laryngeal apparatus	82
i)	<i>Extrinsic muscles</i>	82
ii)	<i>Intrinsic muscles</i>	82
3.4	Histology of the laryngeal apparatus of <i>Caperea marginata</i>	86
CHAPTER 4:	DISCUSSION	105
4.1	Comparison with previous descriptions of <i>Balaenoptera acutorostrata</i>	105
4.2	Comparison of the laryngeal apparatus in <i>Balaenoptera acutorostrata</i> and <i>Caperea marginata</i>	111
4.3	Phylogeny and functions of the laryngeal sac	117
4.3.1	Exclusion of water and food from the respiratory canal	118
4.3.2	Complete utilisation of oxygen in inspired air	118
4.3.3	Phonation	119
CHAPTER 5:	CONCLUSION	123
	SUMMARY	125
	SAMEVATTING	127
	REFERENCES	129

LIST OF TABLES

- Table 1: List of nomenclature used by various authors with current interpretation of the species involved and justifications therefor. Page 13.
- Table 2: Collection details of *B. acutorostrata* specimens during the 1993/94 season. Page 15.
- Table 3: Collection details of *C. marginata* specimens. Page 16.
- Table 4: Measurements associated with the laryngeal apparatus of *B. acutorostrata*. Page 27.
- Table 5: Measurements associated with the laryngeal apparatus of *C. marginata*. Page 72.
- Table 6: Lengths of laryngeal sacs of mysticetes as described by various authors. Page 115.
- Table 7: Percentage that thoracic and lumbar vertebrae constitute of the total vertebral column in mysticete and odontocete families. Page 117.

LIST OF PLATES

- Plate 1: Ventral view of the viscera and laryngeal apparatus of an adult male *C. marginata*, stranded at Bordjies Drif, Cape Point Nature Reserve on 25/05/82 - (# 82/11). Photographs taken by PBB. Note laryngeal sac lying above the heart (arrow). Page 12.
- Plate 2: Ventral view of the laryngeal sac of an adult male *C. marginata*, details as above. Page 12.
- Plate 3: Dorsal view of the laryngeal apparatus of an adult female (# 15) *B. acutorostrata*. Page 21.
- Plate 4: Dorsal view of the laryngeal apparatus of a juvenile female (# 44) *B. acutorostrata*. Page 21.
- Plate 5: Dorsal view of the laryngeal apparatus of a juvenile male (# 13) *B. acutorostrata*. Page 22.
- Plate 6: Dorsal view of the laryngeal apparatus of an adult male (# 159) *B. acutorostrata*. Page 22.
- 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. Page 23.
- Plate 8: Ventral view of the hyoid bones attached to the laryngeal apparatus of a juvenile female *B. acutorostrata*. Page 23.
- 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). Page 25.
- 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. Page 25.
- Plate 11: Ventral view of (a) the os hyoides and (b) styloid bones of an adult male *B. acutorostrata* (# 159) showing an even concave posterior margin. Note scale bar = 10 cm. Page 26.
- 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). Page 26.

- 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. Page 28.
- Plate 14: Ventral view of the laryngeal apparatus of a juvenile male *B. acutorostrata* showing the mid-ventral situation of the thyroid cartilage. Page 28.
- 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. Page 30.
- 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. Page 30.
- 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. Page 32.
- 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. Page 32.
- 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. Page 33.
- Plate 20a: Ventral view of the laryngeal apparatus of a juvenile male *B. acutorostrata* showing the epiglottic projection occurring anterior to the thyroid cartilage. Page 33.
- 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). Page 35.
- 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). Page 35.
- 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. Page 36.
- 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. Page 36.

- 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. Page 37.
- 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). Page 37.
- Plate 26: Dorsal view of (a) the arytenoid cartilages 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. Page 38.
- 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). Page 40.
- 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). Page 40.
- 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. Page 41.
- 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*. Page 41.
- 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. Page 43.
- Plate 31: Ventral view of the (a) thyro-epiglottic, (b) aryteno-epiglottic and (c) hyo-epiglottic muscles of a juvenile female *B. acutorostrata*. Page 43.

- Plate 32: Lateral view of the right portion of the crico-thyroid muscle and the thyroid cartilage of an adult female *B. acutorostrata*. Page 44.
- 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. Page 44.
- 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. Page 45.
- 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. Page 45.
- 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). Page 47.
- Plate 37: Ventral view of the laryngeal apparatus of a juvenile female *B. acutorostrata* showing the grey mucosal tissue (epiglottis is pulled back). Page 47.
- 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. (Mag. 100x, Haemotoxylin & Eosin (H/E) stain). Page 48.
- 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). Page 48.
- 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. Page 50.
- Plate 41: Ventral view of the epiglottis (pulled back) exposing the epiglottic ridge of a juvenile male *B. acutorostrata*. Page 50.
- Plate 42: Transverse section of the epiglottic ridge of an adult female *B. acutorostrata* which is made up primarily of adipose tissue. (Mag. 50x, H/E). Page 51.
- Plate 43: Dorsal view of the nasopharynx of a juvenile male *B. acutorostrata* exposed by a sagittal incision. Note the free end of the epiglottis is inserted into the posterior narial opening (arrow). Page 51.
- Plate 44: Dorsal view of the laryngeal apparatus of an adult female *B. acutorostrata*. Note the lack of grey coloration of the pharynx. Page 52.

- Plate 45: Dorsal view of the pharynx of an adult female *B. acutorostrata* revealing the epiglottis and two clear groups of crypts, as well as the “crypt passage” (arrow) anterior to the tip of the epiglottis. Page 52.
- 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). Page 53.
- Plate 47: Dorsal view of the oesophagus of an adult female *B. acutorostrata* (exposed by a sagittal incision) showing distinct groups of crypts (arrows). Page 53.
- 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). Page 55.
- 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). Page 55.
- 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). Page 56.
- 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. Page 56.
- Plate 52: Dorsal view of the (a) epiglottis, (b) tips of the arytenoid bodies, (c) processi musculares and the (d) laryngeal sac of an adult female *B. acutorostrata*. Note the folded nature of the tracheal/external laryngeal sac mucosa. Page 57.
- 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). Page 57.
- 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). Page 58.
- 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). Page 58.
- 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. Page 59.

- Plate 57: Dorsal view of the body of the cricoid cartilage of a juvenile male *B. acutorostrata* which is continuous with the tracheal rings. Page 59.
- 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). Page 60.
- Plate 59: Ventral view of the muscular wall of the laryngeal sac of a juvenile male *B. acutorostrata*. Page 60.
- 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). Page 61.
- 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). Page 61
- 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). Page 63.
- 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). Page 63.
- 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). Page 64.
- Plate 65: Ventral view of the laryngeal sac of a juvenile female *B. acutorostrata*. Page 64.
- Plate 66: Ventral view of the laryngeal sac of an adult male *B. acutorostrata* (sac turned inside out). Page 65.
- Plate 67: Dorsal view of the laryngeal sac of an adult female *B. acutorostrata* (sac turned inside out). Page 65.
- Plate 68: Dorsal view of the laryngeal apparatus of a juvenile male *C. marginata*. Page 67.
- 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. Page 67.
- Plate 70: Dorsal view of the laryngeal apparatus of a juvenile female *C. marginata* (# 89/3). Page 68.
- Plate 71: Lateral view of the laryngeal apparatus of an adult male *C. marginata* (ventral surface facing upwards). Page 68.

- Plate 72: Ventral view of the hyoid bones attached to the laryngeal apparatus of a juvenile female *C. marginata* (# 89/3). Page 69.
- Plate 73: Dorsal 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. Page 69.
- 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. Page 71.
- 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. Page 71.
- 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). Page 73.
- 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. Page 73.
- Plate 78: Lateral view of the cricoid cartilage of a juvenile female *C. marginata* (# 90/12) showing the lack of distinct ventral cornua (arrow). Page 75.
- 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). Page 75.
- 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. Page 76.
- 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). Page 76.
- 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". Page 77.
- 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. Page 77.

- 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. Page 79.
- 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 processi vocales (arrow). Page 79.
- 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. Page 80.
- 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). Page 80.
- Plate 88: Ventral view of the arytenoid cartilage of a juvenile female *C. marginata* (# 90/12) indicating the opening to the laryngeal sac (arrow). Page 81.
- 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. Page 81.
- Plate 90: Lateral view of the laryngeal apparatus of an adult male *C. marginata*. Note the sterno-thyroid muscle above the thyroid cartilage (arrow). Page 83.
- 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). Page 83.
- 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). Page 84.
- 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). Page 84.
- 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). Page 85.
- Plate 95: Remnants of the nasopharynx of a juvenile female *C. marginata* (# 89/3). Note the abundance of crypts. Page 85.

- 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). Page 87.
- 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). Page 87.
- 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). Page 88.
- Plate 99: Transverse section of the epiglottic "hood". Note spiralling blood vessels (arrow) coursing through the adipocytes. (Mag. 25x, MT). Page 88.
- 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). Page 89.
- 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). Page 89.
- 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). Page 90.
- Plate 103: Ventral view of the pharynx of a juvenile female *C. marginata* (# 89/3). Note the two distinctive groups of elongated cells (arrows). Page 90.
- 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). Page 91.
- Plate 105: Ventral view of (a) the arytenoid bodies and part of the pharynx of an adult male *C. marginata*. Note crypts. Page 91.
- 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). Page 93.
- 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). Page 93

- 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). Page 94.
- 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. Page 94.
- 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). Page 95.
- 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. Page 95.
- 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. Page 97.
- 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). Page 97.
- Plate 114: Ventral view of the laryngeal apparatus of a juvenile male *C. marginata* indicating the position of the laryngeal sac (arrow). Page 98.
- 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). Page 98.
- 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). Page 99.
- 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. Page 99.
- 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. Page 100.
- 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. Page 100.

- Plate 120: Ventral view of the laryngeal sac of an adult *C. marginata*. A sagittal incision reveals the cavum of the laryngeal sac. Note grey coloration of the mucosa. Page 102.
- Plate 121: Longitudinal section of the laryngeal sac of a juvenile male *C. marginata*. Note lymphatic tissue beneath the epithelium (arrow) and ducts associated with serous glands. (Mag. 50x, H/E). Page 102.
- Plate 122: Longitudinal section of the laryngeal sac of a juvenile male *C. marginata* showing proteinaceous secretion moving from a serous gland through a duct to the epidermis. Page 103.
- Plate 123: Longitudinal sections of the laryngeal sac of a juvenile female *C. marginata* (# 89/3) showing undulating chains of adipocyte-type cells (reddish-brown) occurring near the epidermis. (Mag. 50x, MT). Page 103.
- 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. Page 104.
- 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. Page 104.
- Plate 126: Sagittal section through the laryngeal apparatus of *B. acutorostrata* showing the position of the laryngeal sac. Labelling as follows: a: epiglottic cartilage; b: lateral view of the arytenoid cartilage (dashed line); c: arytenoid lip at anterior tip of the arytenoid cartilage; d: cricoid cartilage; e: laryngeal sac; f: inter-arytenoid connective tissue connection; g: thyro-arytenoid muscle; h: tracheal rings. Shaded area represents the air passage. Drawing not to scale. Page 114.
- Plate 127: Sagittal section through the laryngeal apparatus of *C. marginata* showing the position of the laryngeal sac. Labelling as above except for i: opening on the left hand side of the arytenoid cartilages which opens into the laryngeal sac; j: neck of the laryngeal sac. Drawing not to scale. Page 114.