

## CHAPTER 4: DISCUSSION

### 4.1 Comparison with previous descriptions of *B. acutorostrata*

Generally speaking, the structure of the laryngeal apparatus of *B. acutorostrata* agrees with previous descriptions for both this and other mysticetes (Eschricht & Reinhardt 1866; Carte & Macalister 1868; Turner 1872; Beauregard & Boulart 1882; Dubois 1886; Benham 1901; Schulte 1916; Hosokawa 1950; Yablokov, Bel'kovich & Borisov 1974; Quayle 1991; Haldiman & Tarpley 1993; Schoenfuss & Hillmann 1996).

The most detailed structural accounts of the laryngeal apparatus of *B. acutorostrata* are found in the works of Carte & Macalister (1868) and Benham (1901), which served as invaluable guides for the present study. Both accounts concerned subadult or juvenile animals only. Although Benham (1901) refers to Carte & Macalister's (1868) specimen as an adult, the whale measured 18'5" (approx. 5.6 m) in length, which indicates that it was sexually immature (Lockyer 1984) and cannot therefore be regarded as an adult, but rather as a sub-adult.

In this study the nature and positioning of the hyoid bones on the ventral surface of the laryngeal apparatus are shown to be similar to those previously described for *B. acutorostrata* (Carte & Macalister 1868; Benham 1901; Satake & Omura 1974), but the association of the hyoid bones with each other is not entirely consistent with previous descriptions. Drawings by Carte & Macalister (1868) indicate that the styloid bones are closely related to and occur on either side of the anterior notch of the os hyoides. This was found to be the case here in the adult female and the juvenile male. In the adult male and the juvenile female, however, the styloid bones were found with their internal margins in close proximity to each other while the anterior notch of the os hyoides lay beneath the mid-ventral meeting of these bones. The internal extremities of the styloid bones did seem to be attached to the anterior apex of the os hyoides via connective/fibrous tissue. Satake & Omura (1974) noted that the minke whale in the Antarctic has longer styloid bones (stylohyals) than the minke in the North Pacific, though there is rather wide individual variation. Extreme variation in both size and shape of the hyoid bones was also described by Perrin (1975) in the spotted dolphin, *Stenella attenuata*.

The sternum bone described by Carte & Macalister (1868) as somewhat "heart-shaped" differed considerably in shape from those found in this study, although this shape has been described by previous authors (Tomilin 1967; True 1983). Much individual variation is also known to occur in specimens from the North Pacific and Antarctic Oceans, but the form of the sternum is generally cruciate (Omura 1975). Individual variation of the sternum did exist between the juvenile male and female specimens examined in this study, but the general "cross-like" form, also described by Flower (1864), is expressed in these specimens.

The five typical mammalian cartilages described in this study generally conform with previous descriptions for balaenopterids (Carte & Macalister 1868; Benham 1901). The cartilaginous framework is joined by muscles most of which could be identified as following the general mammalian pattern.

The existence of the sterno-thyroid, an extrinsic muscle, was denied by Carte & Macalister (1868) in their description of a specimen of *B. acutorostrata*. Benham (1901), without denying its existence, was unable to determine the relationships of a sterno-thyroid muscle in his specimen of *B. acutorostrata*. Unfortunately I was not able to isolate this muscle in any of the *B. acutorostrata* specimens to which I had access.

The finger-like projections of the dermis which reach into the epidermis of the nasopharynx may possibly provide an anchoring mechanism for the epidermis, which may be placed under considerable strain during respiration. Ling (1974) describes what seems to be the same arrangement (which he terms "rete ridges") on the underside of the epidermis in the integument of *B. physalus*. The presence of melanocytes in the nasopharynx seems to be related to the dark epidermal lining found in the blowholes (Quayle 1991).

The "elasticated" or "gathered" character of the narial opening, together with the presence of muscles directly beneath the epithelium, seem to indicate that this region is structured in order to encourage movement. With the epiglottis being inserted into the posterior narial opening and the whole larynx possibly being pulled upwards during the process of respiration (Benham 1901), movement of this structure seems essential.

Haldiman & Campbell (1985) stated that the fusion of the tracheal rings with the posterior prominence of the cricoid cartilage in *B. mysticetus* may offer a method for aging harvested animals. Although the number of tracheal rings fused with the cricoid cartilage in *B. acutorostrata* varies according to the size of the animal, the difference in the number of fused tracheal rings between the juvenile female and the adult male is very small, although the age difference is quite substantial (Table 2). Clearly this species does not lend itself to the aging method proposed by the abovementioned authors.

Although the illustrations in Benham's (1901) paper do not show the clearly defined tubercles on the anterior margin of the thyroid cartilage as were seen in this study in both the juveniles and the adults, he does note their presence. The distinctive or well-developed structure of the tubercles found in this study may support Benham's (1901) theory that they are representative of anterior cornua.

Carte & Macalister (1868) describe a strong crescentic hood-like fold of mucous membrane two inches (5 cm) in front of the root of the epiglottis. They state that this fold is capable of being drawn over the orifice of the glottis when the margins of that opening are approximated, and that its use appears to be to cover and protect the superior opening of the larynx during the act of deglutition. Benham (1901) did not find any comparable structure except for the epiglottis itself and as such maintained that, although Carte & Macalister's (1868) account in the text was precise, the hood-like fold was in fact the epiglottis. In this study, no evidence of any such hood-like fold was found in any of the specimens. Consequently, I support Benham's (1901) opinion that Carte & Macalister (1868) must have been referring to the epiglottis itself.

Carte & Macalister (1868) did not regard the epiglottic cartilage as a true cartilage as they found that the cartilagenous portion of the epiglottis formed only a small part of the entire organ. Later, Benham (1901) described a 3 inch (7.6 cm) long, horse-shoe shaped cartilage in his juvenile specimen. This study extends Benham's (1901) finding to larger and older animals, where predictably, the epiglottic cartilages are better developed. Therefore, contrary to Carte & Macalister's (1868) findings, the epiglottic cartilage can be considered as one of the five cartilages that form the framework of the cetacean larynx.

The arytenoid "lips", as they were observed in this study, have not been previously described in this species. In other mysticetes (e.g. *E. australis*), two lips formed by the extension of the laryngeal mucosa over the horns of the arytenoids are described (Beauregard & Boulart 1882). These authors also state that in *B. physalus* and *B. musculus* "the lips of the orifice communicating between the sac and the larynx are formed by the arytenoids covered by mucosa". Purves (1967) described "semidiscoid flanges projecting forward from the apex of each arytenoid cartilage" in *B. physalus*, with "closely-packed, warty rugosities" on the mesial surface in the more adult specimens. Haldiman & Campbell (1985) describe elongated "lips" of the laryngeal sac in *B. mysticetus*, whose sac in longitudinal section forms the shape of an anchor. It is the left and right hooks of the "anchor" which the authors refer to as "lips". Consequently these are not comparable to the "lips" described in *B. acutorostrata*. However, apart from the presence of warty rugosities, both the flanges of *B. physalus* and the "lips" (described in the present study) of *B. acutorostrata* occur at the anterior tip of the arytenoid bodies and are composed entirely of connective/elastic tissue, indicating that they are probably analogous structures. The descriptions of the lips found in *E. australis* (Beauregard & Boulart 1882) also seem to match that of the lips of *B. acutorostrata* as described in this study.

In humans, the vocal cords are the only part of the lower respiratory tract which is not lined by respiratory epithelium; they are lined by stratified squamous epithelium which is better adapted to withstand frictional stress (Wheater, P.R., Burkitt, H.G. & Daniels, V.G. 1979).

Being part of the anterior opening to the larynx, it is not unreasonable to expect that the arytenoid bodies, as well as their "lips", would be exposed to considerable strain caused by the movement of air that occurs during respiration. This fact is corroborated by the presence of a stratified squamous epithelial lining which lines the arytenoid bodies and which continues to form the lip-structures.

Benham (1901) stated that in *B. mysticetus*, the two processi vocales of the arytenoid cartilages were continuous at their distal ends, forming a posterior support for the laryngeal opening, while in *B. acutorostrata*, the posterior ends of the processi vocales were connected by dense connective tissue. These findings for *B. acutorostrata* are echoed in this study, although, contrary

to what Benham (1901) suggests, the connective tissue did not become replaced by cartilage in the older animals.

According to Fanning & Harrison (1974), both Simpson & Gardner (1972) and Slijper (1962) maintained that all the epithelial cells in cetacean trachea were ciliated. After consulting Slijper's (1962) original document, however, it is clear that he has been misquoted; in fact he explains that, based on the investigations of other researchers, the trachea is said to be lacking in cilia in various species of odontocetes. The researchers to whom Slijper (1962) refers were also surprised to note the complete absence of mucous (goblet) cells in the epithelium of the trachea and bronchi, and their almost complete absence in the glands terminating in the air passages. However, a pseudostratified ciliated columnar epithelium, containing goblet cells, has since been found lining the crypts on the ventral aspect of the cranial end of the trachea in *Tursiops truncatus* by Fanning & Harrison (1974). On the dorsal wall of the laryngotracheal junction in *B. mysticetus*, stratified squamous epithelium with lymphatic nodules in the lamina propria changed abruptly to ciliated pseudostratified columnar epithelium with diffuse lymphatic tissue underneath (Haldiman, Abdelbaki, Al-Bagdadi, Duffield, Henk & Henry 1981). In this study, changes in the composition of the epithelium of the dorsal wall of the tracheal mucosa from thick stratified squamous cells to thin pseudostratified columnar cells were evident. Small aggregations of goblet cells, together with lymphocytes, were found in the tracheal lining, although no goblet cells were found along any other air passage. No ciliated epithelia nor any remnants thereof were detected at all at the laryngotracheal junction nor in the middle of the trachea.

According to Slijper (1962), the alleged absence of cilia in cetacean trachea may have been due to the poor state of the histological material available. However, the relatively short post-mortem times of the specimens used in this study (Table 2), together with the cool nature of the environment in which they were obtained, should not have produced significant degeneration of the tissue and none was obvious in the histological material examined. As another explanation, Slijper (1962) speculates that ciliated structures may have been dispensed with by cetaceans, as they live in a moist and dust-free environment. Evans (1987) has suggested that secretions produced at the bottom of the junction between the larynx and the trachea are removed by the violent coughing movement of the blow, making the need for cilia redundant. In view of the fact

that ciliated structures have been described in at least some mysticetes and odontocetes (see above), these theories do not seem plausible.

The laryngeal sacs described in other mysticetes namely, *Balaena mysticetus* (Eschricht & Reinhardt 1866; Haldiman & Campbell 1985), *Balaenoptera musculus* (Turner 1872; Beaugard & Boulart 1882; Dubois 1886), *B. physalus* (Beaugard & Boulart 1882), *B. borealis* (Hosokawa 1950) and *M. novaeangliae* (Quayle 1991), seem to follow the same general pattern, *B. acutorostrata* included (Carte & Macalister 1868; Benham 1901). All have the laryngeal sac on the ventral aspect of the larynx, between the thyroid and cricoid cartilages, in a post-thyroideal position. This study concurs with these descriptions.

The ventral muscular wall of the laryngeal sac consists partly of the crico-thyroid, accessory crico-thyroid and thyro-cricoid muscles, together with the circular muscular fibres which immediately surround the cavity of the sac. Benham (1901) only describes the circular muscular fibres, which he says differ from the musculature described by Eschricht & Reinhardt (1866) for *B. mysticetus*. As the latter authors' description concurs with the intrinsic muscle component described in this paper, I am inclined to believe that Eschricht & Reinhardt (1866) were describing the exterior character of the wall of the laryngeal sac, whereas Benham (1901) was describing the interior character of the wall of the laryngeal sac.

All the abovementioned authors seem to agree that the muscular structure of the wall of the laryngeal sacs found in the species of mysticetes studied could allow for extension and contraction of the sacs. Dubois (1886) describes the *N. laryngeus inferior* which innervates the sac and Hosokawa (1950) states that the muscular sheets of the sac are innervated by the vagus. The present histological study revealed nerves coursing through the muscular wall of the sac, as well as an abundance of blood vessels and lymphatic tissue in the mucosa. This, together with the definite ontogenetic development of the laryngeal sac further supports the theory that the structure is functional, at least in adults.

The interior of the laryngeal sac of *B. physalus* has been described as having "numerous voluminous fasciculate folds, subdivided into secondary folds with corrugated edges" as well as

longitudinally directed folds which occupy the sides of the laryngeal sac, and numerous crypts (Beauregard & Boulart 1882). These authors found no such folds in *B. musculus* or in *E. australis*, although crypts were present in both species, being particularly abundant in the former. The arrangement of the crypts in *B. musculus* does seem to most closely represent that found in *B. acutorostrata*. In *B. borealis*, Hosokawa (1950) found many longitudinal folds in the upper part of the sac, while the lower parts showed many reticulated grooves. No evidence of folds was found in the laryngeal sac of *B. acutorostrata*. Apart from the absence of cilia, the pseudo-stratified, columnar nature of the epithelial cells lining the laryngeal sac is consistent with the epithelia almost exclusively confined to the larger airways of the respiratory system in other mammals (Wheater *et al.* 1979).

#### 4.2 Comparison of the laryngeal apparatus in *B. acutorostrata* and *C. marginata*

The gross morphology of the laryngeal apparatus of *C. marginata* generally conforms with that of *B. acutorostrata*. A few structural differences do occur, and these are discussed below.

The identification of the various muscles of *C. marginata* is based on relating their positions to those found in *B. acutorostrata*. On this basis, it is found that the general myology of all the specimens studied is very similar, with a definite sterno-thyroid muscle being discernible in *C. marginata*. I hesitate to infer exactness of the attachment and insertions of the various musculature due to the condition of preservation of the *C. marginata* specimens.

The notable difference in the thyroid cartilage of *C. marginata* is that a distinct ridge was present on the mid-ventral line of the thyroid cartilage in all the specimens examined, whereas in *B. acutorostrata* a slight ridge was only visible in the adult female. The ridge seemed to provide attachment for connective tissue in the juveniles, but which became continuous with the epiglottic protrusion, and hence the epiglottic cartilage itself, in the adult male *C. marginata*.

The general structure of the cricoid cartilage of *C. marginata* differs slightly from that found in *B. acutorostrata*. Although the body does continue laterally and ventrally, no distinctive cornua

are visible. Foramina were not definable along the mid-dorsal line of the body but there is a distinct hump on the anterior, dorsal surface of the body of the cricoid cartilage.

Once again the tracheal rings are seen to be continuous with the rounded prominence on the posterior margin of the dorsal side of the body of the cricoid cartilage. Although (as mentioned for *B. acutorostrata*) the numbers of tracheal rings continuous with the cricoid cartilage varied, the smaller of the juvenile females (89/3) had the highest number of such tracheal rings. This species therefore did not display a correlation between size of the animal and number of tracheal rings continuous with the cricoid prominence. Unfortunately the tracheal rings of the adult male could not be counted.

In *C. marginata*, the epiglottic cartilage is much reduced compared to that found in *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 found in the latter species. A central ridge (as well as the aryteno-epiglottic folds) is barely discernible. The association which occurs between the epiglottic and thyroid cartilages in the adult male *C. marginata* did not occur in any of the *B. acutorostrata* specimens available. The absence of cartilaginous connections to the epiglottic cartilage is consistent with the findings of Schoenfuss & Hillmann (1996) for *B. mysticetus*.

The arytenoid cartilages of *C. marginata* differ from those of *B. acutorostrata* in that the whole structure is more compact in the former species. On first inspection, the arytenoid bodies in *C. marginata* are continuous posteriorly with the processus vocales, with no thinning or tapering evident. However, once dissected out, each arytenoid cartilage seemed to consist of two components which merge to form the arytenoid bodies. The broader tips of the arytenoid bodies of *C. marginata* are ventrally flattened against each other, with the right tip projecting further than the left tip in the juveniles and vice versa in the adult. This difference between the juveniles and the adult may be due to a difference in the rate of growth of the arytenoid cartilages. No "lips" are present at the tips of the arytenoid bodies and the processus vocales do not extend to form the dorsal wall of the laryngeal sac.



In *D. leucas*, Watson & Young (1879) describe the apices and processes of the arytenoid cartilages as being covered with mucous membrane, forming the posterior thickened lip of the superior aperture of the larynx. The thickened character of the arytenoids in *C. marginata* and the nature of the mucosa which was found to cover the tips of the arytenoids suggest that this species may also be evolving towards a similar non-involvement of the arytenoid lip structure in the process of phonation.

In *B. acutorostrata* and *C. marginata* the oesophageal mucosa is folded, but distinct left and right groups of crypts occur on each side in the former, whereas they are almost absent in the latter species.

The laryngeal sac found in *C. marginata* is also present on the ventral surface of the larynx but differs in position from that in *B. acutorostrata* (or any other mysticete so far described) in that it is completely separate from the tracheal rings and lies to the right hand side of the animal (Plates 126 and 127). As such, the dorsal wall of the sac is not made up by the processi vocales and, unlike *B. acutorostrata*, the sac opens into the laryngeal area through a small opening (approx. 1 cm in length) on the ventral side of the processi vocales. The arrangement as well as the nature of the crypts inside the sacs also differ. As in *B. acutorostrata*, there is distinct ontogenetic development of the laryngeal sac, but to a much greater extent, with the adult's sac being almost five times the size of those found in the juveniles. This together with the notable vascularisation and innervation detected in the muscular lining, as well as the presence of lymphatic tissue in the mucosa of the laryngeal sac imply that the structure is functional. The coiled nerves and blood vessels also lend support to the theory which advocates that the laryngeal sac undergoes expansion and contraction.

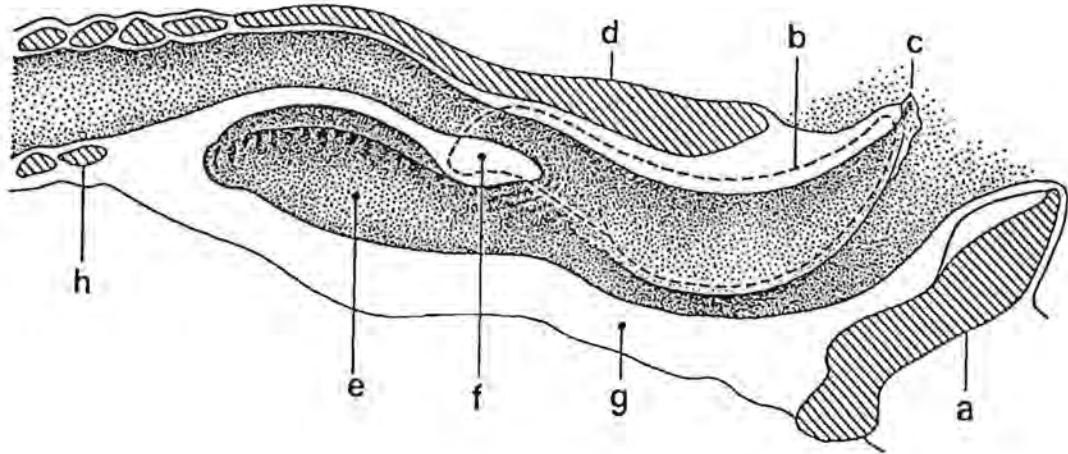


Plate 126:

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.

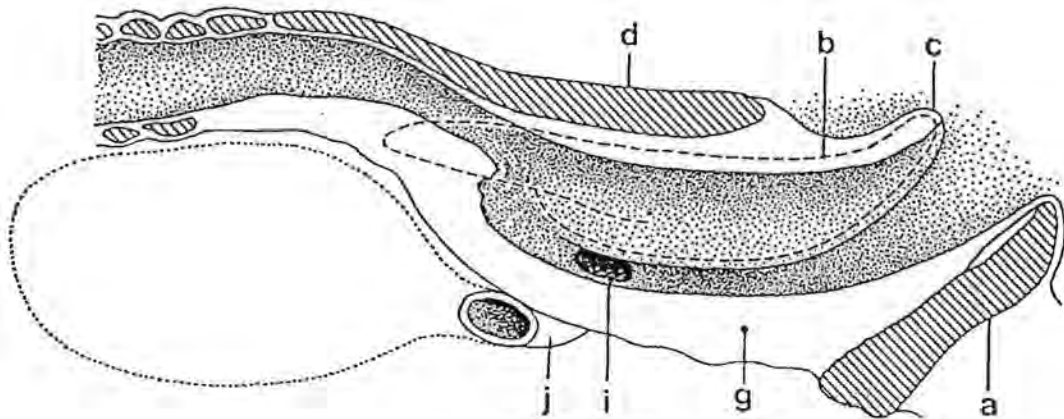


Plate 127:

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.

The most outstanding difference between the laryngeal sacs in the two species is the much greater development of the sac in adult *C.marginata* (at least for males). Table 6 lists the lengths of laryngeal sacs of some species of mysticetes as described by different authors.

Table 6 Lengths of laryngeal sacs of mysticetes as described by various authors.

Author	Species described	Sex	Length of animal (m)	Length of laryngeal sac (cm)	Relative age of specimen
Turner (1872)	<i>B. musculus</i>	♀	23.9	25.4	Adult
Beauregard & Boulart (1882)	<i>B. musculus</i>	♂	3.6	1.0	Foetus
	<i>B. physalus</i>	♀	12.0	≥ 35.0	Adult
	<i>E. australis</i>	♀	0.6	—*	Foetus
Purves (1967)	<i>B. physalus</i>	♀	17.8	120.0	Subadult
Quayle (1991)	<i>M. novaeangliae</i>	♂	4.2	10.0	Juvenile
Reeb (present study)	<i>B. acutorostrata</i>	♂	5.3	11.0	Juvenile
		♂	8.5	22.5	Adult
		♀	5.7	11.3	Juvenile
		♀	8.9	28.8	Adult
	<i>C. marginata</i>	♀	3.3	10.0	Juvenile
	♀	3.7	11.5	Juvenile	
	♂	3.2	12.0	Juvenile	
	♂	5.9	51.2	Adult	

\* “quite rudimentary with respect to Balaenopterids”.

Although the methods of measurement used by the different authors are not known, it seems from Table 6 that (with the possible exception of *B. physalus*) the ontogenetic development of the laryngeal sac in *C. marginata* is not matched by any other mysticete species examined to date.

The size and position of the laryngeal sac are not the only unique anatomical features of *C. marginata*. The structure of the thorax, for instance, is quite different to that seen in any other mysticete. Beddard (1901) found that the ribs of *C. marginata* are only, and not very firmly, attached to the transverse processes of their vertebrae. Davies & Guiler (1957) pointed out that compared to other mysticetes the number and flattening of the ribs are much greater in *C. marginata*. The number of vertebrae (based on seven *C. marginata* specimens) ranges as

follows: cervical, 7; thoracic, 17-18; lumbar, 1-4; caudal, 14-16; total, 40-44 (Baker 1985). The vertebral formula for *B. acutorostrata* (based on two adult specimens from the Antarctic and two juveniles from the North Pacific) was found by Omura (1975) to be cervical, 7; thoracic, 11-12; lumbar, 10-12; caudal, 18-20; total, 48-50.

The marked development of the thorax in *C. marginata* is perhaps best demonstrated by the proportion that the thoracic vertebrae constitute of the whole vertebral column. The data given by Baker (1985) show that thoracic vertebrae composed 41-43% of the vertebral count, compared to 22-25% for *B. acutorostrata* (Omura 1975). The thoracic development in *C. marginata* is in fact unmatched by any cetacean: vertebral counts listed by Watson (1981) show that in no cetacean family, apart from Neobalaenidae, do the thoracic vertebrae make up more than 26% of the total number of vertebrae (Table 7). This thoracic development is perhaps achieved at the expense of the lumbar vertebrae which only make up 2.5-9% in Neobalaenidae (Omura 1975) compared to 21-23% for other mysticetes (Omura 1975, Watson 1981) (Table 7).

Beddard (1901) compares the arrangement of the ribs to armature for the protection of the viscera and explains that if *C. marginata* is capable of longer submersion compared to some other mysticetes, "the lax attachment of the ribs may conceivably allow of a greater expansion of the contained lungs". Davies & Guiler (1957) however doubt whether this hypothesis is consistent with the knowledge of the physiology of diving in whales. These authors believe that the peculiar structure of its skeleton suggests that *C. marginata* may not be an especially deep diver, but rather that it spends abnormally long periods of time beneath the surface and may actually rest on the bottom for much of this time, the ribs acting as support at this time. Bonner (1980) raises the question what a filter-feeder, such as *C. marginata*, would be doing in such bottom-lying activities (except meditating).

Table 7 Percentage that thoracic and lumbar vertebrae constitute of the total vertebral column in mysticete and odontocete families.

Family	Ave. Total No. of vertebrae	Percentage (%) of thoracic vertebrae	Percentage (%) of lumbar vertebrae
Balaenidae	55-57	24-25	21-22
Neobalaenidae	41	42	5
Eschrichtiidae	56	25	21
Balaenopteridae	48-64	23	21-23
Ziphiidae	46-49	20-22	20-29
Platanistidae	40-51	23-26	13-16
Monodontidae	53-54	22-23	15
Physeteridae	50-56	22-23	16
Stenidae	51-67	19-24	22-24
Phocoenidae	62-97	17-19	18-27
Globicephalidae	50-82	17-20	21-26
Delphinidae	63-92	16-19	22-32

It is possible that the unique development and construction of the thorax of *C. marginata* are associated with the unusual positioning and ontogenetic development of the laryngeal sac (as seen in the adult male). Beddard's (1901) hypothesis in fact could be modified to refer to expansion of the laryngeal sac rather than the lungs.

#### 4.3 Phylogeny and functions of the laryngeal sac

Barnes & McLeod (1984) are of the opinion that the order Cetacea is a monophyletic evolutionary group, in which the two modern suborders Odontoceti and Mysticeti both have their ultimate ancestries within the primitive suborder Archaeoceti. Unfortunately there are no fossils of *C. marginata* and therefore no palaeontological data on its familial interrelationships are available. However the fossil record of Balaenopteridae, the family under which *B. acutorostrata* falls, extends back about 10-12 million years ago to the Late Miocene (Barnes & McLeod 1984). According to Arnason & Best (1991), *C. marginata* is genetically closer to Balaenopteridae than to Balaenidae.

The positioning and marked ontogenetic development of the laryngeal sac in *C. marginata* differ significantly from the laryngeal apparatus of *B. acutorostrata* (or any other mysticete described to date). This leads one to speculate whether the functioning of the apparatus differs in *C. marginata* compared to other mysticete species.

"We must consider any such supposition as that the water may penetrate from the cavity of the mouth into the respiratory canals, and particularly into the tracheal bag on the larynx, and be again expelled from thence through the nostrils, to be quite improbable" (Eschricht & Reinhardt 1866). The direct contact the laryngeal sac has with the trachea implies that water entering this sac would inevitably also enter the trachea and thus the lungs. The function of the laryngeal sac, as mentioned in the introduction, has therefore been narrowed down to three main possibilities involving the movement or storage of air.

#### **4.3.1 Exclusion of water and food from the respiratory canal**

The justification given for the sac as a mechanism to preclude the entrance of water and food into the respiratory canal (*vide* page 8) is quite improbable; in order to successfully execute a "blast of air" at the same time that food and water are ingested, as proposed by Rawitz (1900 in Hosokawa 1950), the timing of these activities would have to be very precise. It would also mean that feeding would be a function of sac inflation. Exhalation of air during feeding is also not an obvious feature in Balaenopterids (Best, pers. comm.). Finally, this proposed function of the sac is generally believed to be undertaken by the epiglottis.

#### **4.3.2 Complete utilization of oxygen in inspired air**

Schulte's (1916) speculation that contraction and relaxation of the laryngeal sac during submergence would cause a circulation of air in the trachea and bronchi and thereby encourage oxygen absorption (*vide* page 9) is unlikely when Scholander's (1940) proposal that alveolar collapse occurs in diving mammals at about 100m, is taken into consideration. Such collapse prohibits gaseous exchange during deep dives and possibly reduces the risk of the bends and nitrogen narcosis. Although there are no available data on the dive depths of *B. acutorostrata* and *C. marginata*, data have been collected for a few mysticete species. Maximum dive depths of

272-306 m have been recorded for *E. glacialis* for a period of 2 minutes (Mate, Nieukirk, Mesecar & Martin 1992) and a harpooned *B. physalus* has been recorded diving to 355 m for a period of 20 minutes (Scholander 1940). As the vertical distribution of zooplankton in the world's oceans extends well below 100 m (Van der Spoel & Heyman 1983), it is not unreasonable to assume that most mysticetes can dive to depths greater than 100m.

Based on the laryngeal sac's position as an integral part of the ventral tracheal wall that bulges dorsally into the tracheal lumen, Haldiman & Tarpley (1993) concluded that enlargement of the sac in *B. mysticetus* would close off the trachea. Except for *C. marginata*, this positioning of the laryngeal sac has been found in all studies conducted on mysticetes (Eschricht & Reinhardt 1866; Carte & Macalister 1868; Turner 1872; Beauregard & Boulart 1882; Dubois 1886; Benham 1901; Schulte 1916; Hosokawa 1950; Yablokov, Bel'kovich & Borisov 1974; Quayle 1991; Schoenfuss & Hillmann 1996). The "re-breathing" of air as suggested by Negus (1962), whereby the sac might act as an air reservoir so that when the animal is submerged for a prolonged period of time, the used-up air which has been in contact with the pulmonary epithelium would mix with the relatively unused air which has lain in the sac, is therefore questionable in mysticetes due to the fact that the used-up air which has been in contact with the pulmonary epithelium would not be able to move into the laryngeal sac if it was inflated.

The size of the laryngeal sac should also be considered. Although previous studies of the laryngeal apparatus of various mysticete species involved foetal or juvenile material, the adult *B. acutorostrata* specimens available for this study had laryngeal sacs averaging 25.7 cm in length and 18.2 cm in width. Keeping Boyle's Law in mind (that the volume of a given quantity of gas varies inversely as the pressure on it), it seems that this structure would have to be a lot larger if it was to play any significant role in air storage for more efficient oxygen usage.

### 4.3.3 Phonation

Several authors support the hypothesis that the laryngeal sac is involved in phonation, and have suggested many possible ways in which this is achieved (*vide* page 9). Turner (1872) hypothesised that the processi vocales of the approximated arytenoid cartilages might be made

to vibrate, using air forced from the laryngeal sac. However, although the posterior ends of the *processi vocales* are united only by connective tissue, while at the same time forming the dorsal wall of the laryngeal sac with the rest of the arytenoid cartilages, it is not clear how much vibration can actually be achieved by the portions of these cartilages.

Experiments performed by Schoenfuss & Hillmann (1996) with laminar air flow through the laryngeal diverticulum, and histological as well as anatomical investigations of this structure, in *B. mysticetus*, strongly suggest a sound-producing function. These authors found that when air is forced out of the laryngeal diverticulum, by contraction of the powerful *M. diverticulum laryngeus* (proposed), vibration along the leading edge of the flap (arytenoid lips) produces a high pitched sound. Unfortunately no sounds were recorded during the laminar air flow experiment conducted in this study, but the laryngeal sac inflated, as did the lungs, when air was introduced down the nasopharynx of *C. marginata*, an occurrence which can safely be expected to occur in *B. acutorostrata* considering the large glottis which opens directly into both the laryngeal sac and the trachea.

Schulte (1916) and Carte & Macalister (1868) describe the arytenoid lips as being homologous with the phonatory "arytenoid fold" of ungulate mammals. Purves (1967) states that the functionality of the arytenoid lips in the adult is indicated by "its isogonic [sic] growth in diameter and thickness, and its situation at the apex of the glottis gives support to the notion that the phonatory region of the larynx, is, as in the Odontocete, at the tip of the epiglottic spout".

Quayle (1991) states that the larynx seems too complicated a structure to be a simple valve and the remarkable similarity between the human and whale glottic inlets suggests that it is morphologically capable of phonation.

Sound is produced by the interruption of the flow of air which results in sound waves consisting of alternating compressions and rarefactions that are related to the displacement of molecules (Denny 1993). As such, the larynx provides animals, which possess a pulmonary system, with a convenient method of phonation (Negus 1962). This is also true for cetaceans. However, since most underwater sounds in cetacea are produced without the release of air, the passage of air



across the larynx must involve some means of temporary storage and recycling of air back into the lungs/trachea.

In this study of the laryngeal apparatus of *B. acutorostrata*, the stratified squamous nature of the epithelium lining the arytenoid lips, the highly vascularised and innervated muscles of the laryngeal sac and the spiral nature of its blood vessels and nerves, indicate that (a) the arytenoid lips are able to withstand strain caused by the movement of air over the larynx, and (b) the laryngeal sac is able to expand and contract when air is passed into it, allowing for the recycling of air to occur.

Clark (1983) noted that songs of *B. mysticetus*, which may be produced continuously for 154 seconds, have alternating louder and softer portions that may represent recycling of air. *M. novaeangliae* do not produce bubbles (Silber 1986) during the 7-30 minutes that they are submerged and singing (Payne & McVay 1971); so that recycling of air is likely in that species (Edds, Odell & Tershy 1993). Ridgway (in Edds *et. al.* 1993) observed that during vocalisation, young *T. truncatus* often released bubbles, but that adults do so rarely. He suggested that dolphins learn to recycle air. Although bubble release during vocalisation is not common in *M. novaeangliae* (Watkins 1967; Silber in Edds *et. al.* 1993) and *E. australis* (Clark 1982), bubble production has been observed in specific behavioural contexts as well as during particular sound types (Clark 1983; Silber 1986). Edds *et. al.* (1993) observed air being expelled during phonation by a juvenile *B. edeni*. These authors state that if recycling of air is common during repeated or extended vocalisations by mysticetes, it is possible that the skill is learned, and had not been mastered by the captive juvenile *B. edeni*, or alternatively, the recycling mechanism may not be functional in young animals for developmental or maturational reasons.

In *B. acutorostrata* as well as in *C. marginata* the components of the laryngeal apparatus were all present in the juveniles, but were larger and better developed in the adults. For this reason it seems likely that the apparatus is functional making it possible for the juveniles to begin the process of learning how to phonate. This skill might be developed with age as the laryngeal apparatus matures.

The sounds reported for *C. marginata* by Dawbin & Cato (1992) were of very low frequency, with no high pitched sounds being reported. Although this recording was made from a juvenile (with a possibly reduced repertoire compared to an adult), it is perhaps significant that this study has shown that adult male (and presumably adult female) *C. marginata* do not possess arytenoid lips.

I therefore agree in principle with Purves (1967) and Schoenfuss & Hillmann (1996), that the laryngeal sac as well as the arytenoid lips are implicated in phonation (in animals in which they are found). The force of air from the laryngeal sac through the arytenoid lips may produce high pitched sounds, as indicated by the latter authors, but may well be responsible for other sounds in the live animals, for example, as the air is recycled or redirected to the trachea/lungs. However, I am also of the opinion that Quayle's (1991) hypothesis whereby the air columns in the laryngeal sac and nasopharynx vibrate due to air from the laryngeal sac (as well as the recycled air redirected to the trachea/lungs) being forced between the arytenoids, causing pressure fluctuations that are transmitted through the soft tissues of the whale into the surrounding water, could also provide for the majority of the mysticete repertoire. This hypothesis is supported by the incredible development of the laryngeal sac in adult *C. marginata* which, through expansion and contraction, would allow the recycling of large amounts of air for phonation.

## CHAPTER 5: CONCLUSION

This study adds to the previous descriptions of the laryngeal apparatus of *B. acutorostrata* by including both adult and juvenile specimens of both sexes, and by adding descriptions of the fine anatomy. The larynx of *C. marginata* has not been described previously, nor has the striking ontogenetic development of the laryngeal sac in any baleen whale, as most dissections have been of foetal or juvenile material.

"We know how unsafe it is, both generally and in respect to these organs in particular, to make inferences from parts as they appear in the dead body, as to their appearance during the life of the animal" (Eschricht & Reinhardt 1866).

The above statement summarises one of the greatest hurdles that anatomists have to overcome. For cetacean biologists, due to the inaccessibility of live mysticetes and the general difficulty of obtaining fresh mysticete material, it makes the hurdle an even more daunting one.

Certainly this is the case with regards to the laryngeal sac found in both *B. acutorostrata* and *C. marginata*. The ontogenetic development of the laryngeal sac seen in both species indicates that this structure is functional. The muscular nature and histological organisation of the laryngeal sac in both species is such that it also seems very probable that this structure undergoes expansion and contraction.

Although the positioning of the laryngeal sac differs markedly between *B. acutorostrata* and *C. marginata*, in both of these species the sac is associated with the trachea through non-valvular openings, necessitating that water not be introduced into the sac. This association together with all the characteristics listed above strongly suggest that the laryngeal sac plays a role in sound production, probably through the recycling of air during submergence. The force of air from the laryngeal sac through the arytenoid lips may produce high pitched sounds, but may well be responsible for other sounds in the live animals, for example, as the air is recycled or redirected to the trachea/lungs. The vibrations of the air columns in the laryngeal sac and nasopharynx caused by air from the laryngeal sac (as well as the recycled air redirected to the trachea/lungs)

being forced between the arytenoids, causing pressure fluctuations that are transmitted through the soft tissues of the whale into the surrounding water, could also provide for the majority of the mysticete repertoire.

The size of the sac also differs in the respective species. This feature is directly related to the positioning of the sac i.e. the integration of the sac into the laryngeal apparatus of *B. acutorostrata* limits the extent to which the sac can grow and expand, whereas in *C. marginata*, the “separation” of the laryngeal sac from the tracheal rings as well as the thoracic development of this species allows the sac to grow to the enormous size it attains in the adult male. This development in *C. marginata*, unmatched by any other cetacean may also allow the sac of the adult animal to expand more freely.

Experimental confirmation of the role of the laryngeal sac in phonation really requires access to a live animal that is temporarily or permanently in captivity. Juvenile *C. marginata* have been caught from the beach with seine nets on several occasions in South African waters (Ross, Best & Donnelly 1975), and are nutritionally independent at 3 m in length (Sekiguchi, Best & Kaczmaruk 1992). Adults only grow to 6 m in length; many captive killer whales are substantially larger than this. Furthermore, recordings of sounds from adult free-living *C. marginata* are needed, and these might throw some light on the reason for the unique development of the laryngeal sac and thorax in this species.