

Opening and closing mechanisms of the leatherback sea turtle larynx: a crucial role for the tongue

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SUMMARY

A combination of dissection and computed tomography scanning has provided significant novel insights into the structure and function of the *Dermochelys coriacea* larynx and its associated muscles. Several previously unknown features of the laryngeal aditus (glottis) are described and their functional significance in its opening and closure are considered. The tongue plays an essential part in producing and maintaining closure during dives and feeding bouts. Closure is brought about by compression of the glottis under the action of the two hyoglossus muscles. The tongue thus plays the role of the epiglottis of mammals, sealing the entrance to the larynx. As is already clear, opening is brought about by abduction of the arytenoid cartilages. In addition, there is a powerful mechanism for maintaining the larynx in close apposition to the hyoid plate during feeding and neck flexion, thereby enhancing the efficiency of feeding.

Key words: leatherback turtle, tongue, larynx, hyoid, diving, feeding.

INTRODUCTION

The leatherback sea turtle, *Dermochelys coriacea* (Vandelli 1761), the sole living species of the family Dermochelyidae, is a most unusual chelonian anatomically, physiologically and ecologically. Adult leatherbacks are large animals (typically 300–500 kg, but <916 kg) (Eckert and Luginbuhl, 1988), overlapping in size with many marine mammal species. Leatherbacks have highly reduced shells, thick leathery skins and are the most widely distributed of living reptiles, found as far north as the Arctic Circle and as far south as the Cape of Good Hope and New Zealand. In addition, known summer feeding distributions at high latitudes range widely, from Nova Scotia and Ireland to Japan and Argentina.

Dermochelys coriacea is an obligate feeder on gelatinous organisms, predominantly medusae, pyrosomas and siphonophores throughout its life (den Hartog and van Neirp, 1984; Davenport and Balazs, 1991). Its diet is therefore of poor quality for a carnivore [for discussion, see Doyle et al. (Doyle et al., 2007)], especially as the leatherback is probably the fastest-growing living reptile species (Zug and Parham, 1996; Jones, 2009). This means that it has to eat large quantities of food (Duron, 1978), from more than 100% body mass day⁻¹ in hatchlings (Lutcavage and Lutz, 1986) to at least 50% body mass day⁻¹ in adults (Davenport, 1998). Individual prey items are also large [e.g. single specimens of the medusa *Rhizostoma octopus*, commonly eaten by *D. coriacea* foraging in the North Atlantic (Houghton et al., 2006), may exceed 30 kg wet mass (Houghton et al., 2007)] and *D. coriacea* is unique amongst turtles in that it can simultaneously swallow food material while ingesting more (Bels et al., 1998). It therefore has to have a large head, sharp beak, capacious mouth and large oesophagus. *Dermochelys coriacea* is a suction feeder (Bels et al., 1998) and so generates a substantial negative pressure within the buccopharyngeal chamber to engulf

food and water (see Lemell et al., 2000); this negative pressure is substantially generated by sharp depressions of the hyoid apparatus.

Adult leatherbacks are accomplished divers. Dives beyond 1000 m were first inferred (Eckert et al., 1986; Eckert et al., 1989) and subsequently confirmed by satellite tags (Houghton et al., 2008). Maximum recorded dive depths and dive durations have now been extended to 1280 m (Doyle et al., 2008) and 86.5 min (López-Mendilaharsu et al., 2009), respectively. However, it has recently been determined from satellite telemetry that very deep dives (>300 m) are rare (Houghton et al., 2008), making up only 0.4% of all dives, and exceed the calculated aerobic scope for the species. Leatherbacks are mostly (99.6%) limited to aerobic foraging dives of <300 m, but they conduct thousands of dives per year so there are appreciable total annual numbers of very deep dives as well. A recent study (Davenport et al., 2009b) demonstrated that adult *D. coriacea* (but not hatchlings) have a specialized tracheal structure that facilitates collapse of the respiratory tract during dives.

Leatherbacks, like cetaceans and pinnipeds (seals, sea lions and walrus), capture and swallow food during dives. The oropharynx cannot be hermetically sealed from the environment in turtles (i.e. they have no lips), and the larynx is positioned close to the front of the mouth as in all turtles. This opens up the possibility of the respiratory tract being flooded during dives or when feeding underwater. Marine mammals (like terrestrial mammals) have a muscular/cartilaginous epiglottic mechanism that can close off the respiratory tract anteriorly (Tyack and Miller, 2002). In the case of whales, the respiratory tract is totally isolated from the oropharynx because the epiglottis is mounted far more rostrally than in terrestrial forms and is sealed within the nasal tract (e.g. Reidenberg and Laitman, 1987). A similar separation of digestive and respiratory tracts has evolved separately in beavers (*Castor canadensis*), which

feed and gnaw wood extensively underwater (Coles, 1970). Aquatic birds, though not possessing an epiglottis, are also able to separate the respiratory tract from the oropharynx as the glottis can be sealed into the nasal tract by the lips of the choana. Marine mammals and birds can seal the nostrils when diving.

Like all turtles, *D. coriacea* lacks an epiglottis to cover the entrance to the larynx and protect against inhalation of seawater while diving and feeding. There have been many morphological studies of the hyoid apparatus and larynx of turtles (Henle, 1839; Siebenrock, 1899; Göppert, 1900) (for review, see Schumacher, 1973; Sacchi et al., 2004). These have described in some detail the musculoskeletal structure of the larynx, including that of *D. coriacea*. In addition, several functional studies of the feeding behaviour of turtles have been performed recently (Bels et al., 1998; Lemell et al., 2000; Wochesländer et al., 2000; Lemell et al., 2002). The morphological studies of the *D. coriacea* larynx have described its cartilaginous skeleton and the associated musculature. [The anterior part of the skeleton of the *D. coriacea* respiratory tract consists of a cartilaginous tube. The exact phylogenetic/embryological composition of this is unclear, particularly as to whether the thyroid cartilaginous element contributes to it, in which case the cartilage would be termed thyreocricoid (see Göppert, 1900; Schumacher, 1973). For simplicity, in this study, the term cricoid will be used.] However, these have only partly explained the basis of the mechanisms of opening, closure and protection of the glottis. In the course of the present series of investigations on *D. coriacea* (Davenport et al., 2009a; Davenport et al., 2009b), several previously unknown features of the mechanisms of opening and closure of its laryngeal aditus (glottis) became evident. This study concerns these and considers their functional significance.

MATERIALS AND METHODS

Study specimens

Material was collected from two recently deceased stranded adult leatherbacks. The first turtle (specimen 1) was found close to the shore at Ballycotton, East Cork, Ireland. A female, it was 168 cm in standard curved carapace length, and so would probably have weighed ~450 kg (see Georges and Fossette, 2006). The head and neck were removed (amputated as close as possible to the body) and deep-frozen; the remainder of the carcass was disposed of at sea. The head and neck were later embalmed in the Department of Anatomy, University College Cork. The carotid arteries were isolated on the severed surface of the neck by minor dissection. A straight artery tube (120×6 mm, length × diameter) was inserted into each artery and clamped in place. A 2% aqueous solution of 38% formaldehyde was pumped into each artery using a Duotronic embalming pump (Modesto, CA, USA). Pumping continued until the solution was observed to be emerging from the cut apertures of the jugular veins (as well as the surfaces of the muscle tissues). The carotid arteries were then clamped and the specimen was allowed to settle for 24 h before submerging it in a 2% aqueous solution of 38% formaldehyde, allowing for fixation of the external tissues on the cut surface.

The second adult turtle (specimen 2), a male, was observed live in Strangford Lough, Co. Down, Northern Ireland, on 18 February 2008. It was found dead (apparently of infection following an earlier, partially healed, severe head wound) on 21 February 2008 and autopsied. Its standard curved carapace length was 154 cm, suggesting a live mass of ~350 kg (see Georges and Fossette, 2006). During the autopsy the larynx and a short length of upper trachea were removed and fixed/preserved in formalin.

A single hatchling turtle (specimen 3; Museum code BMNH 1969.2805-2807) was dissected under permit at the Natural History Museum, London, on 20 March 2009. It had originally been collected in French Guiana in 1969, and so was also from the Atlantic population of leatherbacks. It had been stored in alcohol after initial fixing in formalin. Permit and CITES rules prevented the removal of material from the museum, so study was limited to display of the gross anatomy of the larynx and trachea.

Gross anatomy

Gross dissection was conducted on the head and neck of specimen 1. Images of dissections were captured with a Casio 10.1 megapixel digital camera (Shibuyaku, Tokyo, Japan). To examine the mouth, pharynx, tongue, larynx, trachea and hyoid apparatus, the structures within the concavity of the mandible, including all of the above, were removed *en masse* (see Fig. 1A–C). This was done by dissecting them away from the inner surface of the mandible and severing the oral and pharyngeal mucosae at the junction of their dorsal and lateral walls. The isolated tissue mass was then dissected so as to display its component elements, including the tissue layers of the anterior neck, the hyoid apparatus, the tongue, the larynx, the anterior part of the trachea and the muscles related to all of these. All of the muscular actions that are reported below were experimentally tested, demonstrated and verified on the dissections.

Computed tomography (CT) scanning

Prior to dissection, the head and neck of specimen 1 were CT-scanned (1 mm slice acquisition with a bony reconstruction algorithm) using a Somatom Plus 4 scanner (Siemens, Erlangen, Germany). Analysis was conducted using Osirix v 3.2.1 Software (Osirix Foundation, Geneva, Switzerland) on a Macbook Pro workstation (Apple, Cupertino, CA, USA).

RESULTS

Structure of mouth and pharynx

Removal of the structures within the concavity of the mandible shows the most prominent feature in the floor of the mouth to be the tongue (Fig. 1C). This is short and its dorsal surface is smooth and convex. Its posterior surface is concave. Posterior to it are paired swellings that overlie the larynx – the laryngeal folds (Fig. 1D,E). Between the tongue and the laryngeal folds is the deep, transverse linguolaryngeal cleft. This cleft defines the oropharyngeal junction. The larynx opens into this anteriorly and into the pharynx dorsally. The laryngeal opening (the glottis) has two parts. Its larger, dorsal component is a median slit that lies between the laryngeal folds (Fig. 1D). However, the deepest part of the glottis is more rounded in section and opens into the depths of the linguolaryngeal cleft (Fig. 1E). The floor of the pharynx, like the walls of the oesophagus posterior to it, has prominent longitudinal ridges and caudally projecting pharyngeal spines (Fig. 1C). Under the surface epithelium is a substantial layer of fat, 1.5–4 cm thick (Fig. 4C,D) (see also Davenport et al., 2009a).

Laryngeal structure

The skeleton of the larynx rests in a groove on the dorsal surface of the hyoid plate (Fig. 2A,B). The tubular laryngeal skeleton consists of the cricoid cartilage (Fig. 3A,B) and two arytenoid cartilages (Fig. 3D,E). The dorsal surface of the cricoid curves sharply towards the pharynx, and its anterior edge has a prominent transversely running cricoid crest (Fig. 3B,C). Its anterior opening is oblique, facing anteriorly and dorsally (Fig. 3B). Each lateral, sloping wall of the opening has an inwardly directed shelf, with which the

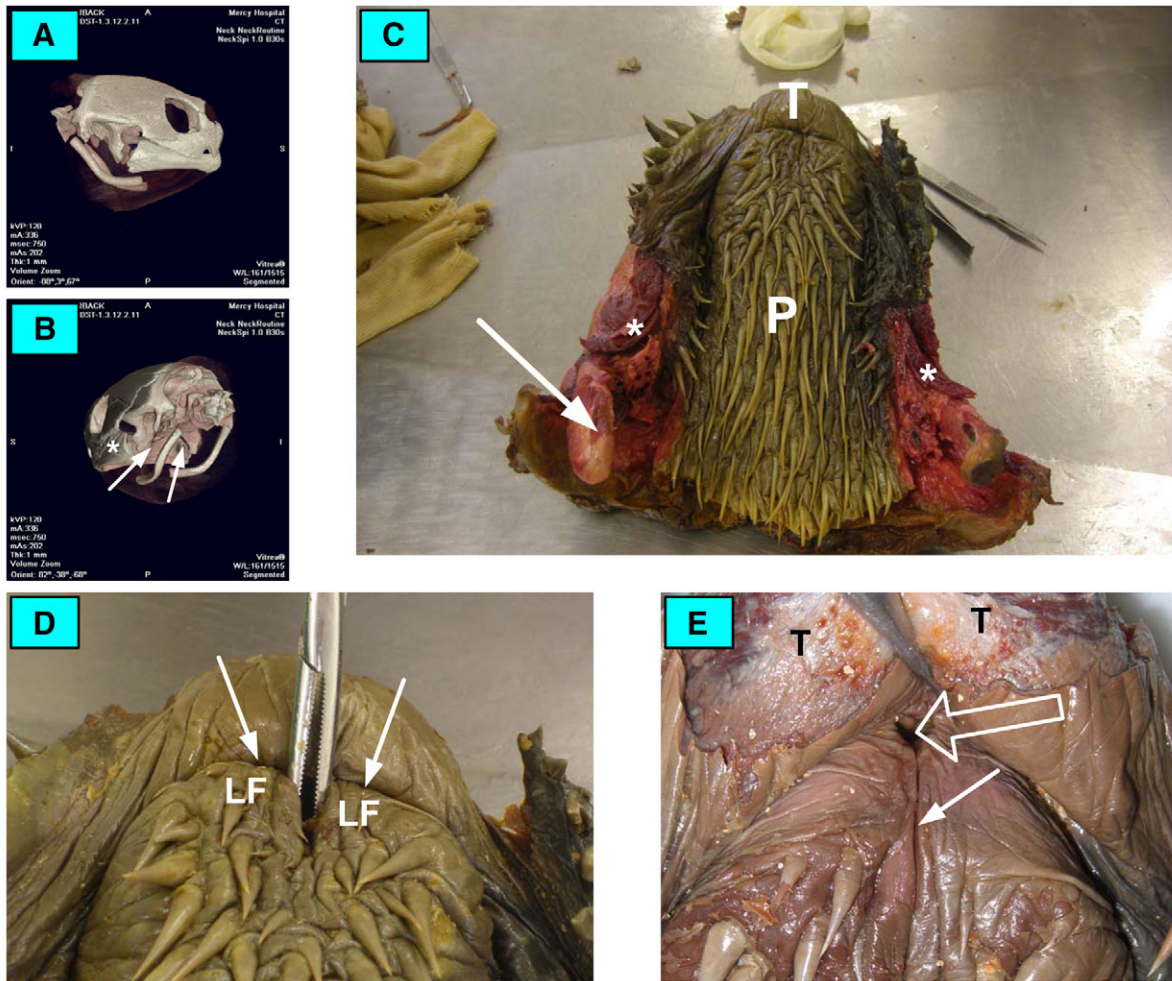


Fig. 1. (A,B) Three-dimensional reconstruction of the skeletal elements of the head and neck of *D. coriacea*: (A) lateral view, (B) inferolateral view, showing the space (solid arrows) within the mandible (asterisk) from which the tissue specimen was removed. (C) Tissue specimen, showing the tongue (T), the pharyngeal floor (P) with spines, tissues between the tongue and mandible (asterisk) and the cornu branchiale II (solid arrow). (D) The linguolaryngeal cleft (solid arrows), between the tongue and larynx, and the glottis (opened with forceps), between laryngeal folds (LF). (E) Opened linguolaryngeal cleft, showing the divided tongue (T) above and components of the glottal openings: the median cleft (solid arrow) and the more rounded opening into depths of the linguolaryngeal cleft (open arrow).

corresponding arytenoid articulates (Fig. 3C). From its anterior end a strong, fibrous cricothyroid ligament connects it to the stem of the processus lingualis of the hyoid (Fig. 7F). The cricoid is continuous posteriorly with the skeleton of the trachea (see Introduction) (Davenport et al., 2009b). The transition between the two is poorly defined, the more anterior tracheal rings being fused not only with the cricoid but also with one another. The anvil-shaped arytenoid cartilage (Fig. 3D,E) has a flattened basal plate that is attached to the cricoid shelf by strong ligaments. A dorsal processus muscularis arises from its anterior part and curves posterolaterally. The abductor arytenoideae muscle is inserted into this (see below).

The thick laryngeal folds consist of fibrofatty tissue and lie immediately anterior to the oblique opening of the cricoid cartilage. Each envelops an arytenoid cartilage and its muscles (Fig. 4C,D). Each projects medially, and where their medial surfaces come into apposition they form a deep cleft, the median part of the glottis (Fig. 1D, Fig. 4, Fig. 5A,B). Their anterior surfaces together form the posterior, convex wall of the linguolaryngeal cleft (Fig. 1D,E, Fig. 7F). The mucosa on their medial surfaces is firmly adherent to an extensive, underlying dense plate of fibrous tissue in each fold

(Fig. 4A,B). This is intimately attached to the arytenoid cartilage and extends anteriorly beyond the latter, through the medial part of the fold. This arrangement ensures that each arytenoid cartilage and its associated laryngeal fold move as a unit during laryngeal opening and closure (see below).

The laryngeal cavity is tubular (Figs 5, 6). It is wide posteriorly, where it is imperceptibly continuous with the trachea. Its anterior part is narrow, where it is impinged upon dorsally by the laryngeal folds (Fig. 6C). The dorsal part of the glottis is a median slit between these (Fig. 5A, Fig. 6C). The cavity opens anteriorly into the linguolaryngeal cleft through the ventral part of the glottis (Fig. 1E, Fig. 6C).

There are two pairs of laryngeal muscles (Fig. 7). The abductor arytenoideae runs anteriorly and dorsally from the lateral aspect of the larynx and trachea to the processus muscularis arytenoideae (Fig. 7A–F). [Muscle nomenclature: the terms abductor arytenoideae and compressor laryngis are preferable to those used previously, namely, dilator laryngis and constrictor laryngis, respectively (Sacchi et al., 2004), because they connote the action of each muscle unequivocally. The former dilates the glottis, and not the larynx,

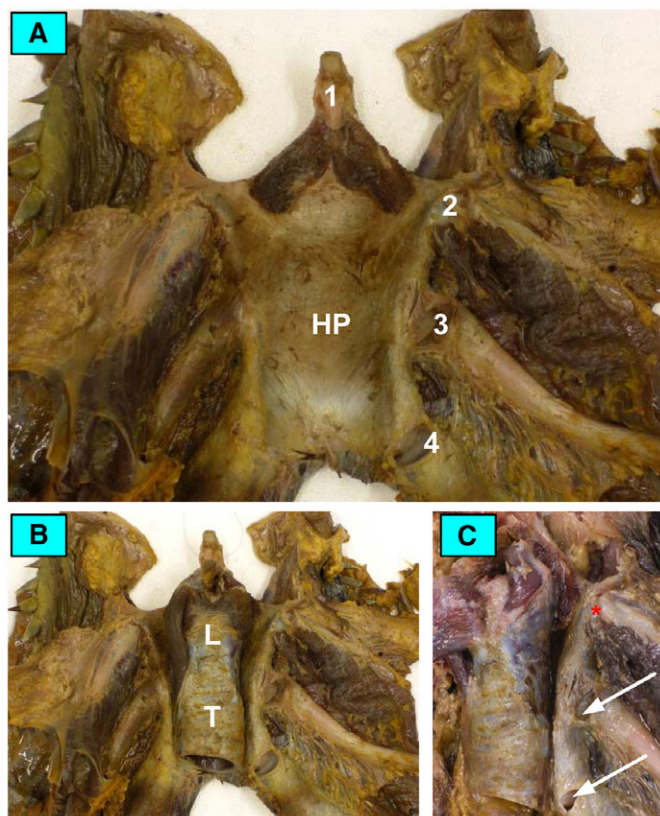


Fig. 2. (A) Dorsal surface of the hyoid plate (HP) of *D. coriacea*, showing: (1) the processus lingualis and (2,3,4) the hyoid prominences with which the cornu hyale and cornua branchialia II and III, respectively, articulate (see below and text). (B) The larynx (L) and trachea (T) *in situ* in the deep groove on the dorsal surface of the hyoid plate. (C) The cornu hyale articulates with the hyoid plate by means of a fibrous joint (asterisk); the articulations of the cornua branchialia II and III are synovial (opened cavities; solid arrows).

by abducting the arytenoid cartilages. The latter arches around the cricoid cartilage and its primary action is to compress the larynx against the hyoid plate.] For actions, see Discussion.

The compressor laryngis muscle (Fig. 7D–G) arises from the hyoid plate (Fig. 7G), lateral and anterior to the laryngeal skeleton. It curves dorsally around the cricoid. Its anterior fibres run obliquely dorsally and posteriorly, parallel to the lateral margin of the cricoid opening, and pass through the groove between the body and the processus muscularis arytenoideae, deep to the abductor muscle. Its deeper fibres are attached to the lateral and dorsal aspects of the cricoid. The superficial parts of the two muscles are continuous with one another dorsal to the cricoid, posterior to the crest (Fig. 7E). The prominence of the crest prevents the muscle from slipping anteriorly over the rim of the cricoid on contraction. For actions, see the Discussion.

Hyoid apparatus

The hyoid apparatus consists of seven elements: a median hyoid plate and three pairs of bilaterally symmetrical elements (Fig. 2A). These are the cornu hyale and the cornua branchialia II and III, in anteroposterior order (Schumacher, 1973). The hyoid plate (Fig. 2A,B, Fig. 8A) lies ventral to the tongue, pharynx, larynx and trachea. It is formed principally of cartilage, with small, bilaterally symmetrical, ossified regions (Fig. 8B). Its thickness varies from *ca.* 1 cm anteriorly to 2.5 cm posterolaterally. It is ventrally convex

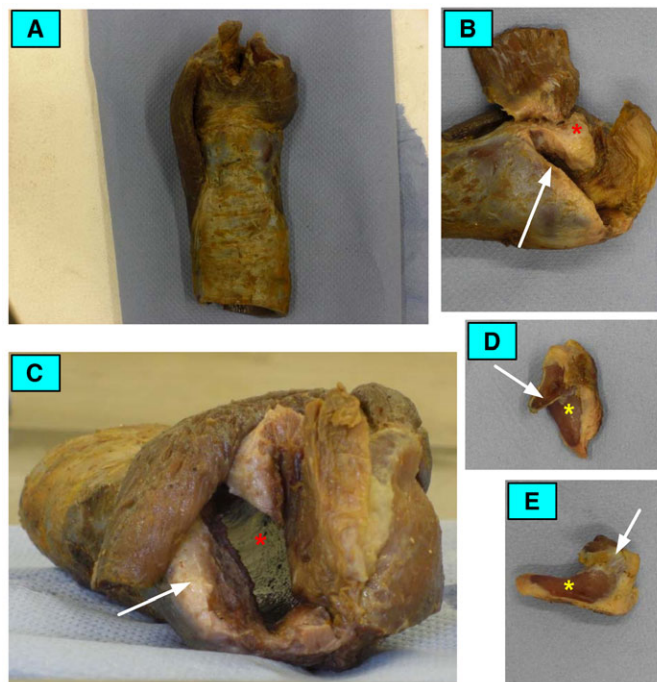


Fig. 3. Skeleton of the larynx and trachea of *D. coriacea*. (A) Dorsal view, showing the continuous nature of the fused cartilaginous components. (B) Lateral view of cricoid, showing the obliquity of its anterior margin (solid arrow). Asterisk, cricoid crest. (C) Oblique view, showing the cricoid shelf (solid arrow) with which the arytenoid cartilage articulates. Asterisk, laryngeal cavity. (D,E) Dorsal and lateral views, respectively, of arytenoid cartilage, showing its processus muscularis (solid arrow) projecting posteriorly and laterally (asterisk).

in both the transverse and longitudinal planes, more so in the former. This resists dorsally directed pressure, exerted by the seawater on the external surface of the floor of the mouth and the neck, which would tend to compress the airway. Its lateral margin has three projections: the anterior, middle and posterior hyoid prominences (Schumacher, 1973). Its anterior extremity curves dorsally into the tongue, forming a median processus lingualis (Fig. 2A). Its dorsal surface has a broad median longitudinal groove. The laryngeal and tracheal cartilages fit closely into this and are firmly attached to it by fibrous tissue. The three hyoid elements articulate with it, each through a highly mobile joint. That for the cornu hyale is fibrous. Those for the cornua branchialia II and III are synovial (Fig. 2C).

Tongue musculature

The tongue substance includes intermingled fibrofatty and diffuse muscular tissue. Poorly developed intralingual muscle is a feature of suction feeders (Lemell et al., 2000). Its best defined components consist of thick fibrous plates located anteriorly and posteriorly. The latter lies immediately anterior to the mucosa of the linguolaryngeal cleft.

There is a pair of extrinsic hyoglossus muscles: each muscle arises mainly from the hyoid apparatus (principally the ventral part of cornu branchiale II) and is composed of four bellies that enter the tongue (Fig. 8A) and are continuous with the fibrous plates of the latter. The two hyoglossus muscles, with the fibrous plates, form a hyoglossal sling which passes anterior to the linguolaryngeal cleft, an arrangement that enables the tongue to be drawn posteriorly against the larynx (see below).

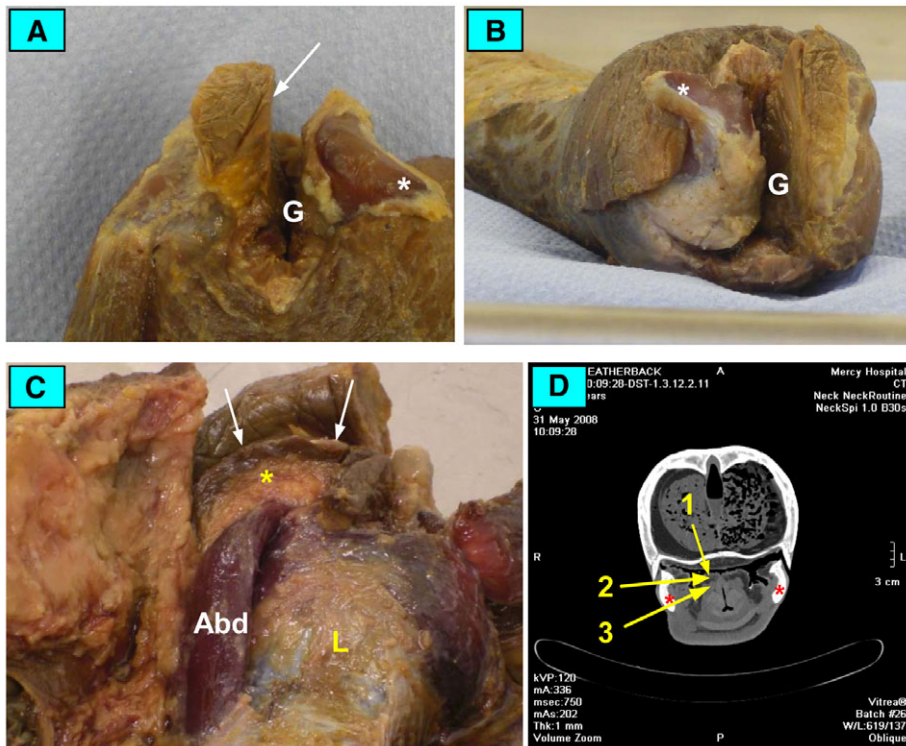


Fig. 4. Dissected glottis of *D. coriacea*. (A) Dorsal view. Left: the mucosa of the left laryngeal fold (solid arrow) with underlying fibrous tissue, bounding the glottis (G). The right laryngeal fold has been removed, exposing the arytenoid cartilage. Asterisk, processus muscularis. (B) Oblique view, showing the same features as shown in A, labelled similarly. (C) Laryngeal cartilage (L) and left laryngeal fold (viewed from the posterior aspect), dissected to show fatty tissue (asterisk) underlying the mucosal surface (solid arrows) and enveloping the abductor arytenoideae (Abd) muscle (see Figs 7, 9). (D) CT transverse sectional image broadly corresponding to C, showing: (1) the laryngeal fold mucosa, (2) the underlying fat and (3) the enveloped abductor arytenoideae muscle. Asterisk, mandible.

Hatchling

All seven hyoid elements were present in the hatchling and were similar in form to those of the adult. Their relationships to the hyoid were also similar, although they are more longitudinally orientated than those of the adult. The glottis is relatively short and its opening is mostly into the linguolaryngeal cleft.

DISCUSSION

Comparative anatomy

The leatherback larynx resembles that of tortoises (Henle, 1839; Siebenrock, 1899; Schumacher, 1973; Sacchi et al., 2004) in many respects: (1) its skeleton consists of a single cricoid and a pair of arytenoid cartilages, each of which articulates with the cricoid by a

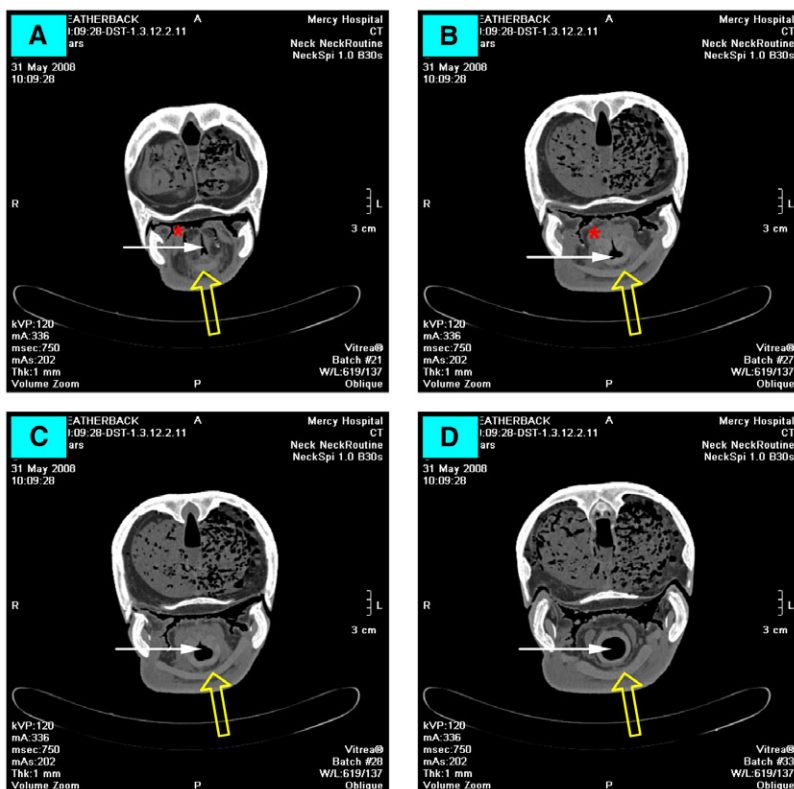


Fig. 5. Laryngeal and tracheal cavities of *D. coriacea*. CT transverse sectional images, showing, in anteroposterior sequence: (A,B) the narrow anterior part of the larynx (below, solid arrows) with laryngeal folds (asterisks) bounding the glottis dorsally; (C) the wide posterior part of the laryngeal cavity (solid arrow); and (D) the wider tracheal cavity (solid arrow). Note the shadow of the hyoid plate (open arrows) ventrally at all levels.

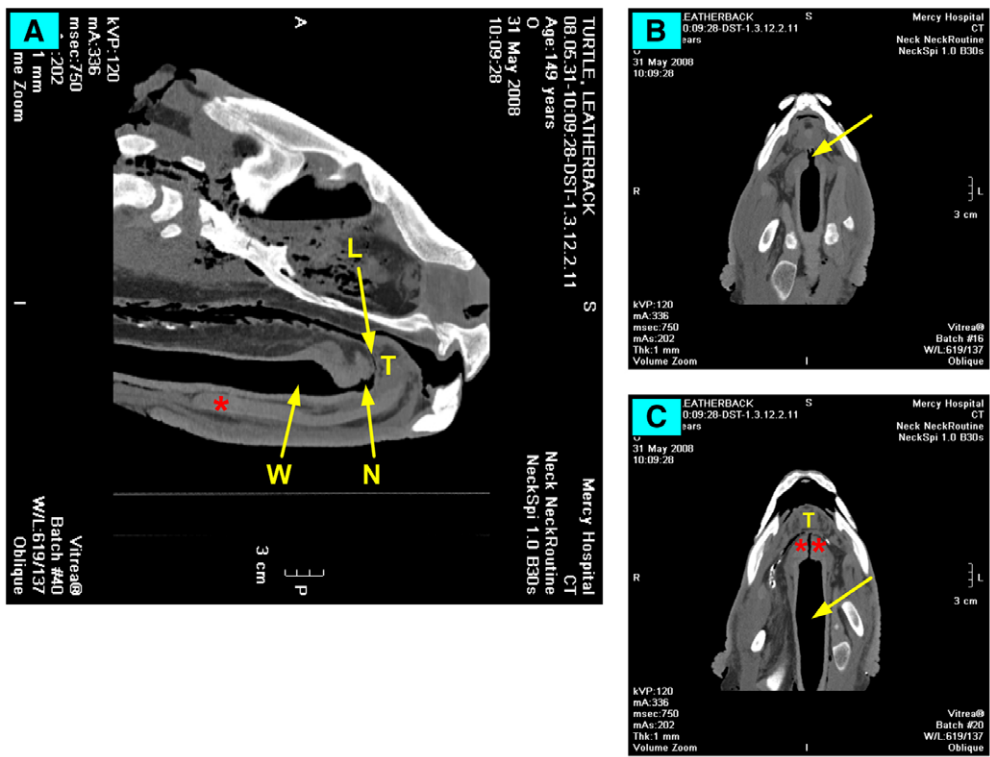


Fig. 6. Laryngeal and tracheal cavities of *D. coriacea*. CT longitudinal sectional images. (A) Sagittal section, showing the wide (W) and narrow (N) parts of the laryngeal cavity, the tongue (T) and the linguolaryngeal cleft (L). Asterisk, hyoid plate. (B,C) Coronal sections in ventro-dorsal sequence, showing: (B) the ventral, narrow part of laryngeal cavity, with the ventral part of the glottal opening anteriorly (solid arrow); and (C) the wide posterior part of the larynx (solid arrow) becoming imperceptibly continuous posteriorly with the trachea (T), and the apposed laryngeal folds (asterisks) bounding the dorsal part of the glottis.

fibrous joint; (2) the arytenoid cartilage has a muscular process; (3) the cricoid cartilage shows a few narrow, transversely orientated clefts; (4) the larynx possesses a pair of muscles; (5) the hyoid apparatus includes an expanded hyoid plate, which is convex ventrally and which possesses a lingual process; and (6) the fused larynx and trachea lie in a groove on the dorsal, concave surface of the hyoid plate.

In the leatherback, the laryngeal mucosa shows no evidence of vocal folds or of any muscles which could be associated with them. This is interesting as leatherbacks have a considerable vocal repertoire (Mrosovsky, 1972), yet do not possess the vibrating structures and diverticula reported for vocal terrestrial tortoises (Sacchi et al., 2004).

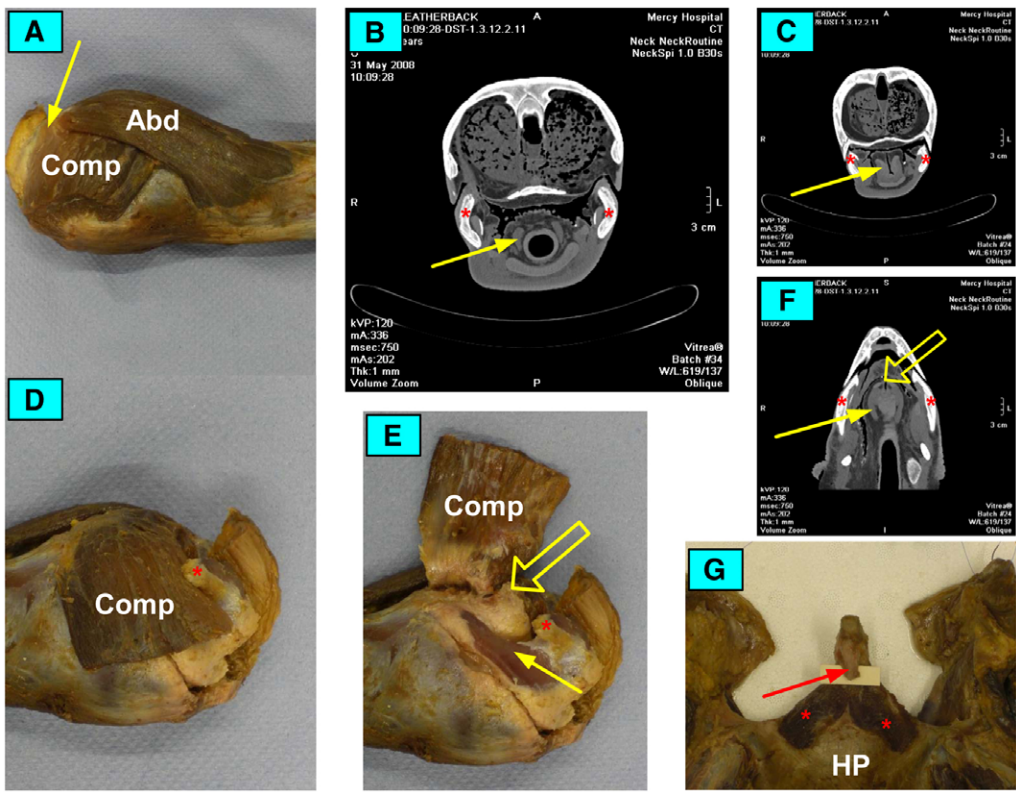


Fig. 7. Laryngeal muscles of *D. coriacea*. (A) Lateral view, showing the abductor arytenoideae (Abd) arising from the cricoid/trachea and inserting into the processus muscularis of the arytenoid cartilage (solid arrow), and the compressor laryngis (Comp). (B,C,F) CT transverse (B,C) and coronal (F) sectional images showing the abductor arytenoideae muscle (solid arrows). Note that the glottis opens into the linguolaryngeal cleft (F; open arrow). Asterisk, mandible. (D) Compressor laryngis (Comp, origin cut) running dorsally and posteriorly between the body and the processus muscularis (asterisk) of arytenoid cartilage. (E) Compressor laryngis (Comp), reflected dorsally to show its dorsal attachment to the cricoid. Solid arrow, body of arytenoid cartilage; asterisk, muscular process of arytenoid; open arrow, cricoid crest. (G) Dorsal view of the hyoid plate (HP), showing the origin of the compressor laryngis (*) and the anterior end of the cut cricohyoid ligament (solid arrow; highlighted against the pale card background).

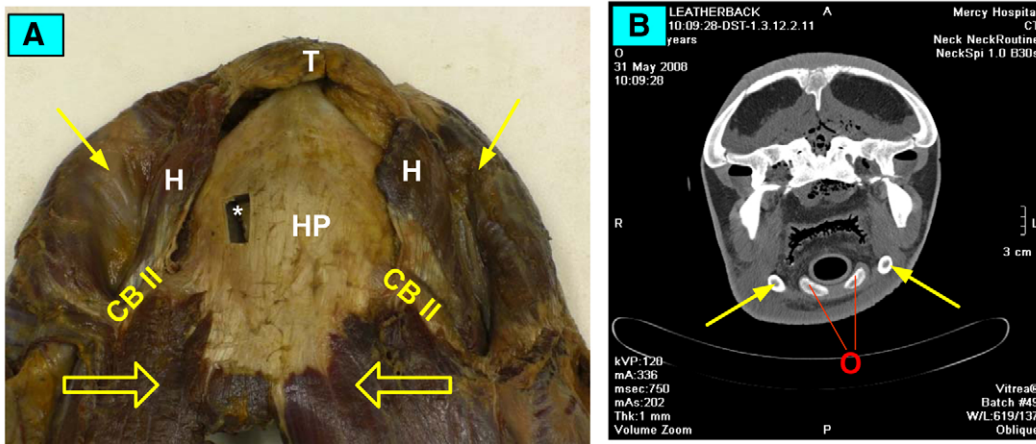


Fig. 8. (A) Ventral view of hyoid plate (HP) of *D. coriacea*, showing the tongue (T) above, dissected free of the hyoid; and the left and right hyoglossus muscles (H) arising from the cornua branchialia II (CBII) and running anteriorly to enter the tongue. Solid arrows indicate M. intermandibularis reflected laterally; open arrows indicate the m. coracohyoideus. (* indicates locus of specimen removed for histology). (B) CT transverse sectional image showing centres of ossification/calcification (O) in hyoid plate. Solid arrows, cornua branchialia II.

Hatchling–postnatal development

It is noteworthy that all seven hyoid elements in the hatchling were similar in form and in their relationships with the hyoid apparatus to those of the adults, though they tended to be more longitudinally arranged. Also, the glottis was relatively shorter than in the adults and it opened principally into the linguolaryngeal cleft.

Functional correlates of the tongue

The hyoid apparatus and of the tongue of vertebrates tend to be inversely proportional in size to one another (Bramble and Wake, 1985); in aquatic feeders, the former is well developed and the latter is small, smooth and relatively immobile, an arrangement that aids suction feeding. The tongue musculature is poorly developed, and the small size of the tongue means that it does not impinge on mouth volume, thereby enabling ingestion of large volumes through suction. High-velocity suction, as well as jaw opening and head thrust, are typical of aquatic turtles during feeding (Lemell et al., 2000; Lemell et al., 2002). The opposite arrangement is typical of terrestrial feeders. In these, the tongue is large and mobile, to aid food capture and swallowing, whereas the hyoid apparatus is small and suction is impossible. The morphological features of the leatherback mouth and pharynx – namely, a small tongue with poorly developed musculature, combined with a powerful hyoid apparatus – are those of a typical aquatic feeder, in which suction plays a key role (Lemell et al.,

2000; Lemell et al., 2002). However, in contrast to this minor role in feeding, the tongue plays a major, indeed essential, part in closure of the glottis (see below).

Laryngeal mechanisms

This study details the morphology of the larynx and related structures, and proposes mechanisms (Fig. 9) of glottal opening and closure. Key findings include: (1) close congruity between the smooth mucosal walls of the linguolaryngeal cleft and the soft, deformable, convex, anterior surface of the combined laryngeal folds, facilitating close apposition between them; (2) close apposition of the laryngeal folds, forming the dorsal part of the glottis; (3) the firm attachment of the glottal mucosa to the arytenoid cartilage, so that the former moves with the latter; and (4) the arrangement of the hyoid sling and the relation of the compressor laryngis muscle to the cricoid cartilage.

Opening

All of the muscular actions considered below were experimentally tested and verified on the dissections. The arytenoid cartilage, together with its associated subepithelial fibrous plate and the attached mucosa of the glottis, comprise key elements in glottal patency. Opening of the glottis is produced by contraction of the two abductor arytenoideae muscles (Schumacher, 1973) (Fig. 9A). These swing the arytenoid cartilages and the attached walls of the

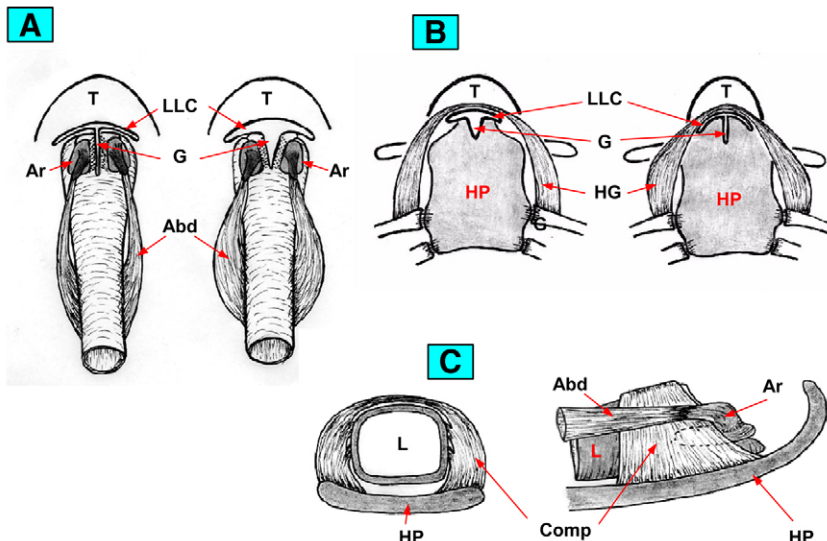


Fig. 9. (A,B) Proposed mechanisms for opening and closing the glottis of *D. coriacea* (see Discussion for details). (A) Left: closed glottis; right: opened glottis with contracted abductor arytenoideae muscles. (B) Left: open glottis; right: closed glottis with contracted hyoglossus muscles. (C) Morphology of the compressor laryngis muscle in transverse sectional and lateral views. Ar, arytenoid cartilage; Abd, abductor arytenoideae muscle; G, glottis; HG, Hyoglossus muscle; Comp, compressor laryngis muscle; HP, hyoid plate; L, larynx; LLC, linguolaryngeal cleft; T, tongue.

glottis laterally and posteriorly, around a fulcrum at the posterior end of the arytenoid. As a result of the lateral component of this movement, the profile of the glottis is transformed from a slit to a triangle, with its base anteriorly. The posterior component of the movement opens the linguolaryngeal cleft, because the laryngeal folds are drawn posteriorly. Opening may also be aided through the tongue being drawn anteriorly by the intrinsic muscles, connecting it to the processus lingualis of the hyoid.

Closure

Dermochelys coriacea, like all other turtles (Schumacher, 1973), lacks an epiglottis. Consequently, maintenance of closure is dependent on close apposition of the walls of the glottis and the linguolaryngeal cleft. Closure of the latter is produced by contraction of the hyoglossal sling. This draws the tongue posteriorly and also compresses the two surfaces of the linguolaryngeal cleft together (Fig. 9B). The function of an epiglottis – namely, closure of the laryngeal opening (aditus) – is thus fulfilled by the tongue instead of by an epiglottal cartilage. This would seem to be a distinctive, if not unique, adaptation of tongue function in *D. coriacea*.

Any tendency for the posterior movement of the larynx as a whole, owing to contraction of the hyoid sling, is prevented by the strong cricohyoid ligament. The efficiency of the sling is thereby enhanced. In addition, because the hyoglossal sling is concave, it tends to become more so on contraction (Fig. 9B). Also, because the two laryngeal folds lie within this concavity, they are compressed against one another, aiding closure of the intervening glottis. These effects combine to provide a seal between the gas in the respiratory tract and that in the oropharyngeal cavity and, thence, the exterior.

The morphology of the well-developed compressor laryngis muscle (Fig. 9C) clearly indicates a number of actions (tested on the dissections). First, because the major part of the muscle arches dorsally around the cricoid and the body of the arytenoid, its contraction draws the cricoid ventrally, stabilises it and compresses it against the hyoid plate. This obviates the tendency for the negative buccopharyngeal pressure generated during feeding (Lemell et al., 2000; Lemell et al., 2002) to elevate the larynx into the pharynx. It also maintains the larynx in close apposition to the hyoid during the neck flexion that occurs during feeding, when the rigidity of the trachea and larynx would tend to elevate the anterior end of the larynx into the pharynx. This is particularly important as the leatherback trachea consists of a continuous cartilaginous tube that is likely to resist bending (Davenport et al., 2009b), rather than the flexible sequence of tracheal rings interspersed with connective tissue that characterises other turtles. Second, the muscle may also deform the cricoid, flattening the laryngeal cavity dorsoventrally, thereby also aiding the free passage of food. Third, the anterior, oblique fibres pass over the body of the arytenoid on each side and draw each medially and forwards (Schumacher, 1973). The medial component of this movement compresses the attached fibro-epithelial plates together and aid closure of the glottis. The anterior component draws the arytenoids and thence the laryngeal folds anteriorly and compresses them against the tongue, maintaining closure of the linguolaryngeal cleft. Fourth, contraction of the anterior, oblique fibres draws the larynx anteriorly against the tongue, thereby reinforcing closure of the linguolaryngeal cleft. And fifth, the most anterior fibres arise close to the midline and pass lateral to the ventral, rounded part of the glottis. Accordingly, on contraction they may close the glottis.

Maintenance of a tight seal is aided by the smooth consistency of the mucosal tissues bounding the glottis and the linguolaryngeal

cleft. This enables intimate apposition between the apposed walls. In addition, the extensive amount of fat in the underlying tissues facilitates mutual adaptation of form.

This is the first description of a mechanism for laryngeal opening and closure in a suction-feeding chelonian species. The comprehensive sea turtle anatomical manual of Wyneken (Wyneken, 2001) confirms the close association of the hyoid and larynx in the hawksbill turtle *Eretmochelys imbricata*, but the larynx is situated much more posteriorly than in *D. coriacea* and does not appear to be closely associated with the (relatively much larger) tongue. More research is needed to determine whether the opening/closure mechanism of the leatherback larynx is unique amongst aquatic turtles.

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