Journal of Experimental Marine Biology and Ecology 450 (2014) 40–46

Contents lists available at ScienceDirect

Journal of Experimental Marine Biology and Ecology

journal homepage: www.elsevier.com/locate/jembe

Special issue: Charismatic marine mega-fauna

Unique characteristics of the trachea of the juvenile leatherback turtle facilitate feeding, diving and endothermy

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ARTICLE INFO

Available online 31 October 2013

Keywords:
Cross-sectional shape
Juveniles
Leatherback turtle
Luminal vascular plexus
Ontogenic changes
Tracheal structure

ABSTRACT

The adult leatherback turtle *Dermochelys coriacea* overlaps in body size (300–500 kg) with many marine mammals, yet develops from a 50 g hatchling. Adults can dive deeper than 1200 m and have core body temperatures of 25 °C; hatchlings are near-surface dwellers. Juvenile leatherbacks have rarely been studied; here we present anatomical information for the upper respiratory tract of 3 turtles (66.7–83.0 cm straight carapace length; 33.2–53.4 kg body mass) incidentally captured by long-line fisheries. Combined with existing information from adults and hatchlings, our data show that there is an ontogenic shift in tracheal structure, with cartilaginous rings becoming broader and eventually fusing anteriorly. This ontogenic shift during independent existence is unique among extant deep-diving air breathing vertebrates. Tract wall thickness is graded, becoming progressively thinner from larynx to bronchi. In addition, cross-sectional shape becomes increasingly dorsoventrally flattened (more elliptical) from anterior to posterior. These characteristics ensure that the tract will collapse from posterior to anterior during dives. This study contains the first report of a double (=internally bifurcated) posterior section of the trachea; it is suggested that this allows continuous food movement along the esophagus without tracheal collapse. The whole upper respiratory tract (from larynx to lungs) has a vascular lining (thicker anteriorly than posteriorly) that appears to be a simple analog of the complex turbinates of birds and mammals. Our study confirmed that the leatherback tracheal structure represents a distinctive way of dealing with the challenges of diving in deep, cold sea water.

1. Introduction

The leatherback sea turtle, *Dermochelys coriacea* (Vandelli 1761), the sole living species of the Family Dermochelyidae, is a very unusual turtle. Dermochelyidae diverged from other (non-marine) chelonians 100–150 million years ago (MYA; Wood et al., 1996) and represent a separate evolution of sea turtles from all other living species (which form the hard shelled Family Cheloniidae). Adult leatherbacks are large animals (typically 300–500 kg), overlapping in size with many marine pinniped and cetacean species. However, in contrast to marine mammals, they start their aquatic life as 40–50 g hatchlings, so undergo a 10,000-fold increase in body mass during independent existence, much of which is still enigmatic as post hatchlings and juveniles are rarely seen in the wild (c.f. Grant, 1994).

The leatherback is a strange chelonian anatomically, with a highly modified and reduced shell structure that, with the thick leathery skin, allows the animals to change shape considerably and escape some of the limitations of the turtle shell (Davenport et al., 2011). It is also highly unusual in terms of its feeding ecology, biogeography and physiology. *Dermochelys* feeds mainly on cnidarians and tunicates throughout its life (den Hartog and van Nierop, 1984; Davenport and Balazs, 1991; see Jones and Seminoff, 2003 for review). Its diet is therefore of poor quality for a carnivore (Doyle et al., 2007), especially as the leatherback is probably the fastest-growing living reptile species (Jones et al., 2011; Rhodin, 1985). It consequently has to eat great quantities of food (Jones et al., 2012). Although most observers have suggested that leatherbacks eat large prey items such as the jellyfish *Rhizostoma octopus* (Hays et al., 2003; Houghton et al., 2006), Fossette et al. (2012) have recently shown that they can also gain adequate quantities of food from dense patches of jellyfish individuals as small as 4 g. The prey densities of adult leatherbacks are geographically patchy and leatherbacks migrate over long distances (thousands of kilometers) between breeding areas in the tropics and feeding areas in cool temperate coastal waters (e.g. Hays et al., 2006).

Adult *Dermochelys* are well known to have core body temperatures elevated substantially above ambient (to around 25 °C) when in cool water (e.g. off Nova Scotia) by virtue of their large size ('gigantothermy'), exercise, thick subcutaneous blubber (unique in living reptiles), plus vascular countercurrent heat exchangers in the flippers (Bostrom and

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http://dx.doi.org/10.1016/j.jembe.2013.10.013

Jones, 2007; Davenport et al., 1990; Frair et al., 1972; Greer et al., 1973; James and Mrosovsky, 2004; Paladino et al., 1990). They even have extensive intracranial insulation to keep brain and salt glands warm (Davenport et al., 2009a). A recently published review (Wallace and Jones, 2008) considers the gigantothermic/endothermic status of the species in the context of metabolic rate, concluding that they are true endotherms (though see Bradshaw et al., 2007). There is good paleoecological evidence that the link between the distribution of Dermochelyidae into cool waters (and hence of gigantothermy/endothermy) is of great antiquity (>40 MYA; Albright et al., 2003). Bostrom et al. (2010) have recently shown that even relatively small juvenile leatherback turtles (16–37 kg) can sustain significant temperature gradients between the body and the external environment.

Adult leatherbacks are also accomplished divers and can be regarded as the living deep-diving vertebrate with the longest evolutionary history. They forage regularly to depths of several hundred meters, making tens of thousands of dives annually (Houghton et al., 2008). Dives beyond 1000 m were first inferred (Eckert et al., 1986, 1989) and subsequently confirmed (to levels deeper than 1200 m) by satellite tags (Houghton et al., 2008), though such deep dives are rare.

In terms of the respiratory system, all air-breathing vertebrate lineages have been constrained by the nature of structures evolved primarily for a terrestrial existence. These consist of lungs of varying degrees of complexity, plus the upper respiratory system: the larynx and the trachea, together with bronchi that connect the trachea to the lungs (in some groups via a branching bronchial tree). Lungs have little resistance to compression, while the tracheae and bronchi of terrestrial reptiles, birds and mammals have a series of complete-to-incomplete circular, semi-rigid cartilaginous rings interspersed with elastic connective tissue designed to maintain a patent airway and provide flexibility in the neck region.

Diving air-breathing vertebrates encounter a number of problems that are exacerbated by increasing depth and duration of dives (Kooyman, 1989). First, they require adequate blood and tissue oxygen supplies for each dive. Second, the air spaces of the respiratory system become compressed and this decreases buoyancy which affects descent and ascent phases of dives. Third, the possibility of highly compressed air being in close proximity to moving blood has the potential for causing N_2 accumulation and decompression sickness (DCS). Scholander (1940) developed a simple ‘balloon and pipe’ model that addressed the DCS problem. He envisaged that the rib cage and lungs of a diving mammal would be compressed and the latter finally collapse, at relatively shallow depths (30–50 m), displacing air into the rigid (and poorly vascularized) tubes of the upper respiratory system, where little gaseous exchange would be possible and the threat of DCS eliminated. In support of this concept, it was observed that the tracheae of diving mammals tended to have much wider tracheal rings, with far less connective tissue between them than terrestrial mammals, and that the rings were composed of more rigid materials, sometimes calcified. Marine mammals also had cartilage support much further down the bronchiolar tree than terrestrial mammals. Such bronchiolar trees are absent in marine reptiles.

Subsequently this model has become extensively modified as understanding of the complexity of diving physiology and biochemistry has improved. Evidence indicates that lung collapse and gaseous exchange can be delayed to depths of well over 100 m in some seals (Kooyman and Sinnett, 1982; Moore et al., 2011b). A recent comprehensive review (Hooker et al., 2012) argues that diving mammals “manage DCS” rather than eliminate it. Whereas several shallow divers (e.g. marine otters and extinct mosasaurs) feature calcified tracheal rings that help to provide the rigid pipes envisaged by Scholander (1940), this appears not to be the case in deep divers such as Weddell seals and northern elephant seals (both of which exceed 1000 m depth on many dives). They show reduced tracheal volume when compressed in hyperbaric chambers (Kooyman et al., 1970), and it is now clear that this is caused by ‘slipping’ of overlapping cartilaginous rings (Moore et al., 2011a). Bostrom et al. (2008) demonstrated that a compliant trachea causes increased depth of alveolar collapse and a gradual rather than abrupt collapse.

Davenport et al. (2009b) and Murphy et al. (2012) showed that adult *Dermochelys* (but not hatchlings) have a specialized tracheal structure that facilitates collapse of the respiratory tract during dives. As in other reptiles, the larynx and the tracheal structure begins at the anterior of the floor of the mouth. The adult larynx has a somewhat rectangular cross section and is thick-walled. At the rear of the hyoid plate (Fraher et al., 2010) it joins the trachea, which is a continuous long tube, consisting of fused, irregularly shaped, tracheal rings, with minimal amounts of connective tissue between them (Davenport et al., 2009b). The cross section of the trachea is near-elliptical in shape, but thinner-walled dorsally than ventrally. The material of this nearly-elliptical tube is predominantly uninterrupted, uncalcified cartilage. Davenport et al. (2009b) reported that the trachea could easily be compressed between the fingers, suggesting that it should collapse progressively given small pressure differences between lumen and exterior; this was confirmed by the biomechanical study of Murphy et al. (2012) who showed that the trachea had elastic properties ideally suited to repeated collapse and dilation. However, Murphy et al. (2012) also demonstrated mathematically that collapse of the upper respiratory tract would not be initiated until the lungs themselves had collapsed; they recognized that air moving from the collapsing lungs into the trachea and larynx would keep the latter two structures inflated until depths of several hundred meters had been attained.

Davenport et al. (2009b) also showed that the adult leatherback trachea was lined with an extensive, dense vascular plexus that should warm and humidify cold inspired air and possibly retain heat on expiration. They suggested that this structure was functionally equivalent to the nasal turbinates of birds and mammals and similarly diagnostic of endothermy.

All of the investigations of leatherback tracheal structure described above had the following short comings. First, all of the adult studies were conducted on sections of the upper respiratory tract between buccal cavity and the base of the turtle neck; no data were available from the more posterior parts of the trachea and bronchi between neck and lungs. Second, although some details of the structure in hatchling leatherbacks were given by Davenport et al. (2009a), who showed that their trachea was circular in cross section and dominated by connective tissue rather than cartilaginous rings (which were narrow), no information about juvenile leatherback turtles has ever been published. Here we present data derived from three juvenile turtles (70.9–87.3 cm curved carapace length; 33.2–53.4 kg mass) that shed light on ontogenic changes in respiratory tract structure and also yield novel information about likely functionality. Turtles of this size have rarely been encountered, have unknown diving capabilities, but are now known to be capable of several degrees of endothermy (Bostrom et al., 2010).

2. Methods

The three study specimens of juvenile leatherbacks (see Table 1 for their basic dimensions and body masses) were collected as bycatch by observers (NOAA Fisheries Service, Pacific Islands Regional Office, Observer Program) on longline fishing vessels operating in the equatorial Pacific. All were immediately frozen after death and so were in good post-mortem condition. Turtles were thawed 24 h before necropsy, which entailed a complete external and internal examination with procurement of tissues for routine histopathology in attempts to confirm cause of death (drowning) (c.f. Work and Balazs, 2002, 2010). Note that previous work has indicated that drowning damages the lungs (Work and Balazs, 2010); there is no evidence that drowning damages the larynx or trachea. Histological study of the tracheal lining of a drowned adult leatherback (Davenport et al., 2009b) exhibited no obvious damage. The upper respiratory tracts (from larynx to anterior of bronchi) were harvested and refrozen before further investigation. After thawing,