Fat head: an analysis of head and neck insulation in the leatherback turtle (*Dermochelys coriacea*)

John Davenport[1,2,*], John Fraher[3], Edward Fitzgerald[4], Patrick McLaughlin[4], Tom Doyle[1,2], Luke Harman[1] and Tracy Cuffe[3]

[1]Department of Zoology, Ecology and Plant Science and Environmental Research Institute, University College Cork, Distillery Fields, North Mall, Cork, Ireland, [2]Coastal and Marine Resources Centre, University College Cork, Naval Base, Haulbowline, Cork, Ireland, [3]Department of Anatomy, University College Cork, College Road, Cork, Ireland and [4]Radiology Department, Mercy Hospital, Cork, Ireland

*Author for correspondence (j.davenport@ucc.ie)

SUMMARY

Adult leatherback turtles are gigantothermic/endothermic when foraging in cool temperate waters, maintaining a core body temperature within the main body cavity of *ca.* 25°C despite encountering surface temperatures of *ca.* 15°C and temperatures as low as 0.4°C during dives. Leatherbacks also eat very large quantities of cold, gelatinous prey (medusae and pyrosomas). We hypothesised that the head and neck of the leatherback would have structural features to minimise cephalic heat loss and limit cooling of the head and neck during food ingestion. By gross dissection and analytical computed tomography (validated by ground truthing dissection) of an embalmed specimen we confirmed this prediction. 21% of the head and neck was occupied by adipose tissue. This occurred as intracranial blubber, encapsulating the salt glands, medial portions of the eyeballs, plus the neurocranium and brain. The dorsal and lateral surfaces of the neck featured thick blubber pads whereas the carotid arteries and jugular veins were deeply buried in the neck and protected laterally by blubber. The oesophagus was surrounded by a thick sheath of adipose tissue whereas the oropharyngeal cavity had an adipose layer between it and the bony proportion of the palate, providing further ventral insulation for salt glands and neurocranium.

Key words: leatherback turtle, cranial insulation, blubber, gigantothermy.

INTRODUCTION

Adult leatherback sea turtles, *Dermochelys coriacea* (Vandelli 1761), are large animals [typically 300–500 kg but <916 kg (Eckert and Luginbuhl, 1988)], overlapping in size with many marine pinniped and cetacean species. *Dermochelys coriacea* is an obligate feeder on gelatinous organisms, predominantly medusae, pyrosomas and siphonophores throughout its life (den Hartog et al., 1984; Davenport and Balazs, 1991). Its diet is therefore of poor quality for a carnivore (for details, see Doyle et al., 2007), especially as the leatherback is probably the fastest-growing reptile (Rhodin, 1985; Snover and Rhodin, 2008). This means that it has to eat exceptionally 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).

The prey densities of adult leatherbacks are geographically very patchy and leatherbacks migrate over long distances (thousands of kilometres) between breeding areas in the tropics and feeding areas in cool temperate coastal waters (e.g. Hays et al., 2004; Hays et al., 2006; Ferraroli et al., 2004; James et al., 2005). Adult *Dermochelys* are well-known to have core body temperatures elevated substantially over ambient sea surface temperatures (to around 25°C) when in cool water (e.g. off Newfoundland) by virtue of: large size ('gigantothermy'), exercise, thick subcutaneous blubber (unique in living reptiles), plus vascular countercurrent heat exchangers in the flippers (Frair et al., 1972; Greer at al., 1973; Davenport et al., 1990; Paladino et al., 1990; James and Mrosovsky, 2004; Bostrom and Jones, 2007). Wallace and Jones have recently published a review that considers the gigantothermic/endothermic status of the species

in the context of metabolic rate (Wallace and Jones, 2008). There is good palaeoecological evidence that the link between distribution of Dermochelyidae into cool waters (and hence of gigantothermy) is of great antiquity [>40 million years (Albright et al., 2003)].

Adult leatherbacks are also accomplished divers. Dives beyond 1000 m were first inferred by Eckert et al. (Eckert et al., 1986; Eckert et al., 1989) and 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., 2008), respectively. Diving to such abyssal depths exposes leatherbacks to environmental temperatures of about 5°C regardless of latitude (Sverdrup et al., 1946; Houghton et al., 2008). Although 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, leatherbacks can still encounter low temperatures even during shallow dives. James et al. reported repeated 50–100 m dives into water of 0.4–2.5°C for a female foraging in the Gulf of St Lawrence (from surface waters of around 15–19°C) (James et al., 2006).

There is good understanding of how the heart, lungs and viscera are kept warm in *Dermochelys* exposed to low temperatures. Plentiful blubber lining the thick leathery skin, plus heat exchangers allowing the limbs to operate at lower temperature than the core, are responsible. However, no published data are available concerning the means by which the cephalic structures are kept warm. The turtle head contains the brain and eyes; it also contains extremely large lachrymal salt glands (Hudson and Lutz, 1986; Wyneken, 2001) that produce highly concentrated salt secretions almost continuously (Reina et al., 2002), as well as the jaw muscles that permit food

A

- Vertebral column
- Position of great vessels
- Blubber
- Oesophagus
- Trachea

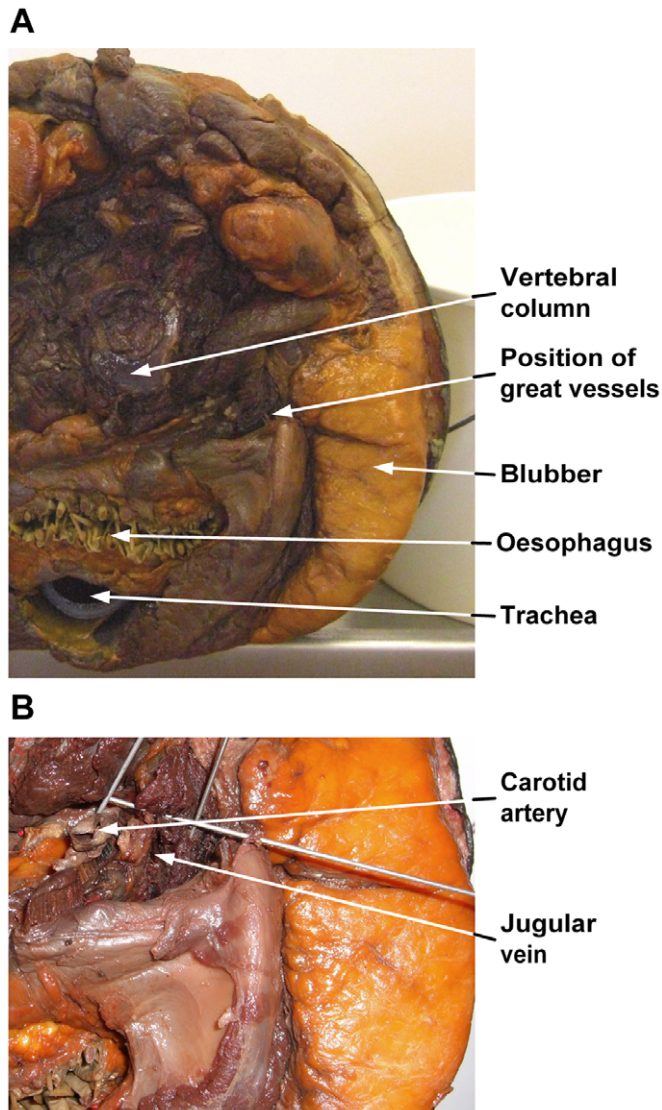**B**

- Carotid artery
- Jugular vein

Fig. 1. (A) Photograph of cut surface of neck of Specimen 1. (B) Close-up of great vessels, showing that the carotid artery is medial to the jugular vein; both are medial to a thick lateral pad of blubber.

capture and handling (Bels et al., 1998). All of these structures are likely to function suboptimally if their temperature drops significantly during exposure to low environmental temperature. The head is also the route of passage of large quantities of cold gelatinous food to the stomach (Davenport, 1998; Bostrom and Jones, 2007).

We predicted that the structure of the leatherback head and neck would have characteristics that would minimise general cephalic heat loss as well as limiting cooling of the head and neck by the passage of food through the oesophagus. In the present study, we report anatomical information gained by dissection and analytical computed tomography (CT) that confirms this hypothesis.

MATERIALS AND METHODS
Study specimens

Material was collected from two freshly stranded adult leatherback turtles. 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, so would probably have weighed around 450 kg (cf. Georges and Fossette, 2006). The head and neck were removed (amputated as close as possible to the body) and transferred to a freezer; 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 large straight artery tube (length 120 mm, diameter 6 mm) was inserted into each artery and clamped into place. A 2% aqueous solution of 38% formaldehyde was pumped into each artery using a Duotronic embalming pump (Modesto, CA, USA), and 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 carotids were then clamped and the head/neck 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 trauma) on 21 February 2008 and autopsied. Its standard curved carapace length was 154 cm, suggesting a live mass of about 350 kg (cf. Georges and Fossette, 2006).

Gross anatomy

Gross dissection was conducted on the head and neck of Specimen 1, partly to 'ground truth' CT analysis. Images of dissections were captured with a Casio 10.1 megapixel digital camera (Shibuyaku, Tokyo, Japan). The autopsy of Specimen 2 was outside our control but the brain [which was in good condition, unusual in stranded leatherbacks (Wyneken, 2001)] was removed and photographed.

CT scanning

The head and neck of Specimen 1 were CT-scanned (1 mm slice acquisition with a bony reconstruction algorithm) using a Siemens Somatom Plus 4 scanner (Erlangen, Germany). Analysis of adipose tissues and false colour image production was conducted using OsiriX v. 3.21 Software (Rosset et al., 2004) on a Macbook Pro workstation (Cupertino, CA, USA). OsiriX is an open source DICOM image analysis software package (Osirix Foundation, Geneva, Switzerland). Such CT analysis is routinely used clinically in the study of conditions such as congenital lipodystrophy (e.g. Shinya et al., 2007).

RESULTS
Initial dissection

The cut surface of the neck of Specimen 1 (Fig. 1A and Fig. 1B) shows that the great vessels run very deep in the neck, protected from the external environment by thick lateral pads of fat. The jugular veins (presumably carrying cooler blood than the arterial supply to the head) are lateral to the carotids. The photograph also shows that the oesophagus is empty and has collapsed. In life, the oesophagus will regularly be dilated during feeding, as the species consumes large medusae and pyrosomas.

Fig. 2 shows a size/shape comparison of the brain of leatherback Specimen 2 and the brain of a cat. The cat had a brain volume of about 35 ml, and the leatherback a brain volume of about 30 ml. While the cat brain is ovoid, the turtle brain is essentially cylindrical (diameter ~1 cm), although with swollen cerebral hemispheres (3 cm max. diameter) and cerebellum (2 cm max. diameter). Assuming a density close to $1 \, g \, ml^{-1}$, the brain of the turtle had a
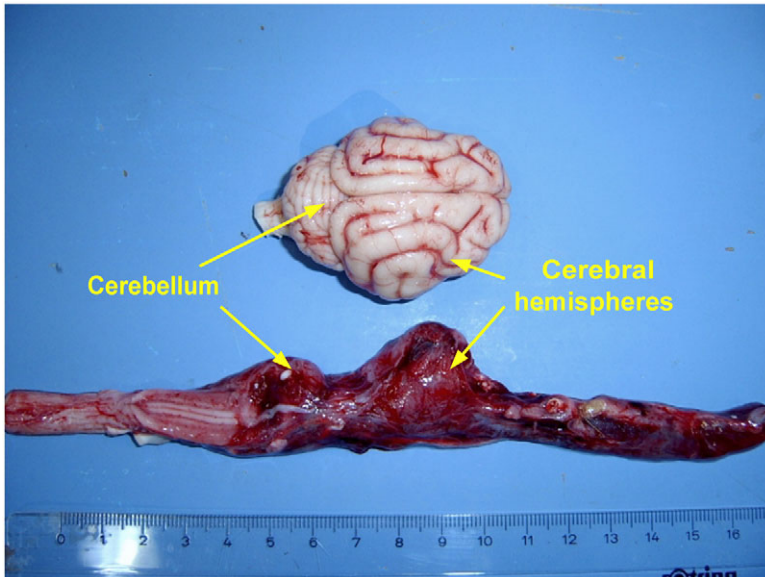
Fig. 2. Comparison of sizes of brains of: (top) cat (*Felis catus*), ~3.9 kg body mass; (bottom) leatherback turtle (Specimen 2), ~350 kg body mass.

mass approximating to 0.009% body mass, the brain of the cat 0.9%. Taken with the CT-scan data described below, it is evident that the small, tubular brain, situated deep within the neurocranium of the skull, is surrounded by a considerable thickness of varied tissues.

CT scan images and data

Fig. 3 displays a transverse CT section of the neck of Specimen 1, together with the same image as shown in Fig. 1A but re-sized and rotated to coincide as far as possible as possible with the CT section (the CT section is about 5 cm anterior to the cut edge of the neck). It may be seen that there is a good match between the yellow adipose tissue of the actual specimen and the red false colour of adipose tissue identified by the CT software.

Fig. 4 shows a sequence of 13 regularly spaced transverse CT sections from neck (image 1) to snout (image 13). Fig. 5 shows enlargements of images 6, 9 and 12, with some structures identified. Inspection of these sections yielded the following findings: (1)

posterior to the skull, fat forms a prominent dorsal, posterior pad superficial to a dorsal muscle mass, the neck extensors. This adipose tissue extends anteriorly into the skull, deep to the dermal bones. (2) Posteriorly, fat is arranged as a prominent, thick sheath around the oesophagus (images 1–4). (3) Fat forms thick lateral pads, immediately under the skin surface of the neck (images 1–4). (4) The anterior continuation of the dorsal, posterior fat pad encapsulates the salt glands within the confines of the skull (images 7–11), isolating them almost completely from the surrounding bones, including the palate, and from the external surface of the head. The salt glands have therefore a virtually complete peripheral covering of fat within the surrounding bone. Further fat insulation is provided ventrally by a second layer ventral to the bony palate (best seen in image 9). (5) The vertebral canal and neurocranium are variously surrounded by bone, fat, muscle and salt gland tissue (images 2–11). Anteriorly, the dorsal part of the neurocranium is only overlaid by bone (images 9–11) but the bone is thick. (6) A thick layer of fat
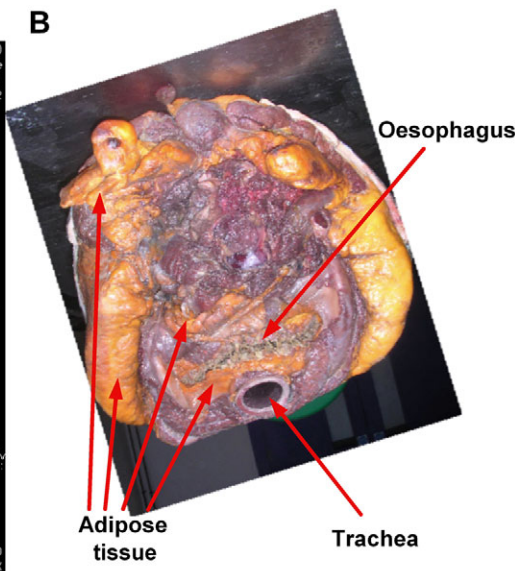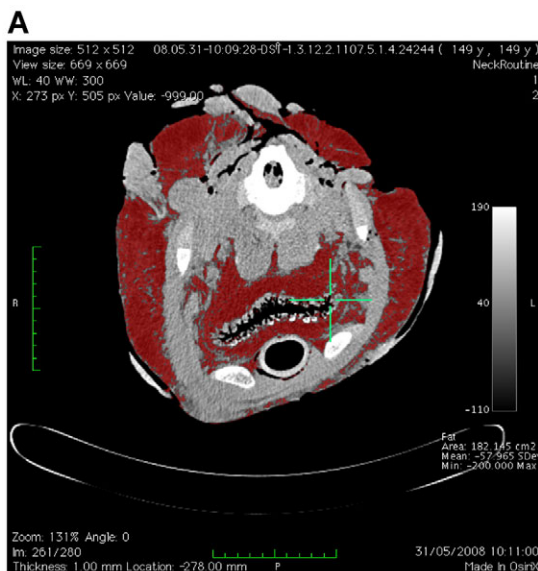

Fig. 3. Comparison of (A) transverse computed tomography (CT) scan of neck of Specimen 1 with (B) photograph of cut surface of neck at similar, but not identical, anteroposterior levels. Red false colour indicates adipose tissue.
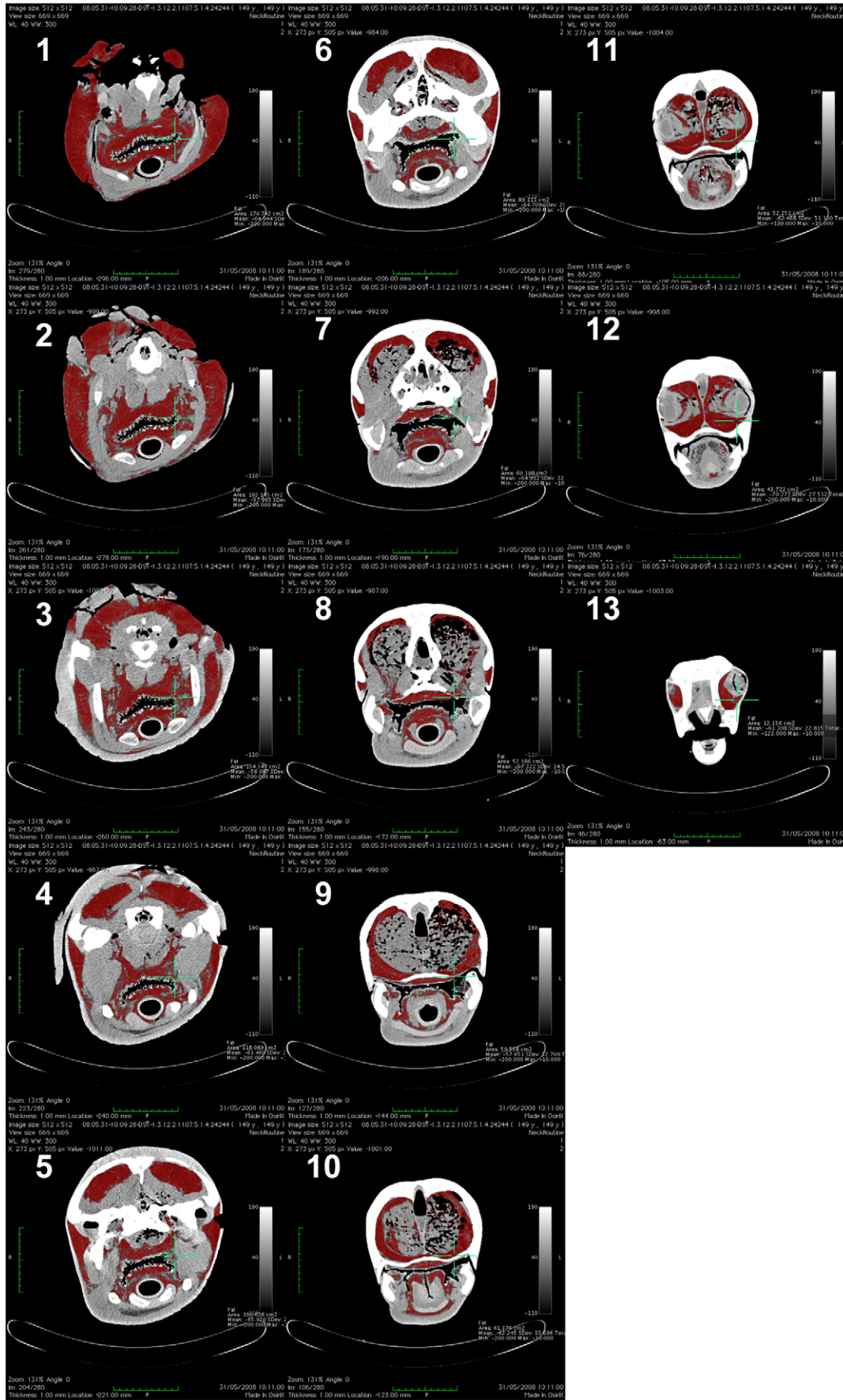
Fig. 4. Sequence of 13 computed tomography (CT) transverse sectional images of head and neck of Specimen 1. From neck (image 1) to snout (image 13). Red false colour indicates adipose tissue.
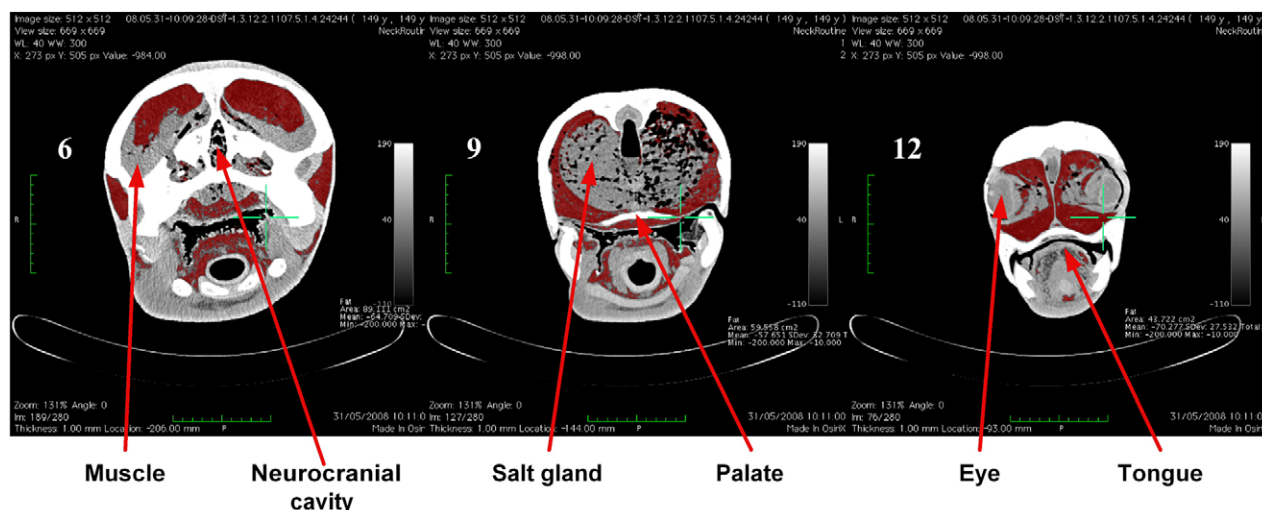
Fig. 5. Selected images from Fig. 4 (images 6, 9 and 12) with labels indicating important structures.

is related to the eyeball medially, dorsally and ventrally (images 11–13). This is continuous with the sheath around the salt glands. Fat covers only just over one half of the eyeball. It underlies the part of the eyeball to which the retina is related. Thus, nearly half of the eye surface is unprotected by fat, and of course the retina is distal to it and therefore not protected either. (7) Fat is absent from
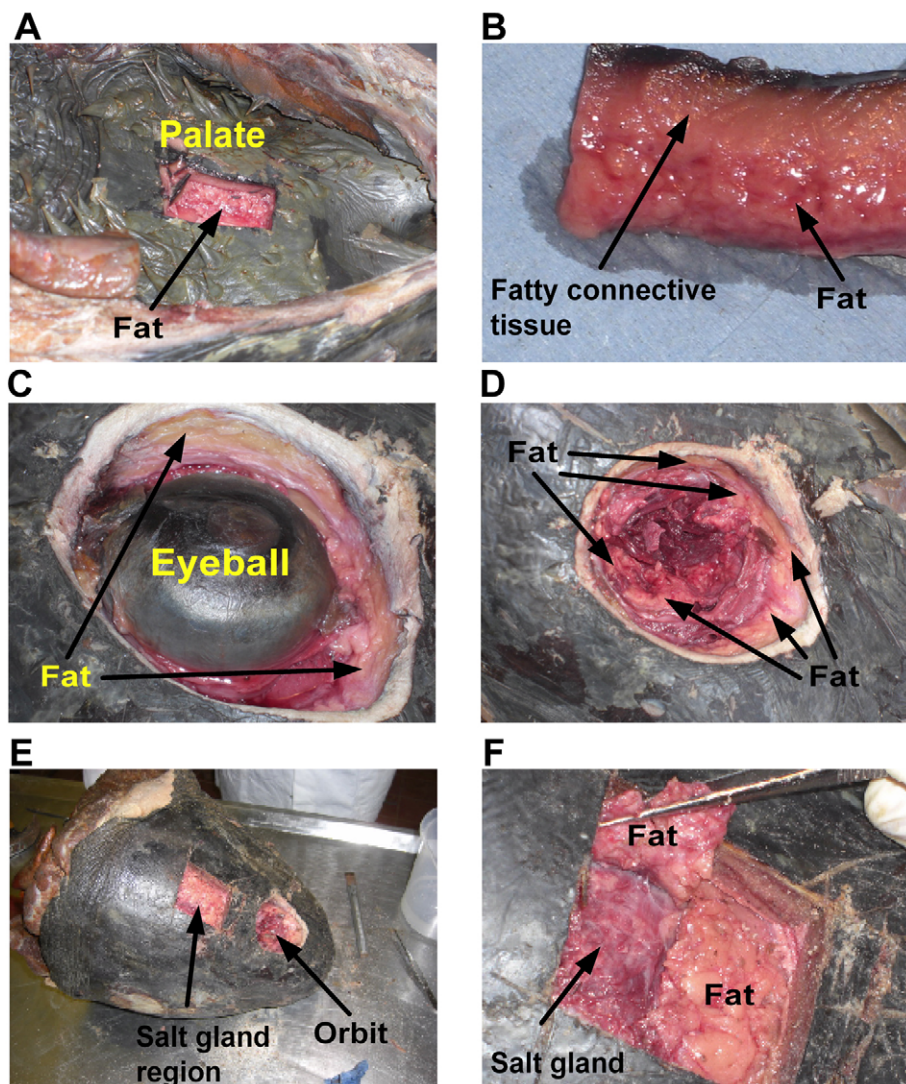

Fig. 6. Photographs of ground truthing dissections. (A) Photograph of palate, showing removal of epidermis over a rectangular section, revealing underlying fat. (B) Slice through epidermis, underlying fatty connective tissue and fat. (C) Left orbit of leatherback, showing fat tissue around eyeball. (D) Enucleated orbit with most of muscle cone removed. Extensive fat deposits indicated. (E) Dorsolateral view of left side of leatherback turtle skull, showing enucleated orbit and trephined cranium in region of left salt gland. (F) Image of trephined area, showing fat and underlying salt gland.

the tongue anterior to the glottis. (8) In the respiratory tract, the trachea is covered dorsally and laterally, but not ventrally, by a thin layer of fat (images 4–8). Heat loss due to the absence of fat ventrally may be compensated for by the highly vascularised ventral mucosal surface. By contrast, the larynx is completely surrounded by a thin layer of fat. This is thickest around the glottis. (9) The jaw muscles are somewhat less completely insulated than the other elements. In many areas a fatty covering is absent and bone is the principal material superficial to them and contributing to the layers separating them from the exterior (images 6–8). (10) Calculations (employing standard CT software) showed that the total volume of the head and neck of Specimen 1 was 9685 ml. Of that volume, 2041 ml (21%) was adipose tissue.

Ground truthing dissections

Fig. 6 shows the results of three ground truth dissections. Fig. 6A and Fig. 6B demonstrate that there is a layer of fat and fatty connective tissue between the bony palate and the palatine epidermis. Fig. 6C and Fig. 6D show that the orbit is lined with fat; further probing showed that this fatty tissue continued all the way to the midline of the skull and into the snout region. Fig. 6E and Fig. 6F demonstrate that there was a thick fat layer between the cranium and salt gland. Overall, these dissections (carried out subsequent to the CT-scan analysis) showed that the match between actual and predicted fat occurrence was accurate.

DISCUSSION

Dermochelys is unique among living reptiles in possessing blubber (i.e. peripherally distributed fibro–adipose tissue); in this respect it shows convergent evolution with marine mammals and penguins. The blubber differs in fatty acid composition from seal/cetacean blubber and has a higher melting point (Davenport et al., 1990; Holland et al., 1990). Our study has revealed that intracranial blubber is also present, protecting the neurocranium and the enormous salt glands [which are richly vascularised, secrete extremely salty tears (<1800 mOsm kg^{-1}) and are continuously active because of the salt loads taken on during feeding (Reina et al., 2002)]. Although no cranial temperatures are available, the combination of deeply situated great vessels and substantial quantities of encapsulating adipose tissue make it likely that there is little reduction of temperature below core levels in the brain and salt glands. The fatty covering is less complete over the jaw muscles than elsewhere. While this might predispose to heat loss though the overlying skull bone and skin, the muscles are almost continuously active during feeding and are also active during dives; Myers and Hays recorded rhythmic mouth openings, mainly during descents (Myers and Hays, 2006). Muscular thermogenesis would presumably compensate for any loss by conduction through the overlying tissues.

The situation is more complicated in the case of the eyes. Medially they are encapsulated by adipose tissue but the cornea is exposed directly to the sea and the aqueous humour is likely to have much the same thermal conductivity as water. The eyes will undoubtedly be sites of heat loss, as they are in marine mammals. The retina is unprotected by the adipose capsule, and avascular, but has a well vascularised choroid applied to it (Brudenall et al., 2008), so will easily be kept warm as the volume of retinal tissue is small.

The oesophagus is surrounded by a thick sheath of fat. Unlike the majority of carnivores, the feeding of *Dermochelys* is more akin to that of browsing herbivores; leatherback turtles even have the ability to capture new prey items whilst handling and swallowing earlier prey (Bels et al., 1998). Although leatherbacks can avoid taking in much seawater with their prey by contracting the oesophagus and expelling water through the mouth and nostrils (Reina et al., 2002), they ingest large quantities of food [perhaps 200 kg per day in a 400 kg turtle (Davenport, 1998)] that is initially at ambient temperature. This food has to be warmed to core temperature whilst passing along the long oesophagus, and this is a significant cost of ingestion (Davenport, 1998; Bostrom and Jones, 2007). However, it is evident from our observations that the cold food is isolated from the respiratory tract, the great vessels, the neurocranium and its contents, as well as the salt glands, by insulating layers of fat.

While leatherback turtles remain active in relatively cold water, other species of marine turtle (e.g. green turtles *Chelonia mydas* and loggerhead turtles *Caretta caretta*) either suffer hypothermia and die or become quiescent for long periods on the seabed (e.g. Hochscheid et al., 2005). We would therefore predict that cranial fat deposits will be far less extensive in these other species.

REFERENCES

Albright, L. B., 3rd, Woodburne, M. O., Case, J. A. and Chaney, D. S. (2003). A leatherback sea turtle from the Eocene of Antarctica: implications for antiquity of gigantothermy in Dermochelyidae. *J. Vertebr. Paleontol.* **23**, 945-949.

Bels, V. L., Davenport, J. and Renous, S. (1998). Food ingestion in the estuarine turtle *Malaclemys terrapin*: comparison with the marine leatherback turtle *Dermochelys coriacea*. *J. Mar. Biol. Assoc. UK* **78**, 953-972.

Bostrom, B. L. and Jones, D. R. (2007). Exercise warms adult leatherback turtles. *Comp. Biochem. Physiol. A Mol. Integr. Physiol.* **147**, 323-331.

Brudenall, D. K., Schwab, I. R. and Fritsches, K. A. (2008). Ocular morphology of the leatherback sea turtle (*Dermochelys coriacea*). *Vet. Ophthalmol.* **11**, 99-110.

Davenport, J. (1998). Sustaining endothermy on a diet of cold jelly: energetics of the leatherback turtle *Dermochelys coriacea*. *Br. Herpetol. Soc. Bull.* **62**, 4-8.

Davenport, J. and Balazs, G. H. (1991). 'Fiery bodies': are pyrosomas important items in the diet of leatherback turtles? *Br. Herpetol. Soc. Bull.* **37**, 33-38.

Davenport, J., Holland, D. L. and East, J. (1990). Thermal and biochemical characteristics of the fat of the leatherback turtle *Dermochelys coriacea* (L.): evidence of endothermy. *J. Mar. Biol. Assoc. UK* **70**, 33-41.

den Hartog, J. C. and van Nierop, M. M. (1984). A study on the gut contents of six leathery turtles, *Dermochelys coriacea* (Linnaeus) (Reptilia: Testudines: Dermochelydae) from British waters and from the Netherlands. *Zool. Verh.* **200**, 1-36.

Doyle, T. K., Houghton, J. D. R., McDevitt, R., Davenport, J. and Hays, G. C. (2007). The energy density of jellyfish: estimates from bomb-calorimetry and proximate-composition. *J. Exp. Mar. Biol. Ecol.* **34**, 239-252.

Doyle, T. K., Houghton, J. D. R., O'Súilleabháin, P. F., Hobson, V. J., Marnell, F., Davenport, J. and Hays, G. C. (2008). Leatherback turtles satellite tagged in European waters. *Endanger. Species Res.* **4**, 23-31.

Duron, M. (1978). Contribution à l'étude de la biologie de *Dermochelys coriacea* (Linné) dans les Pertuis Charentais. Thesis, University of Bordeaux, Talence, France.

Eckert, K. L. and Luginbuhl, C. (1988). Death of a giant. *Mar. Turtle Newsl.* **43**, 1-3.

Eckert, S. A., Nellis, D. W., Eckert, K. L. and Kooyman, G. L. (1986). Diving patterns of two leatherback sea turtles (*Dermochelys coriacea*) during inter-nesting intervals at Sandy Point, St. Croix, US Virgin Islands. *Herpetologica* **42**, 381-388.

Eckert, S. A., Eckert, K. L., Ponganis, P. and Kooyman, G. L. (1989). Diving and foraging behaviour of leatherback sea turtles (*Dermochelys coriacea*). *Can. J. Zool.* **67**, 2834-2840.

Ferraroli, S., Georges, J. Y., Gaspar, P. and Le Maho, Y. (2004). Endangered species: where leatherback turtles meet fisheries. *Nature* **429**, 521-522.

Frair, W., Ackman, R. G. and Mrosovsky, N. (1972). Body temperature of *Dermochelys coriacea*: warm turtle from cold water. *Science* **177**, 791-793.

Georges, J. Y. and Fossette, S. (2006). Estimating body mass in leatherback turtles *Dermochelys coriacea*. *Mar. Ecol. Prog. Ser.* **318**, 255-262.

Greer, A. E., Lazell, J. D., Jr, and Wright, R. M. (1973). Anatomical evidence for a counter-current heat exchanger in the leatherback turtle (*Dermochelys coriacea*). *Nature* **214**, 181.

Hays, G. C., Houghton, J. D. R. and Myers, A. E. (2004). Pan-Atlantic leatherback turtle movements. *Nature* **429**, 522.

Hays, G. C., Hobson, V. J., Metcalfe, J. D., Righton, D. and Sims, D. W. (2006). Flexible foraging movements of leatherback turtles across the North Atlantic Ocean. *Ecology* **87**, 2647-2656.

Hochscheid, S., Bentivegna, F. and Hays, G. C. (2005). First records of dive durations for a hibernating sea turtle. *Biol. Lett.* **1**, 83-87.

Holland, D. L., Davenport, J. and East, J. (1990). The fatty acid composition of the leatherback turtle, *Dermochelys coriacea* L. and its jellyfish prey. *J. Mar. Biol. Assoc. UK* **70**, 761-770.

Houghton, J. D. R., Doyle, T. K., Davenport, J., Wilson, R. P. and Hays, G. C. (2008). The role of infrequent and extraordinary deep dives in leatherback turtles (*Dermochelys coriacea*). *J. Exp. Biol.* **211**, 2566-2575.

Hudson, D. M. and Lutz, P. L. (1986). Salt gland function in the leatherback sea turtle, *Dermochelys coriacea. Copeia* **1986**, 247-249.

James, M. C. and Mrosovsky, N. (2004). Body temperatures of leatherback turtles (*Dermochelys coriacea*) in temperate waters off Nova Scotia, Canada, *Can. J. Zool.* **82**, 1302-1306.

James, M. C., Ottensmeyer, C. A. and Myers, R. A. (2005). Identification of high-use habitat and threats to leatherback sea turtles in northern waters: new directions for conservation. *Ecol. Lett.* **8**, 195-201.

James, M. C., Davenport, J. and Hays, G. C. (2006). Expanded thermal niche for a diving vertebrate: a leatherback turtle diving into near-freezing water. *J. Exp. Mar. Biol. Ecol.* **335**, 221-226.

López-Mendilaharsu, M., Rocha, C. F. D., Domingo, A., Wallace, B. P. and Miller, P. (2008). Prolonged, deep dives by the leatherback turtle *Dermochelys coriacea*: pushing their aerobic dive limits. *J. Mar. Biol. Assoc. UK Biodiversity Records* 1-3.

Lutcavage, M. and Lutz, P. L. (1986). Metabolic rate and food energy requirements of the leatherback sea turtle, *Dermochelys coriacea. Copeia*, 796-798.

Myers, A. E. and Hays, G. C. (2006). Do leatherback turtles *Dermochelys coriacea* forage during the breeding season? A combination of data-logging devices provide new insights. *Mar. Ecol. Prog. Ser.* **322**, 259-267.

Paladino, F. V., O'Connor, M. P. and Spotila, J. R. (1990). Metabolism of leatherback turtles, gigantothermy, and thermoregulation of dinosaurs. *Nature* **344**, 858-860.

Reina, R. D., Jones, T. T. and Spotila, J. R. (2002). Salt and water regulation by the leatherback sea turtle *Dermochelys coriacea. J. Exp. Biol.* **205**, 1853-1860.

Rhodin, R. G. J. (1985). Comparative chondro-osseous development and growth of marine turtles. *Copeia*, 752-771.

Rosset, A., Spadola, L. and Ratib, O. (2004). OsiriX: an open-source software for navigating in multidimensional DICOM images. *J. Digit Imaging* **17**, 205-216.

Shinya, T., Sato, S., Akaki, S., Ogata, T., Kato, K., Tone, A. and Kanazawa, S. (2007). Computed tomography findings of congenital generalized lipodystrophy: multiple nodular fatty liver and diffuse sclerosis of bones. *Radiat. Med.* **25**, 484-487.

Snover, M. L. and Rhodin, R. G. J. (2008). Comparative ontogenetic and phylogenetic aspects of chelonian chondro-osseous growth and skeletochronology. In *Biology of Turtles: From Structure to Strategy of Life* (ed. J. Wyneken, M. Godfrey and V. Bels), pp. 17-43. Boca Raton, FL: CRC Press.

Sverdrup, H. U., Johnson, M. W. and Fleming, R. H. (1946). *The Oceans: Their Physics, Chemistry and General Biology*, 1087pp. New York: Prentice-Hall,.

Wallace, B. P. and Jones, T. T. (2008). What makes marine turtles go: a review of metabolic rates and their consequences. *J. Exp. Mar. Biol. Ecol.* **356**, 8-24.

Wyneken, J. (2001). *The Anatomy of Sea Turtles.* NOAA Technical Memorandum NMFS-SEFSC-470. http://courses.science.fau.edu/~jwyneken/sta/