



Research

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Physiology

Topsy-turvy: turning the counter-current heat exchange of leatherback turtles upside down

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Counter-current heat exchangers associated with appendages of endotherms feature bundles of closely applied arteriovenous vessels. The accepted paradigm is that heat from warm arterial blood travelling into the appendage crosses into cool venous blood returning to the body. High core temperature is maintained, but the appendage functions at low temperature. Leatherback turtles have elevated core temperatures in cold seawater and arteriovenous plexuses at the roots of all four limbs. We demonstrate that plexuses of the hindlimbs are situated wholly within the hip musculature, and that, at the distal ends of the plexuses, most blood vessels supply or drain the hip muscles, with little distal vascular supply to, or drainage from the limb blades. Venous blood entering a plexus will therefore be drained from active locomotory muscles that are overlaid by thick blubber when the adults are foraging in cold temperate waters. Plexuses maintain high limb muscle temperature and avoid excessive loss of heat to the core, the reverse of the accepted paradigm. Plexuses protect the core from overheating generated by muscular thermogenesis during nesting.

1. Introduction

Limb counter-current heat exchange arrangements have been identified in birds and mammals living under cold terrestrial or aquatic conditions [1–4]. Heat exchangers feature bundles of closely applied arterial and venous vessels. The accepted paradigm is that, under cold conditions, heat from warm arterial blood travelling into the appendage crosses into the cool venous blood returning towards the body, facilitating maintenance of core body temperature. However, the corresponding appendage functions at low temperature [5,6].

Dermochelys coriacea is the sole living species of the chelonian family Dermochelyidae, which has a long history (*ca* 50 Myr) of foraging in cool water [7]. The largest of extant sea turtles, leatherbacks, also have the longest fore- and hindlimbs [8]. Limb blades are essentially composed of *manus* and *pes*. Muscles that drive them are associated with the pectoral and pelvic girdles, humerus plus radius and ulna, and femur plus tibia and fibula [8]. Propulsion in water is produced by synchronous action of the foreflippers, with the hindlimbs acting as rudders [9] and perhaps elevators. On land, all limbs are involved in propulsion [10], and the hindlimbs used to excavate nests.

Adult leatherbacks have elevated core temperatures (25–27°C) in cold (10.9–16.7°C) surface seawater [11–13] and regularly dive into near-freezing water [14]. Whether the leatherback is endothermic [15], or gigantothermic [16] has been controversial because of low metabolic rate in adults. Current consensus is that they derive heat from exercise [13,17,18]. Leatherbacks have arteriovenous

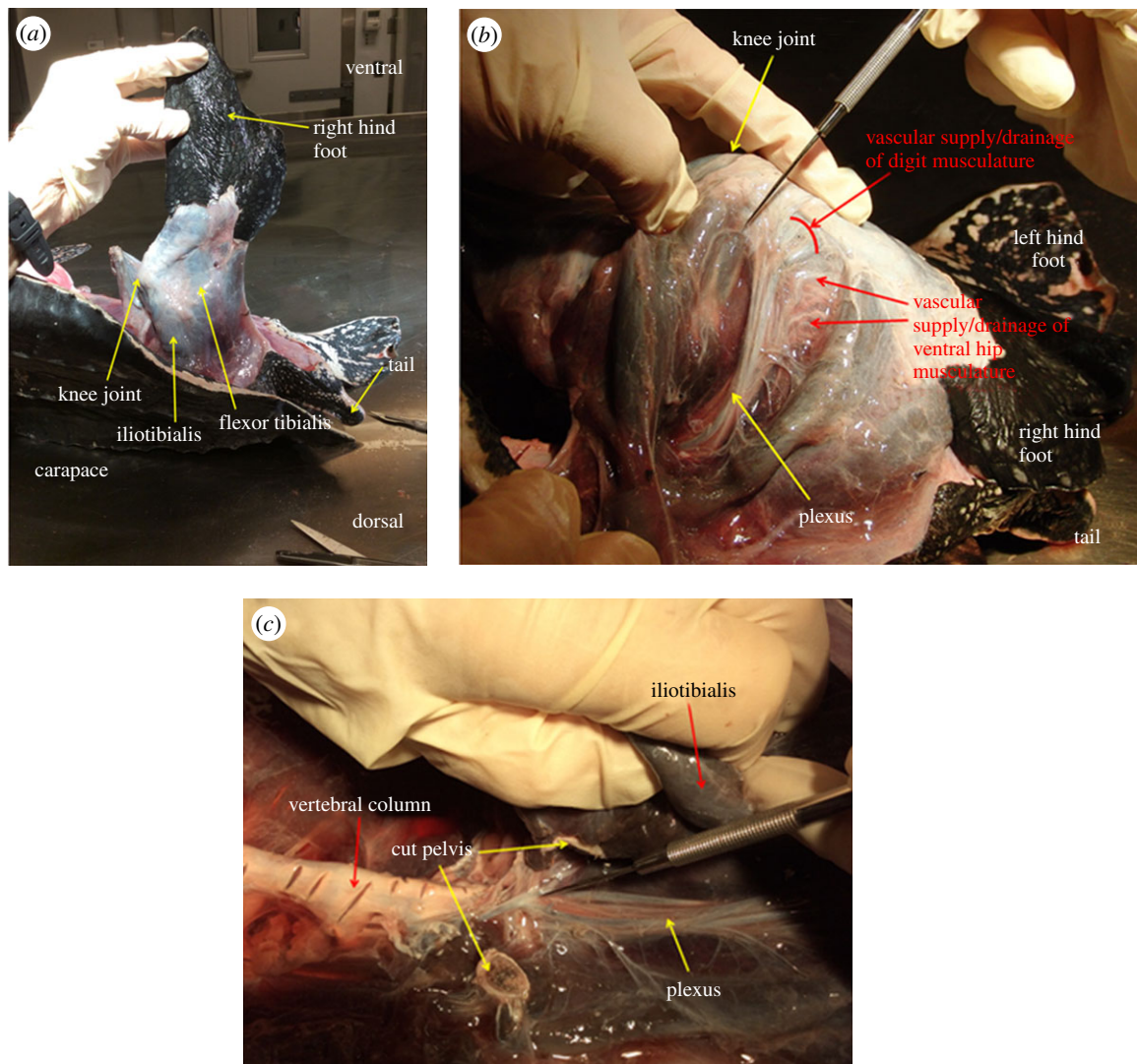


Figure 1. (a) View of hindlimb from laterodorsal aspect. Skin and superficial connective and adipose tissue have been removed from thigh and tibial areas. Two dorsal hip muscles are identified. (b) Laterodorsal view of hindquarter vascular plexus. Iliotibialis and flexor tibialis muscles have been parted. Needle indicates artery curving from distal end of plexus towards hip along posterior surface of iliotibialis. Note numerous vessels leaving/entering plexus that supply/drain flexor tibialis and ventral hip muscles, plus muscles of digits. Note also that some vessels that supply/drain the flexor tibialis loop hipwards from their connection with the plexus. (c) Dorsolateral view of distal origin (indicated by needle) of plexus. Cut pelvis and vertebral column (with necropsy cut marks) provide orientation.

counter-current plexuses at the roots of all four limbs, which have been assumed to avoid heat loss from the body core [19].

Leatherback turtles swim continuously when in water [20], even when foraging [13,21]. In cool temperate waters (14–15°C), Atlantic leatherbacks swim at 2.7 km h⁻¹ [13], similar to modal speeds of 2.0–3.0 km h⁻¹ recorded off the US Virgin Islands [22], where sea surface temperatures are about 28°C. Locomotory muscle performance is therefore little affected by the ranges of latitude and temperature routinely encountered, implying similar muscle temperatures in cold and warm environments. Muscular thermogenesis has not been studied directly in *Dermochelys*, but has been investigated in the pectoral muscles of smaller green turtles (*Chelonia mydas* [21]). In active adult green turtles, pectoral muscles were 8°C warmer than the sea; other tissues were not. There is indirect evidence that leatherback forelimb blades function at lower temperatures than more central tissues; cooled lipid samples taken from blade adipose tissue initiate crystallization at 11°C, whereas samples from carapace fat start to crystallize at 17–18°C [23]. Our study demonstrates that the vascular arrangements of the hindquarter plexus of *Dermochelys* result in a counter-current function

opposite to that described for birds and mammals exposed to cold conditions.

2. Methods

Six juvenile leatherbacks (59.5–84.1 cm, straight carapace length, 26.0–70.9 kg body mass) were collected as bycatch by observers (NOAA Fisheries, Pacific Islands Regional Office, Observer Programme) on longline fishing vessels operating in the equatorial Pacific. Frozen on death, they were in good post-mortem condition. Turtles were thawed 24 h before routine necropsy and histopathology to confirm cause of death [24] (drowning). The hindquarter plexus and its relationships with hindlimb musculature and hindlimb anatomy were investigated by gross dissection, tissue manipulation, histology and digital photography.

3. Results

Dissection of the hindquarter plexus of all six turtles revealed that its proximal end was at the pelvic girdle and that it ran deep within the hip muscles, alongside and posterior to the femur (figure 1a,b). It consisted of numerous bundles of

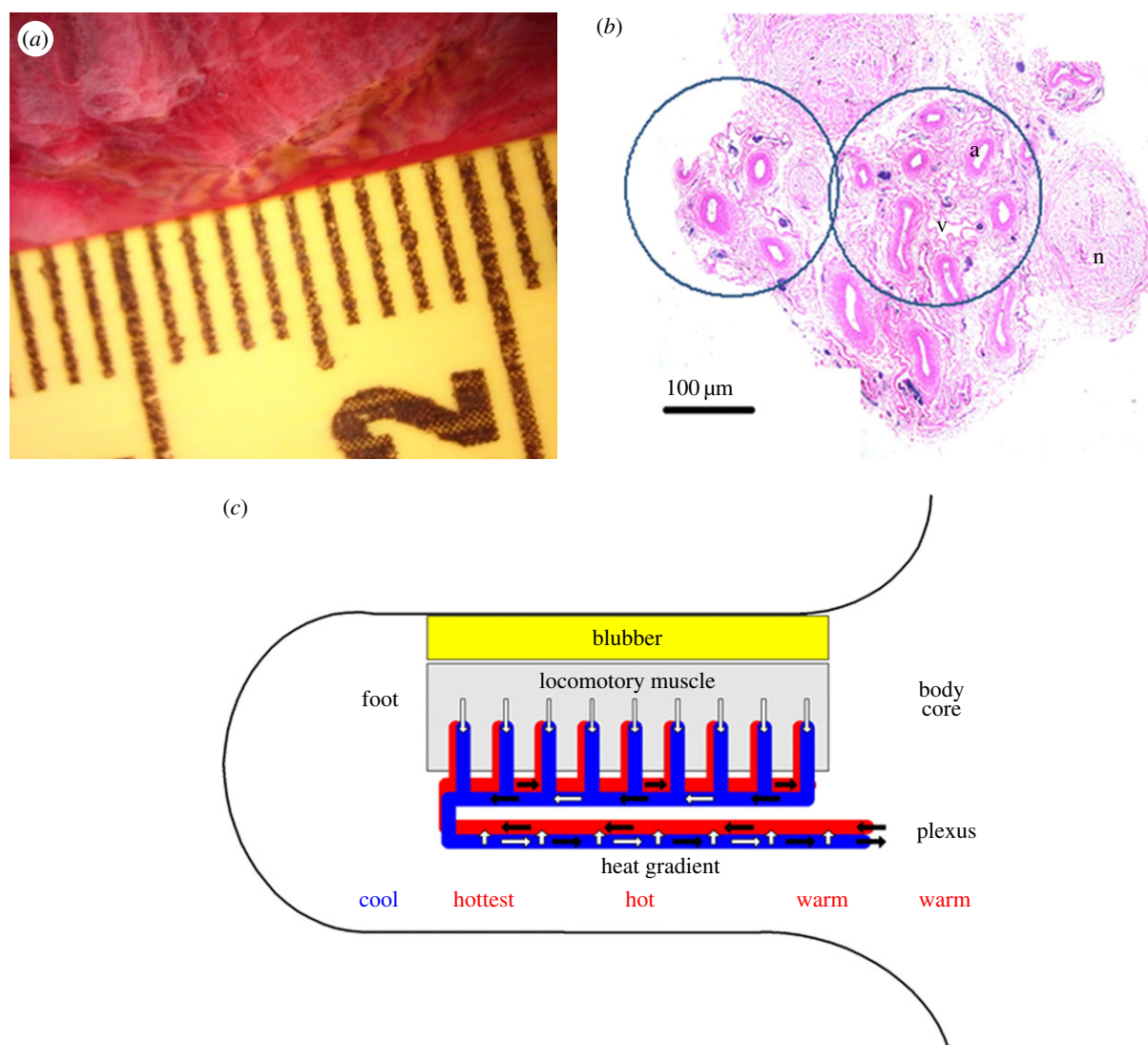


Figure 2. (a) Macrophotograph of cut end of plexus. Individual bundles (about 1 mm diameter) have tubular structures within them. (b) Cross section of part of plexus. Artery (a), vein (v), nerve bundle (n). Circles indicate areas of mixed arteries and veins. Veins are collapsed; arteries with thick smooth muscle walls have diameter about 25 μm. (c) Schematic diagram of function of hindlimb vascular plexus in *Dermochelys coriacea*. Black arrows indicate blood flow, white arrows indicate heat flow. Red indicates arterial supply, blue indicates venous drainage. Limb root blubber not present in hatchlings, juveniles or nesting adult female turtles, but characteristic of adult turtles on high-latitude feeding grounds [25].

closely applied veins and arteries interspersed with nerve bundles (figure 2a,b) as is normal in vertebrate limbs. No venous valves were seen. The two types of closely packed vessels are known to be arranged randomly, but with more veins than arteries [19]. The plexus was situated wholly within the core of the thigh musculature; it did not project beyond the knee joint into the lower limb and foot. Distally, most of the plexus broke up into less-packed vessels that supplied the hip muscles before the knee was reached. It was evident that some vessels that supply/drain the hip muscles loop proximally from the distal part of the plexus. In consequence, in the live animal, where the hip muscles are close to one another, the looped vessels will also be close to the plexus. This means that, upon circulating to the limb, some distally directed arterial blood in the plexus will flow proximally, whereas some venous blood will flow distally before entering the plexus and flowing proximally.

4. Discussion

The anatomical arrangements of leatherback hindlimb plexuses appear incompatible with accepted function [5,6,19]

for counter-current heat exchangers. Instead of the limbs having lower temperatures than the body core, we believe that the exchangers function primarily to retain thermogenic heat within the locomotory muscles themselves (see figure 2c for schematic diagram), thus allowing the muscles to be kept warm enough to work effectively in cold water, even though hindlimb function is primarily for steering [9] and may be mostly isometric. This implies that the muscle temperatures will usually be above those of the core, and also that the muscles generate enough heat for some to be transferred to the core, where large body size and very effective insulation will combine to retain it and thus maintain a steady 25–27°C core temperature [11–13].

Bird tibiotarsal counter-current vascular arrangements are phylogenetically/structurally varied [2], some species having complex intermingled networks of arteries and veins (rete), others having arrangements in which a single artery is surrounded by counter-current veins (venae comitantes). The lower bird leg is largely composed of bones (tarsometatarsi), tendons and skin with little muscle. In all cases, the exchanger is in the distal tibiotarsal region, so that returning cold blood is already warmed before it

passes through the muscular femoral region. The intramuscular placement of the leatherback plexuses is the reverse of this arrangement.

Overheating is a risk for *Dermochelys* in the tropics. Adults shuttle between warm surface waters and cool deeper water, thereby moderating their body temperatures [26,27]. Nesting female leatherback turtles (which use their hindlimbs for locomotion and nest digging) have core body temperatures of about 32°C (around 8–10°C above air/sand temperatures and 2.5–5°C above surface seawater temperatures) [28]. We suggest that our model of counter-current heat exchange (figure 2c) will protect the core against hyperthermia, by retaining heat generated by muscular thermogenesis within the limb musculature; enhanced blood perfusion of the turtle's skin (nesting turtles show flushed forearms/wrists, throats and undersides) will aid heat dispersion, working synergistically with plexus function.

In summary, the adult leatherback turtle exhibits a different form of endothermy in cold water from that exhibited by birds and mammals. Instead of depending upon heat generated by central nutrient-derived thermogenesis in the liver, *Dermochelys* relies upon continuous exercise of the peripheral locomotory muscles to generate heat that keeps them warm and is mostly retained in the musculature by counter-current heat exchange. Endogenous heat transferred from muscles to core is held there by thermal inertia

and effective insulation, rather than by counter-current heat exchange.

Ethics. All investigations were carried out upon dead leatherback turtles that had been accidentally caught (and drowned) by commercial fishers unconnected with any of our institutions. Their necropsies therefore posed no ethical problems whatsoever. No live animals were studied, and none were collected deliberately for our research.

Data accessibility. No data were collected beyond the photographic material used in the paper. No supplementary material is referred to in the paper.

Authors' contributions. All four authors conducted the necropsies, photography and histology in collaborative fashion following joint discussions of hypotheses to be addressed. J.D. led the analysis of the material and the writing of the various drafts of the manuscript, but all authors contributed to that analysis and writing (plus responding to reviewers' criticisms).

Competing interests. We have no competing interests.

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