

Chondro-osseous morphology of *Dermochelys coriacea*, a marine reptile with mammalian skeletal features

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The marine leatherback turtle, *Dermochelys coriacea* (Testudines, Dermochelyidae), is the largest known extant reptile, reaching weights >680 kg. It has a cosmopolitan oceanic distribution, nesting in tropical climates but migrating widely into colder temperate and boreal waters¹. Recent studies have shown that the leatherback has certain well developed thermoregulatory adaptations: vascular counter-current heat exchangers in the flippers, thick subcutaneous insulation beneath its leathery shell and effective inertial homoiothermy, if not endothermy^{2,3}. Whether this ability to maintain a body temperature higher than the ambient is due to endogenous endothermy or thermal inertia remains unclear^{4,5}. The skeleton of *Dermochelys* remains extensively cartilaginous even in adult animals^{6,7}, which has been attributed to neoteny secondary to its highly pelagic habitat, based on the assumption that its skeleton resembled that of typical embryonic turtles⁸. However, up to now there have been no studies of the internal architecture of the leatherback appendicular skeleton. We report here that the chondro-osseous morphology of *Dermochelys* is unlike that of any other known extant turtle or reptile but is more similar to that of marine mammals, notably Cetacea (whales) and Sirenia (manatees).

The typical hard-shelled marine turtles (Cheloniidae—genera *Chelonia*, *Caretta*, *Eretmochelys* and *Lepidochelys*) show a pattern of chondro-osseous morphology highly reminiscent of terrestrial or aquatic turtles^{9,10}. A thick, distinct compacta is clearly delineated from a medullary cancellous region and the epiphyses are covered by a very thin avascular cartilage which serves the purpose both of articular cartilage and physis, or growth plate. The subchondral plates of the epiphyseal bone surfaces are smooth and perfectly parallel to the articular cartilages. The only difference in marine turtles is the failure of development of a medullary cavity.

Dermochelys shows several important differences in skeletal morphology. In dried whole bones (with cartilage removed) the epiphyseal subchondral plates are not smooth, but instead present a rough, undulated, fenestrated surface which is not parallel to the contours of the articular cartilage surface (Fig. 1). In longitudinal sections of fixed whole bones each epiphyseal end has large cartilaginous epiphyses. Each of these, whether large or small, is filled with an extensive cartilage canal vascular system (Fig. 1). The vessels are both perichondral and transphyseal in origin and allow continuity of circulation between metaphysis and epiphysis. Both large and small vessels cross the physis: the smaller ones probably participate in endochondral chondro-osseous replacement, and the large ones are probably involved in cartilaginous expansion and nutrition of the epiphysis itself. No secondary calcification or ossification centres develop in any of these cartilaginous areas.

The diaphysis and metaphysis are filled with relatively dense cancellous trabecular bone without secondary medullary cavity formation. The metaphysis seems to be almost totally derived from endochondral bone formation and the diaphysis from a combination of endochondral and periosteal membranous growth. This is dramatically evident because of a combination of

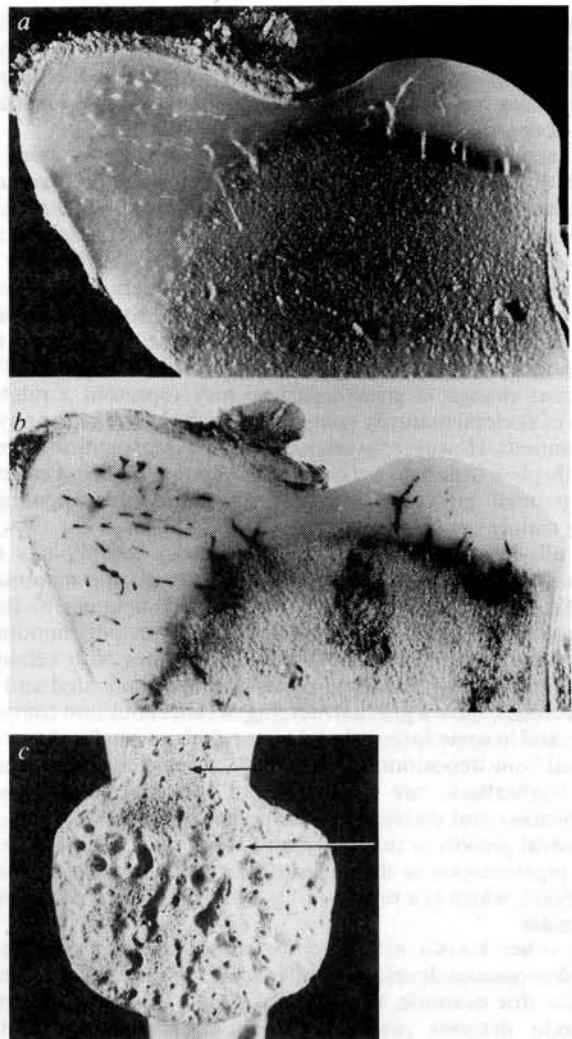


Fig. 1 Dried whole humeri were prepared by dermestid beetle maceration from two *Dermochelys coriacea*, one *Eretmochelys imbricata* (hawksbill), three *Chelonia mydas* (green turtle), two *Caretta caretta* (loggerhead) and two *Lepidochelys kempii* (ridley). Sections of whole formalin-fixed humeri, radii, ulnas and metacarpals were examined from two *C. caretta*, two *L. kempii* and four *D. coriacea* (straight-line carapace lengths 135, 153, 175 and 178 cm, estimated weights 260, 360, 470 and 470 kg; specimens found stranded in New Jersey during August–October 1979, and obtained from the Marine Mammal Stranding Center, Atlantic City). *a, b*, Natural and dye-injected longitudinal sections of the proximal humerus in a *D. coriacea* of 135-cm carapace length: medial process apophysis on the left, proximal epiphysis on the right. Small vessels of perichondral origin are seen in the centre of the apophysis; large transphyseal vessels are seen in both the epiphysis and the apophysis. *c*, View end-on of dried proximal humeral epiphyseal subchondral plate (cartilage removed) in a *D. coriacea* of ~190-cm carapace length. Arrowhead points to small metaphyseal end-arterioles participating in endochondral osteogenesis; black arrow points to large transphyseal fenestrations allowing vascular access to the centre of the cartilaginous epiphysis. Also seen are coarse growth plate undulations, which probably serve as stabilization for the large chondroepiphysis.

dark pigmentation in the periosteally derived trabecular bone and lack of internal ontogenetic remodelling (Fig. 2). Cones of light-coloured endochondral and dark-coloured periosteal bone are therefore formed, which radiate in a well delineated manner from the central nutrient artery located at the anatomic site of the initial diaphyseal ossification centre (see radiograph, Fig. 2).

Transverse sections of the mid-humerus show a cyclical variation in bone deposition which is mainly peripheral, both in the endochondral and periosteal portions. Other than pigmentation differences it is difficult to delineate grossly endochondral and

periosteal bone and the impression gained is of an amedullary cancellous region merging gradually peripherally into a slightly denser compacta, which is extensively vascular in the deeper portions but less so superficially, where it becomes a very thin shell of dense subperiosteal bone.

In reconstructing the hypothetical growth of this bone, it seems that both patterns of bone formation occur contiguously for a certain period of time, with the endochondral cones of bone progressively diverging from each other at their bases and the intervening space being filled in by periosteal bone. However, in the sub-adult animal it seems that further elongation of the bone becomes solely derived from endochondral growth, with very little contribution from the periosteal bone apart from the continued formation of a very thin cortical compacta. This apparent change in growth pattern may represent a relative onset of skeletal maturity comparable with closure of the physis in mammals. However, as secondary epiphyseal ossification and growth-plate fusion do not occur in the leatherback, it is capable of continual growth throughout adulthood, this apparently being mainly endochondral.

In all these features of chondro-osseous morphology the leatherback turtle appears most similar to marine mammals, notably the Cetacea (whales)¹¹ and Sirenia (manatees)¹². Both of these groups also vascularize their epiphyses perichondrally and transphyseally, develop amedullary bones with retained endochondral and periosteal cones that are pigmented and do not remodel, show a gradual merging of cancellous into compact bone, and in some forms (the migratory beluga whale) also show cyclical bone deposition^{11,12}. The only discernible differences in the leatherback are the lack of secondary epiphyseal calcification and ossification, the point of relative cessation of periosteal growth in the sub-adult animal, and the presence of dark pigmentation in the periosteal rather than the endochondral bone, which is a reversal of the pattern seen in the marine mammals.

No other known extant reptile shows this combination of chondro-osseous developmental features. Whereas some extant reptiles (for example, the varanid lizards, including the large Komodo dragon) vascularize their chondroepiphyses, this vascularization is always perichondrally or circumphyseally derived, never transphyseally¹³. In addition, the vascularization is invariably followed by secondary calcification and ossification of the epiphysis. All other turtles and all crocodylians previously examined, including species of large body size, fail to vascularize their thin chondroepiphyses, which also remain cartilaginous throughout adulthood^{8,13}. However, certain extinct reptiles show some similarities to the leatherback: plesiosaurs have been described as having endochondral and periosteal cones that do not remodel¹⁴; ichthyosaurs, plesiosaurs, nothosaurs and mesosaurs are known to have amedullary bones with cancellous-compacta differentiation paralleling that of marine mammals^{15,16}, and protostegid turtles have also been noted briefly to be somewhat similar in this respect¹⁷. All these fossil reptiles were highly adapted to a marine existence as shown by other skeletal features. Some fossil amphibians with pronounced marine modifications (certain stegocephalian species) also show a pattern of bone histology very similar to that described for marine mammals¹⁸. Other extant vertebrates with marine adaptations have similar developmental patterns, notably pinnipeds (seals)¹⁹ and penguins²⁰. However, some marine vertebrates do not show this spectrum of characteristics—notably the typical hard-shelled marine turtles (Cheloniidae) which are, in most respects, similar to freshwater or terrestrial species.

No terrestrial vertebrate has these chondro-osseous developmental features. The fact that such diverse groups as cetaceans, sirenians, pinnipeds, penguins, extinct marine reptiles and amphibians, and leatherback turtles have such a high degree of physical similarity in bone morphology suggests an underlying mechanism of marine adaptability which has led to a highly developed pattern of skeletal evolutionary convergence. The failure of some marine vertebrates (for example, hard-shelled turtles) to develop these characteristics fully may

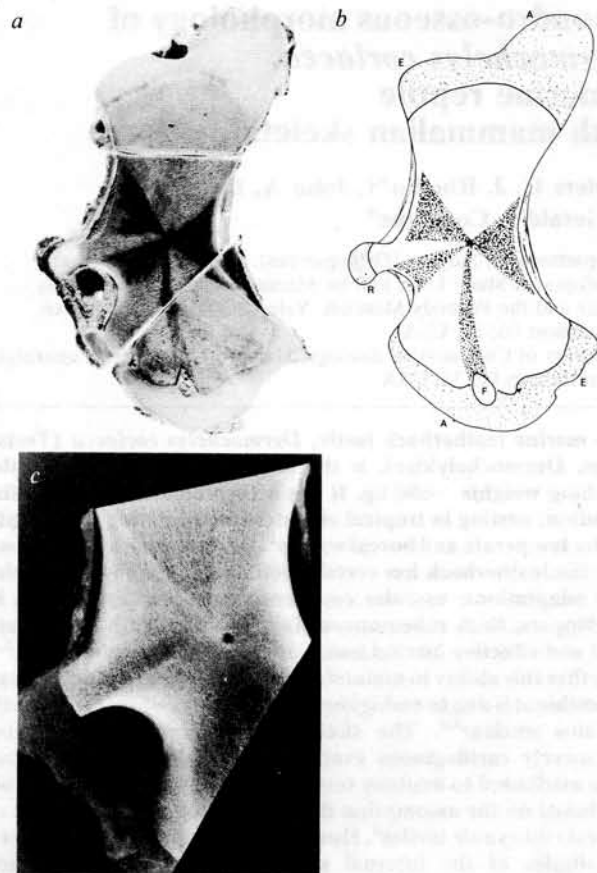


Fig. 2 a, b. Actual and schematic longitudinal sections of unstained humerus of a *D. coriacea* of 135-cm carapace length. Endochondral bone is light coloured whereas membranous (periosteal) bone is dark. Note also the amedullarity, lack of clear cancellous-compacta differentiation and disappearance of pigmentation at the superficial cortical margin. E, epiphyses; A, apophyses; F, ectepicondylar foramen; R, radial process apophysis. c. Radiograph of thin longitudinal slice of central diaphyseal portion of humerus showing central nutrient foramen and radiating cones of endochondral and membranous bone. Orientation as in Fig. 2a.

be related either to an incompletely evolved system due to relatively recent marine adaptation, or to a different set of physiological demands being required for differing life habits. Some studies have suggested that the marine pattern of bone development may be related to the homeostatic requirements of prolonged deep diving^{19,21,22}. It has been hypothesized that the intense dysbaric and acidotic challenges produced by repetitive deep diving can be countered by a skeletal buffering system which becomes more effective through increased vascularity in denser, amedullary bone¹⁹. Probably also of significance are the altered skeletal biomechanics of a marine existence where the limbs are not needed to support weight but instead are subject to entirely different forces produced by propulsion or steering in a medium much denser than air. Theories have also been advanced supporting hypothyroidism¹² and altered thermal relationships¹¹ as the underlying mechanisms leading to marine skeletal characteristics.

With regard to the phylogeny of *Dermochelys*, theories have vacillated between those supporting extreme specialization in a recently derived form and those favouring extreme primitiveness. Current taxonomic opinion accepts the former theory and is based on many similarities to the hard-shelled turtles²³⁻²⁸. However, strong arguments supporting the latter have also been advanced in the past^{7,8,29,30}. We suggest that the chondro-osseous morphology of *Dermochelys* emphasizes its extreme distinctness from other extant marine turtles (and turtles and reptiles in general). Whether this distinctness is recently derived or primitive cannot yet be answered.

Theories concerned with the phylogeny of endothermy and the origin of mammals from reptiles have stressed the relationships of increased body size and thermal inertia³¹ as well as altered bone histology³². It has been suggested that endothermy evolved separately in a number of extinct reptile groups³¹, and that transphyseal vascularization of a permanently cartilaginous epiphysis may have been the pattern in early mammal-like reptiles³³. The striking similarities in bone growth between *Dermochelys* and certain marine mammals, the presence of transphyseal vessels without secondary epiphyseal ossification, and the well developed homiothermic (or endothermic) thermoregulatory adaptations suggest that this large animal may have developed along a course parallel to certain extinct endothermic reptiles, although in a group not previously thought to be undergoing this evolutionary process. In addition, the leatherback turtle's chondro-osseous morphology represents a striking and seemingly unique parallel between an extant reptile and modern marine mammals.

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