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Comparative Chondro-osseous Development and Growth of Marine Turtles

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Longitudinal skeletal growth in appendicular long bones of *Caretta caretta* resembles the patterns in *Pseudemys scripta* and *Carettochelys insculpta*. A metaphyseal cone of cartilage becomes transiently isolated through the formation of a subphyseal plate of calcified cartilage which undergoes early peripheral vascular irruption and ossification. The noncalcified epiphyseal cartilage remains thin and avascular. Skeletal growth in *Dermochelys coriacea* is remarkably divergent from other living chelonians. Primary vascular irruption occurs into the noncalcified hypertrophied cartilage of the metaphysis with rapid extension of vascularity also into the non-hypertrophied epiphyseal cartilage. Endochondral ossification of the metaphysis advances contiguously from the diaphysis, a subphyseal calcified cartilage plate does not form, and there is no isolation of a metaphyseal cartilage cone. The noncalcified epiphyseal cartilage remains thick with transphyseal as well as perichondral vascularization through cartilage canals. The pattern in *Dermochelys* may be due to very rapid skeletal growth to a large body size. The giant Cretaceous *Archelon ischyros* has a similar skeletal vascular pattern, whereas the giant Tertiary *Stupendemys geographicus* resembles normal chelonians. In many respects, skeletal growth of *Dermochelys* resembles marine mammalian patterns.

ANY discussion of the regulatory biology of marine turtles would be incomplete without reference to mechanisms of growth. I have attempted to shed light on the developmental patterns of skeletal growth, as it relates to growth of both bone and cartilage. Knowledge of the skeletal developmental mechanisms of marine turtles can augment and clarify our ecological observations regarding such life history strategies as postnatal growth rates, age and size at sexual maturity, migratory and reproductive cycles and potential metabolic energy requirements. In addition, the study of skeletal development can add perspective to our analysis of the phylogenetic history of marine turtles.

In the marine turtles we have a group where tremendous growth occurs. A hatchling leatherback (*Dermochelys coriacea*) weighs about 30 gm and measures about 6 cm in carapace length. The adult can weigh as much as 650 kg and attain a carapace length of up to 180 cm. This represents a nearly 22,000 fold increase in body weight. An animal with such an incredible growth increment would appear irresistible for anyone interested in the study of chondro-osseous development. Yet aside from our work on the gross morphology of leatherback bones (Rhodin et al., 1980, 1981), no investigations of longitudinal skeletal growth patterns have been carried out on any of the marine turtles.

The only thorough research on longitudinal skeletal growth patterns in turtles was by Suzuki (1963), working on *Pseudemys scripta elegans*. This small, freshwater emydid turtle hardly compares with the giant leatherback, but its skeletal growth pattern has come to represent the typical and, presumably, only known pattern for all turtles, living and extinct. This generalization is primarily the result of writings by Haines as late as 1969, who also examined skeletal growth patterns in eight species of small freshwater and terrestrial chelonians of the families Emydidae, Testudinidae and Pelomedusidae (*Emys orbicularis, Terrapene* sp., *Chrysemys picta, Graptemys geographica, P. s. elegans, Homopus areolatus, Geochelone pardalis,* and *Pelusios* sp.) (Haines 1938, 1942, 1969). Other investigations by Moodie (1908) on *Chelydra serpentina* and *Chrysemys picta,* Lubosch (1910) on *E. orbicularis* and *C. serpentina,* and Wallis (1927) on *Mauremys leprosa* have revealed patterns similar to those described by Suzuki and Haines.

As a generalization for most turtles, the skeletal growth mechanisms of *P. s. elegans* are im-

portant to understand before examining the patterns in the larger, faster-growing marine turtles.

Suzuki (1963) and Haines (1969) both described the growth mechanism of *P. s. elegans* in similar fashion (Fig. 1). The appendicular bones are laid down originally as cartilaginous anlagen. A periosteal cuff forms around the cartilaginous diaphysis and grows out towards the metaphysis, depositing lamellar periosteally-derived cortical bone. The central diaphyseal cartilage cells then undergo hypertrophy, calcification, and early vascular irruption from the central nutrient artery perforating the mid-diaphyseal periosteal bone cuff. A primary ossification center forms in this mid-diaphyseal area and begins to advance slowly towards the metaphysis through endochondral ossification. At this time cartilage cells in the physeal zone between the epiphysis and metaphysis begin to hypertrophy, forming a subphyseal plate of hypertrophied cartilage with its circumferential origin at the periosteal-perichondrial interface of the zone of Ranvier. The subphyseal plate then quickly calcifies and undergoes rapid ingrowth of periosteally-derived vascularization leading to ossification. This creates a subphyseal bone plate and leaves an isolated cone of undifferentiated cartilage in the metaphysis separated from the cartilage in the epiphysis. As ossification proceeds both from the primary diaphyseal center and from the subphyseal plate, the metaphyseal cone of cartilage is gradually eroded and obliterated. In the epiphysis itself, endochondral ossification proceeds in fairly typical mammalian fashion, with zones of resting cartilage cells, proliferating cells, maturing cells in vague columns and columnar hypertrophic cells with calcification and vascularily-mediated endochondral bone formation (Fig. 5). The epiphysis gradually becomes thinner as the animal matures, with less and less hypertrophied cells contributing to longitudinal physeal growth. At no point does any vascular ingrowth occur into any non-calcified cartilage and the epiphysis itself remains avascular. With continued growth and remodeling of the diaphysis and metaphysis a limited medullary cavity also develops.

With an understanding of the mechanisms of skeletal growth in generalized, small, relatively slowly growing turtles such as *P. s. elegans*, I then investigated the patterns of growth in certain specialized, large and relatively fast growing turtles, especially turtles with marine adaptations.

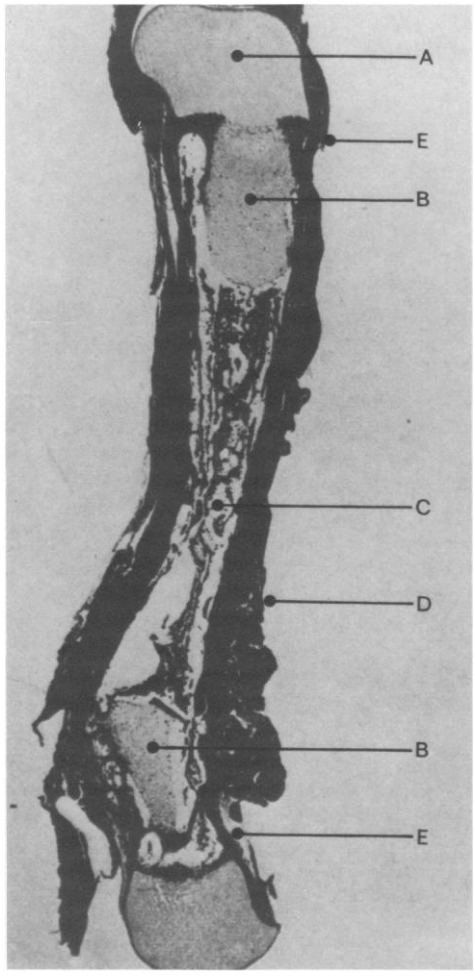

Fig. 1. Longitudinal section of femur of *Pseudemys scripta elegans* hatchling with 35 mm carapace length (ca 12×—from Suzuki, 1963). A, epiphysis with resting cartilage; B, metaphyseal cartilage cone, in the process of becoming isolated in the upper end of the bone, already isolated in the lower end; C, primary diaphyseal ossification center with medullary endochondral bone; D, circumferential periosteal lamellar bone cuff; E, subphyseal bone plate, beginning to form in the upper end of the bone, already formed in the lower end.

In two earlier papers on gross morphology of marine turtle bones (Rhodin et al., 1980, 1981) we reported the major discovery that the leatherback turtle develops well-vascularized thick cartilaginous epiphyses in contradistinction to

the pattern in all other Recent turtles. This paper now presents the first histological investigations of longitudinal skeletal growth in Recent marine turtles, further delineating the morphological distinctiveness of the leatherback. In addition, the paper provides comparative data from certain extinct turtles, describing for the first time the presence of vascularized epiphyses in one of these species as well.

Materials and Methods

I prepared decalcified longitudinally sectioned hematoxylin and eosin stained sections of appendicular long bones (humerus, radius, ulna, metacarpals, femur, tibia, fibula, and metatarsals) of three species of formaldehyde-fixed and ethanol-preserved Recent marine turtles (Cheloniidae and Dermochelyidae). I utilized bones from five loggerhead turtles (*Caretta caretta*) with carapace lengths of 44, 45, 46, 70, and 124 mm, one Kemp's ridley (*Lepidochelys kempi*) with a carapace length of 275 mm, and six leatherbacks (*Dermochelys coriacea*) with carapace lengths of 65, 70, 73, 125, 405, and 1,350 mm. In addition, I investigated six Fly River turtles (*Carettochelys insculpta*) (Carettochelyidae) with carapace lengths of 60, 69, 81, 137, 153, and 394 mm. Though phylogenetically quite distinct, *Carettochelys* was examined because of its superficial resemblance to marine turtles, presumably related to convergent adaptation to a partially marine environment. *Carettochelys* is a large turtle from the New Guinea region with marine-type flippers that inhabits large rivers and coastal marine waters.

For comparative purposes I also examined gross specimens and ground histologic sections of fossil bones from the extinct giant marine protostegid turtle, *Archelon ischyros*, the extinct marine desmatochelyid turtle, *Rhinochelys pulchriceps*, as well as the extinct giant estuarine pelomedusid turtle, *Stupendemys geographicus*. Regular decalcified sections were also prepared of the Recent pelomedusid turtle, *Podocnemis unifilis*, utilizing a specimen with 420 mm carapace length. In addition, decalcified histological sections were also prepared of a large Recent tortoise, *Geochelone elephantopus* (420 mm carapace length), and a large Recent chelydrid turtle, *Macroclemys temmincki* (460 mm carapace length). Examination of gross skeletal specimens was also undertaken of three other Recent marine turtle species (*Chelonia mydas, Eretmochelys imbricata*, and *Lepidochelys olivacea*) as well as representatives of most genera of Recent chelonians, including species from all Recent families not already mentioned (i.e., Trionychidae, Platysternidae, Dermatemyidae, Kinosternidae, and Chelidae).

Results-Histology

Carettochelys insculpta.—The pattern of skeletal growth in *C. insculpta* (Fig. 2) is very similar to that of *P. s. elegans*. Metaphyseal cartilage cones are transiently isolated by the rapid formation of a subphyseal bone plate. All noncalcified cartilage remains avascular. One difference in the growth of *C. insculpta* from that of *P. s. elegans* appears to be the relatively greater prominence and complete calcification of the subphyseal plate prior to ossification. In *P. s. elegans* ossification appears to begin peripherally in the subphyseal plate before central calcification has started. In addition, *C. insculpta* has less of a medullary cavity than *P. s. elegans*. Also, no evidence was found of the occurrence in *C. insculpta* of the basophilic network known as Suzuki's tissue normally found in the epiphysis of *P. s. elegans* and other turtles (Suzuki, 1963; Haines, 1969).

Caretta caretta.—The pattern of skeletal growth in *C. caretta* (Figs. 3–4) is also quite similar to that of *P. s. elegans* and *Carettochelys insculpta*.

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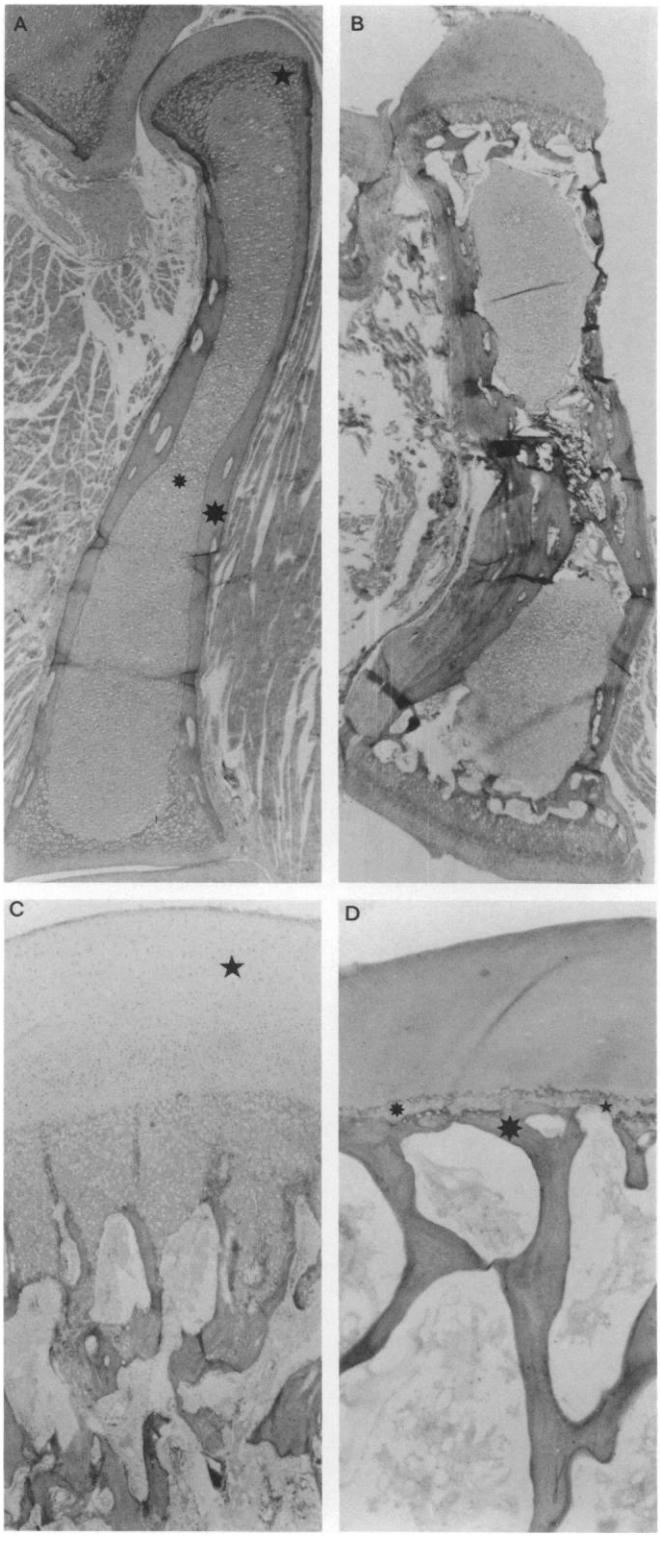
Fig. 2. Chondro-osseous development in *Carettochelys insculpta*. A. Metacarpal of hatchling with carapace length of 60 mm (ca 30×), demonstrating the initial periosteal lamellar bone cuff (large asterisk), early cartilaginous hypertrophy in the mid-diaphysis (small asterisk), and hypertrophic calcified cartilage in the subphyseal plates (star). B. Radius of young juvenile with carapace length of 81 mm (ca 15×), demonstrating isolation of metaphyseal cartilage cones and formation of subphyseal bone plates (see Fig. 1 for terminology). C. Proximal humeral epiphysis of older juvenile with carapace length 153 mm (ca 30×), demonstrating thick physeal growth plate (see Fig. 5 for terminology) and avascular epiphyseal cartilage (star). D. Proximal humeral epiphysis of adult with carapace length 394 mm (ca 20×), demonstrating thin avascular epiphyseal cartilage overlying very thin physeal zone (small asterisk) and subchondral bone plate (large asterisk), perforated only by occasional small metaphyseal vascular foramina (small star).



Noncalcified cartilage remains avascular, and a subphyseal plate is formed, causing transient isolation of a metaphyseal cartilage cone. Two features, however, differentiate the growth pattern of *C. caretta* from the other two species. First, the formation of the subphyseal plate differs in the larger bones of *Caretta* in that the central cartilaginous zone remains unhypertrophied and uncalcified even as the peripheral zone of the plate is already becoming ossified (Fig. 3D). This may be related to the relatively fast growth of the large bones in *Caretta*, where failure of closure of the subphyseal plate may allow faster growth and more rapid cartilaginous expansion in the center of the bone than would be possible if the entire subphyseal plate underwent early and complete calcification and ossification, as it does in the smaller, slower growing bones of *Caretta* (Fig. 3C), and the other slower growing turtle species (*P. s. elegans* and *C. insculpta*). Secondly, there is evidence of the occurrence in *Caretta* of the basophilic network of Suzuki's tissue, localized not in the epiphysis as it is in *P. s. elegans* (Suzuki, 1963; Haines, 1969), but in the zone of cartilaginous expansion in the center of the subphyseal plate (Fig. 4). As Hooff (1964) and Haines (1969) have postulated, this basophilic network may reflect rapid cartilaginous expansion through the unbonding of collagen fibers and localized increase in chondroitin sulphate. This strengthens the supposition that rapid growth is occurring in this noncalcified central portion of the subphyseal plate.

Lepidochelys kempi.—Only a single subadult specimen of *L. kempi* was examined, but its pattern of skeletal growth (Fig. 5) appears very similar to that of *Caretta*, *P. s. elegans*, and *Carettochelys insculpta*. Noncalcified cartilage remains avascular.

Dermochelys coriacea.—The pattern of skeletal growth in *D. coriacea* (Figs. 6–8) is remarkably divergent from all other living turtles. Initial growth resembles other turtles: appendicular bones are laid down originally as cartilaginous anlagen, a periosteal cuff forms in normal fashion, followed by typical vascular irruption into the mid-diaphysis, and subsequent formation of a primary ossification center. At this point, however, *D. coriacea* begins to follow a different growth pattern. In the smaller bones, rapid vascular ingrowth into the nonhypertrophied and noncalcified cartilage of the metaphysis occurs from the central diaphyseal ossification center. In larger bones, this ingrowth occurs simultaneously with the ingrowth leading to the formation of the central primary ossification center (Fig. 6A). The vascularity extends rapidly through the metaphysis and into the epiphyseal areas as well, creating cartilage canals. Cartilage hypertrophy, calcification, and ossification occurs along a narrow zone surrounding the metaphyseal (but not epiphyseal) portions of the cartilage canals, extending distally with the growth of the canal (Figs. 6B, 6C).

At the same time that rapid vascular ingrowth is occurring into the metaphysis and epiphysis, there is some growth activity in the subphyseal zone reminiscent of the subphyseal plate formation which occurs in other turtles (Fig. 6B). A thin circumferential band of cartilaginous hypertrophy, calcification and minimal vascular ingrowth occurs along the zone of Ranvier. There is, however, no formation of a subphyseal plate, and with continued growth, this thin circumferential band of calcified cartilage be-

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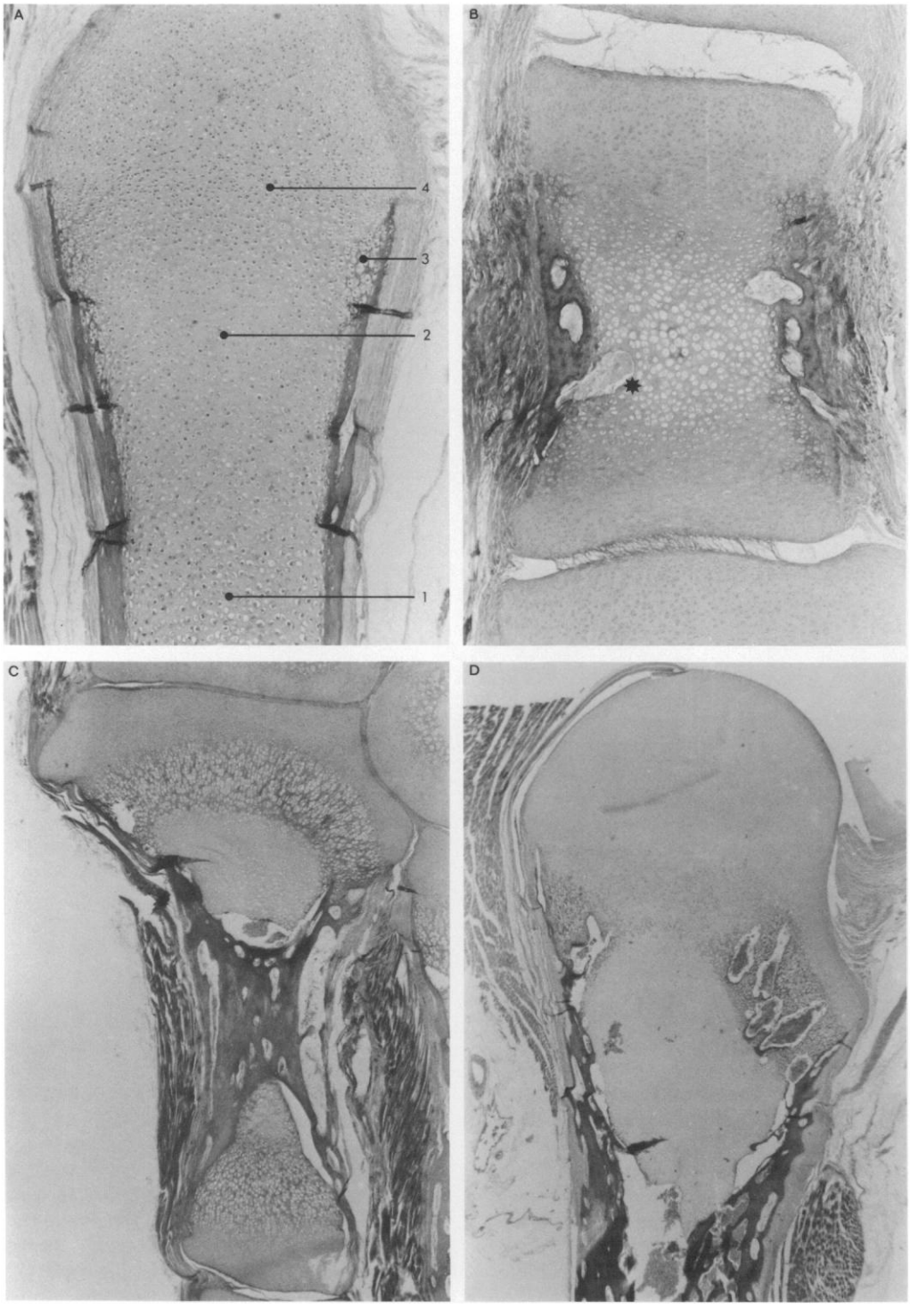
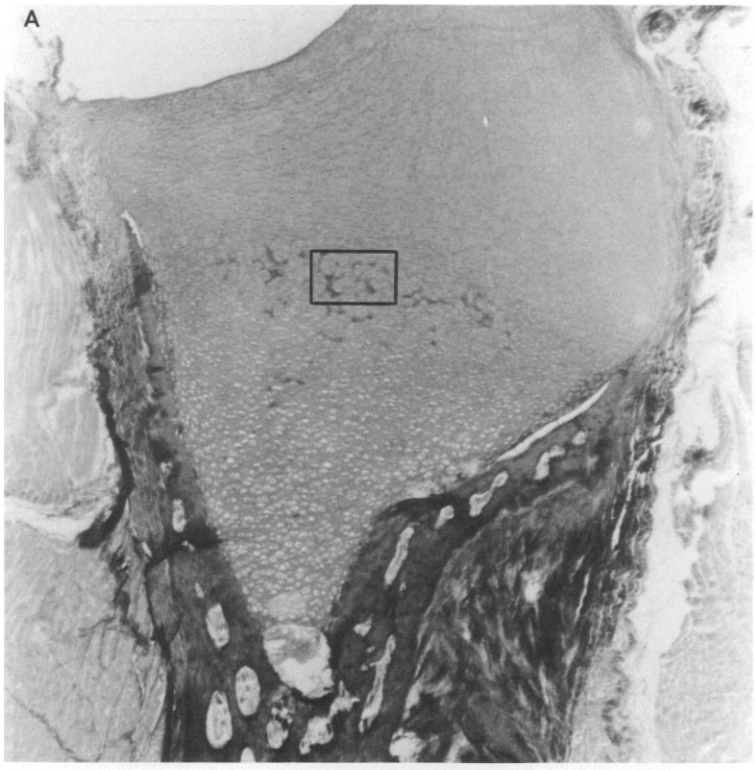
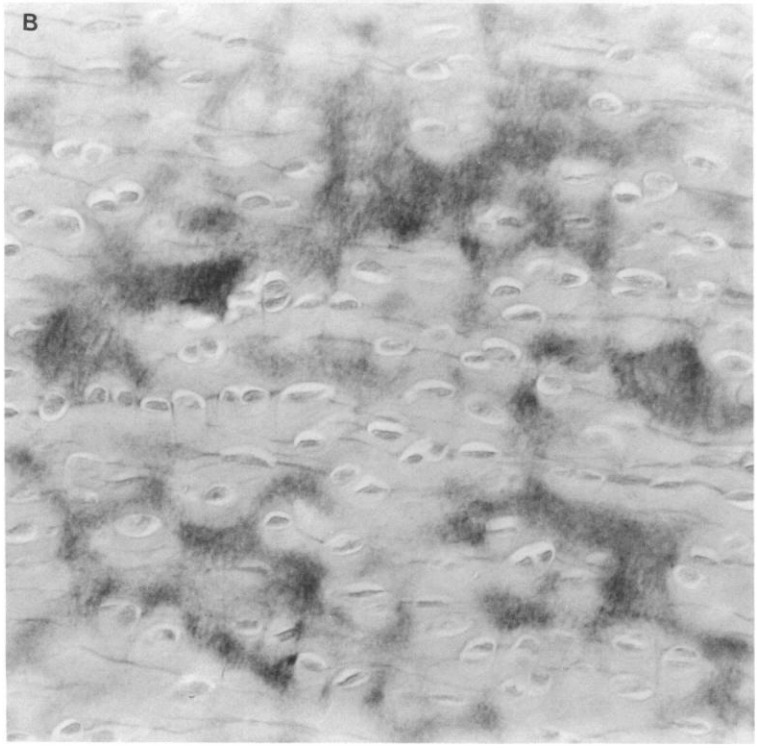
Fig. 3. Early chondro-osseous development in *Caretta caretta*. A. Distal ulna of hatchling with carapace length 46 mm (ca 40×), demonstrating: 1) hypertrophying cartilage in mid-diaphysis beneath periosteal cuff at site of eventual vascular irruption and primary ossification; 2) resting cartilage in metaphysis at site of eventual formation of isolated metaphyseal cartilage cone; 3) circumferential hypertrophy and early peripheral calcification of subphyseal plate beginning to differentiate; and 4) proliferating cartilage indicative of rapid cartilaginous growth delineating the arched outline of the eventual subphyseal plate. B. Metacarpal of hatchling with carapace length 44 mm (ca 40×), demonstrating primary vascular irruption (asterisk) through periosteal cuff into hypertrophied mid-diaphyseal cartilage, leading to formation of primary ossification center. C. Metacarpal of juvenile with carapace length 70 mm (ca. 30×), demonstrating primary diaphyseal ossification, fully formed subphyseal plates of hypertrophied and calcified cartilage, and isolated metaphyseal cones of resting cartilage, one of which is nearly obliterated. D. Proximal femur of juvenile with carapace length 70 mm (ca 20×), demonstrating vascular irruption and ossification occurring peripherally in the subphyseal plate while the central portions of the plate remain unhypertrophied and noncalcified (see text for details).







comes less prominent and eventually obliterated as endochondral ossification extends contiguously towards the epiphysis from the diaphysis. At no point is there formation of an isolated metaphyseal cone of undifferentiated cartilage, such as occurs in other turtles.

As the contiguously expanding primary diaphyseal ossification center reaches the subphyseal area, a typical mammalian type growth plate (physis) forms (Figs. 7A, 7B). This is composed of several different zones, from the resting cartilage in the epiphysis, through zones of cartilage cell proliferation, maturation, hypertrophy, and calcification, with the last three zones forming columnar rows of cells. In the zone of calcification vascular ingrowth of small metaphyseal vessels occurs, mediating endochondral ossification. Much of the physeal pattern resembles the growth plate present in normal turtles (Fig. 5), with two major exceptions. The physis in *D. coriacea* is much thicker with more clearly developed column formation, and traversing the growth plate are the large vascularized cartilage canals which enter the nonhypertrophied, noncalcified cartilage of the epiphysis.

In rapidly growing juveniles, the epiphyseal cartilage canals are surrounded by a narrow zone of rapid cartilage cell production, proliferation, and maturation (Fig. 7C), but without the cartilaginous hypertrophy and calcification which occurred in the metaphysis during early growth of the canals.

In sexually mature adults, the growth plate with its separate zones becomes much thinner, reflecting slowed growth (Fig. 8A). Epiphyseal cartilage canals are still present, but now surrounded by evidence of slower cartilage cell proliferation (Fig. 8B).

Of note is the apparent absence in *D. coriacea* of Suzuki's basophilic network in areas of expanding cartilage.

In the diaphysis and metaphysis there is no evidence of remodeling, a medullary cavity does not form, and endochondrally-derived bone cones can be differentiated from intervening periosteally-derived bone. Grossly, these different types of bone can be distinguished by the light color of the endochondral bone, and dark color of the periosteal bone (Fig. 9). Histologically, the periosteally-derived dark bone is differentiated from the endochondrally-derived light bone by having a denser array of bone trabeculae, increased bone mass, decreased medullary stroma, and scattered pigment (Fig. 7A). The lack of internal ontogenetic remodeling allows these cones to remain well differentiated throughout life.

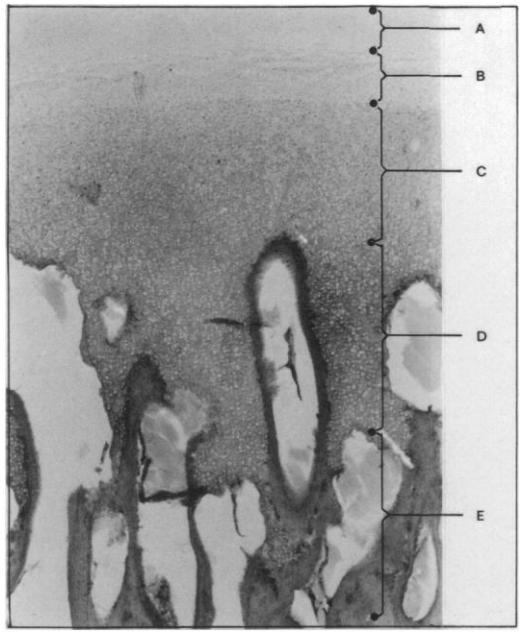


Fig. 5. Growth plate (physis) of proximal humerus in *Lepidochelys kempi* subadult with carapace length 275 mm (ca 30×), demonstrating endochondral ossification zones: A) resting epiphyseal cartilage, B) proliferating cartilage, C) maturing cartilage, blending gradually into D) hypertrophying and calcifying columnar cartilage, which is invaded at different levels by E) metaphyseal vascular channels mediating ossification.

On cross-section of the mid-humerus in a sexually mature adult female (Fig. 10), two growth rings are evident, where periosteal new bone formation has slowed gradually, before suddenly growing very rapidly for a while and then slowing again. This pattern differs from the regular tightly-spaced periosteal annuli previously noted in cross-sections of turtle bones by Mat-

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Fig. 4. Suzuki's tissue in *Caretta caretta*. A. Proximal radius in hatchling with carapace length 44 mm (ca 30×), demonstrating occurrence of Suzuki's tissue at rectangle in the central portions of the subphyseal plate during the early stages of its formation. B. Enlargement of rectangle in A (ca 200×), demonstrating the basophilic network of Suzuki's tissue in area of rapid cartilaginous expansion.

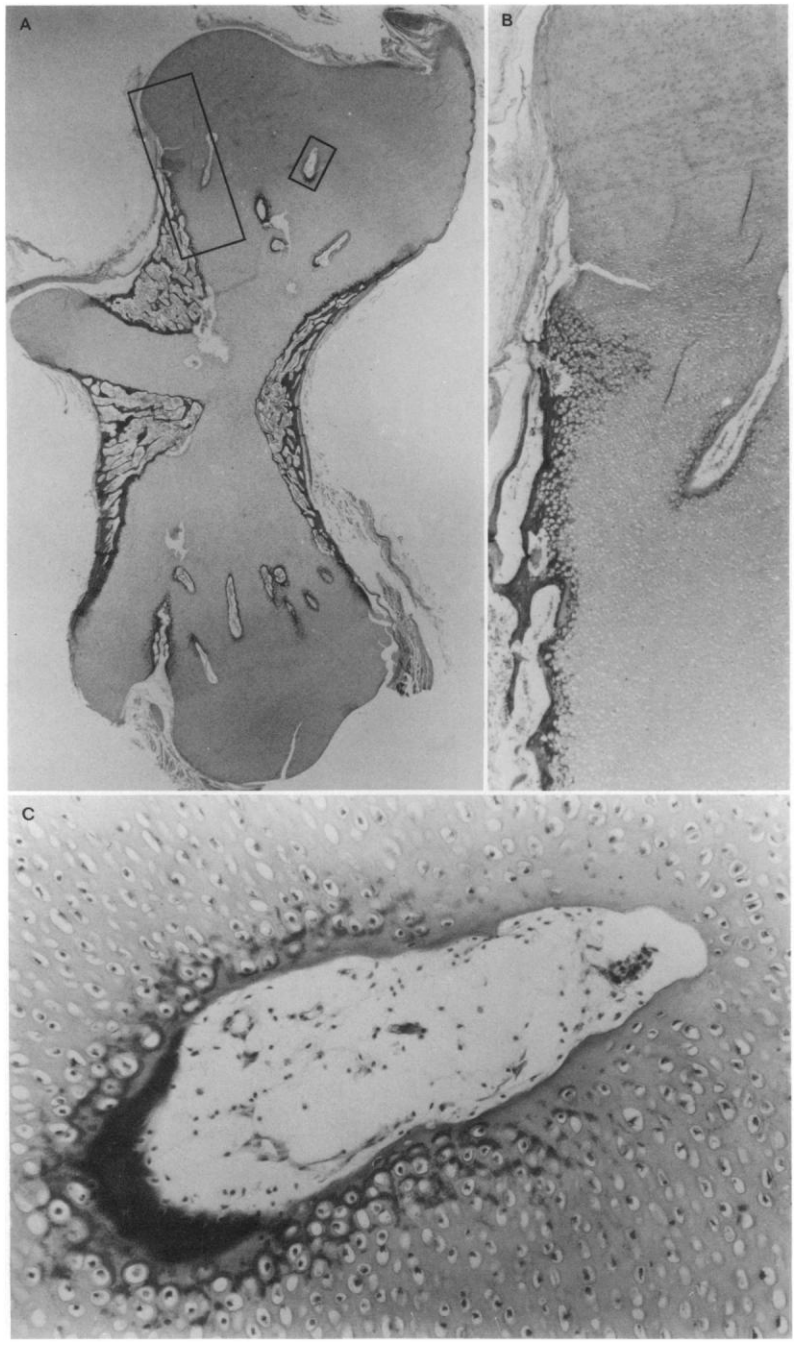

Fig. 6. Chondro-osseous development in *Dermochelys coriacea* hatchling with carapace length 70 mm. A. Longitudinal section of humerus (ca 12×), demonstrating vascularity spreading through metaphyses towards epiphyses prior to formation of primary diaphyseal ossification center. B. Enlargement of larger rectangle in A (ca 30×), demonstrating small transient zone of peripheral cartilaginous hypertrophy, calcification, and minimal vascular irruption (see text for details). C. Enlargement of smaller rectangle in A (ca 100×), demonstrating cartilage canal penetrating epiphysis (to the right) from the metaphysis (to the left), accompanied by cartilaginous hypertrophy, calcification, and ossification on the metaphyseal side (same pattern in another canal also visible in B at lower magnification).

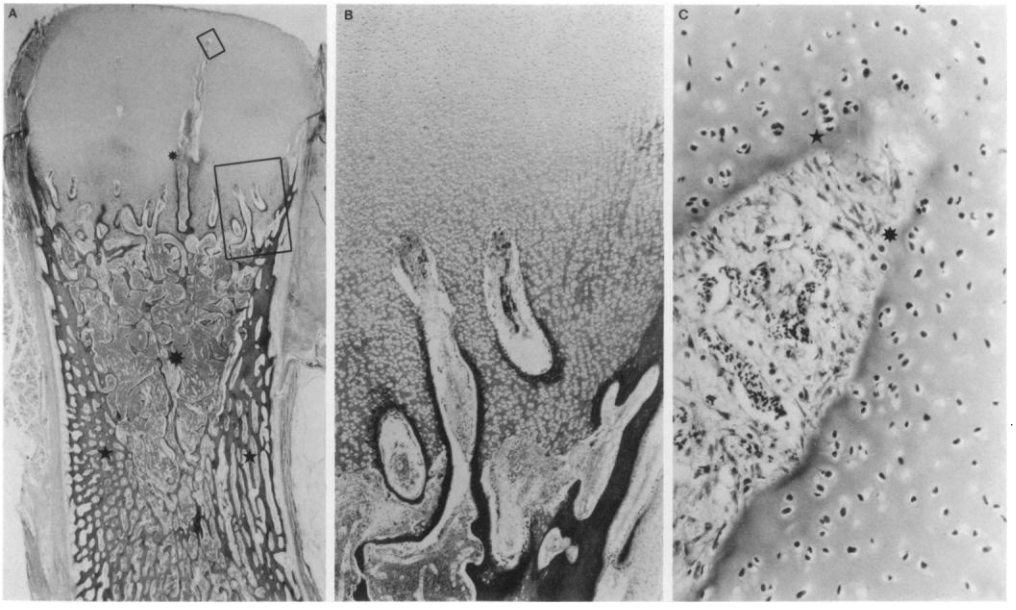

Fig. 7. Chondro-osseous development in *Dermochelys coriacea* juvenile with carapace length 405 mm. A. Distal ulna (ca 15×), demonstrating clearly differentiated cone of endochondral medullary bone (large asterisk) between denser periosteal bone (stars), as well as large transphyseal vascular channel (small asterisk). B. Enlargement of larger rectangle in A (ca 40×), demonstrating growth zone (physis) with columnar cartilage maturation, hypertrophy, and calcification (see Fig. 5 for terminology). C. Enlargement of area similar to small rectangle in A (ca 100×), demonstrating rapid cartilage growth (most pronounced at star) along periphery of epiphyseal cartilage canal, and apparent rapid transformation of pre-chondral mesenchymal cells from the canal itself to true cartilaginous cells (asterisk) (see also Fig. 8B for contrast).

tox (1936) for *Chrysemys picta marginata*, Peabody (1961), Hammer (1969), and Enlow (1969) for *Chelydra serpentina*, Suzuki (1963) and Enlow (1969) for *Pseudemys*, Enlow (1969) for *Gopherus* and *Podocnemis expansa*, Castanet and Cheylan (1979) for *Testudo hermanni* and *T. graeca*, and Zug et al. (1983) for *Caretta caretta*.

Discussion

The leatherback turtle, *Dermochelys coriacea*, is unique among living chelonians in its pattern of chondro-osseous development (Rhodin et al., 1980, 1981). In fact, no other known extant reptile demonstrates a similar pattern (Rhodin et al., 1981). Though some lizards, notably large varanids such as the Komodo dragon (*Varanus komodoensis*) as well as some small lizards such as chamaeleons and certain agamids vascularize their chondroepiphyses (Haines, 1969), such vascularization is always perichondrally or circumphyseally derived, never transphyseally as in the leatherback. In addition, the vascularization is invariably followed by secondary epiphyseal calcification and ossification, unlike in the leatherback where the epiphysis remains cartilaginous.

In fact, in many respects, the skeletal growth pattern of *Dermochelys* resembles that of marine mammals such as whales (Rhodin et al., 1981; Felts and Spurrell, 1965, 1966). The leatherback resembles marine mammals in many ways, exhibiting: 1) perichondral and transphyseal vascularization of epiphyses; 2) failure of formation of a subphyseal bone plate; 3) well delineated endochondral and periosteal bone cones in minimally remodeled amedullary bone; 4) gradual merging of cancellous into well vascularized compact bone on cross section; 5) physiologic inertial homoiothermy or possible endothermy (Frair et al., 1972); and 6) heat retention mechanisms such as thick subcutaneous fibrous adipose tissue insulation and vascular counter-current heat exchangers in the flippers (Greer et al., 1973).

Of note is that marine mammals differ significantly from the leatherback in that they go on to secondarily ossify their vascularized epiphyses. However, Ricqles (1979) has theorized that early mammal-like reptiles probably

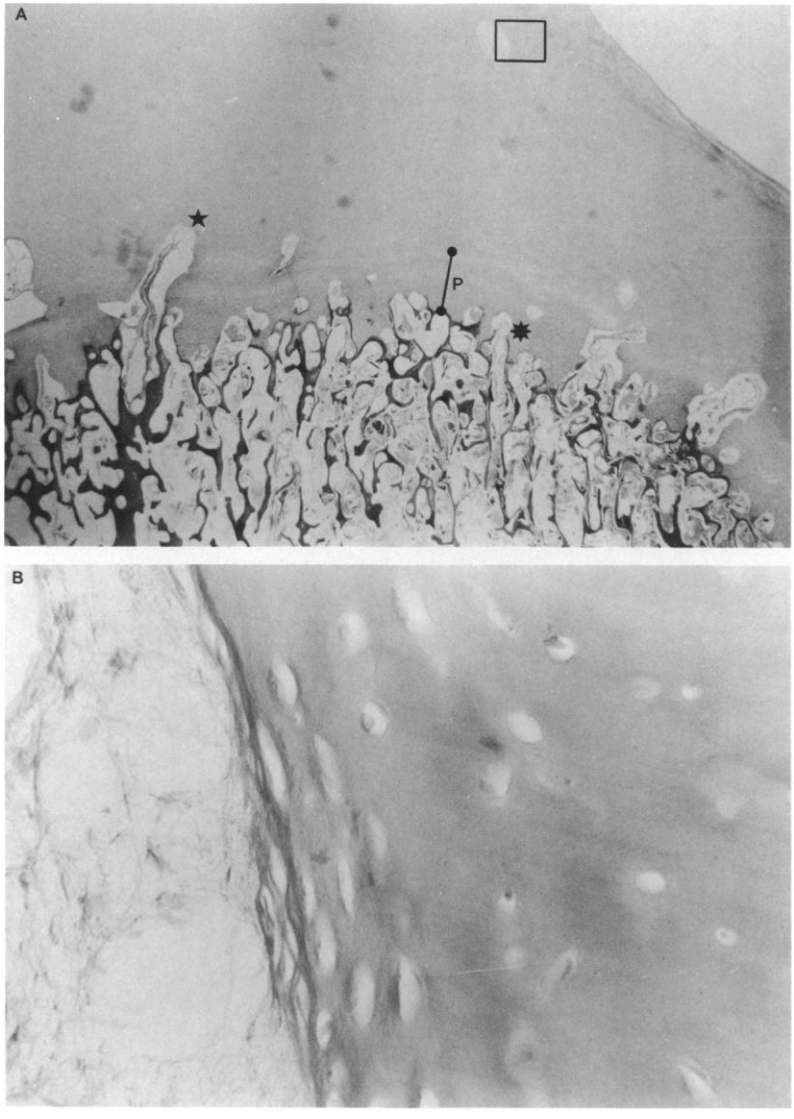

Fig. 8. Chondro-osseous development in *Dermochelys coriacea* adult with carapace length 1,350 mm. A. Proximal radius (ca 10×), demonstrating relatively thin physis (P), large transphyseal vascular channels (star), smaller metaphyseal vascular foramina for endochondral ossification (asterisk), and epiphyseal cartilage canal (at rectangle). B. Enlargement of rectangle in A (ca 200×), demonstrating apparent slow production of cartilage cells from pre-chondral mesenchymal cells in the cartilage canal (contrast with Fig. 7C).

developed non-ossified vascularized epiphyses much like those here demonstrated for the leatherback. It appears possible, based on the above data, that the leatherback could be an extremely derived species, evolving along a course parallel to certain extinct endothermic reptiles. If true, then it is the only extant mammal-like reptile, though a member of a lineage previously felt to be typically primitively reptilian. The potential for further comparative research appears highly promising.

As noted above, no other living turtle shares the leatherback's skeletal developmental pattern. However, certain extinct turtles evidently did. The giant Cretaceous protostegid marine turtle *Archelon ischyros* (carapace length ca 190

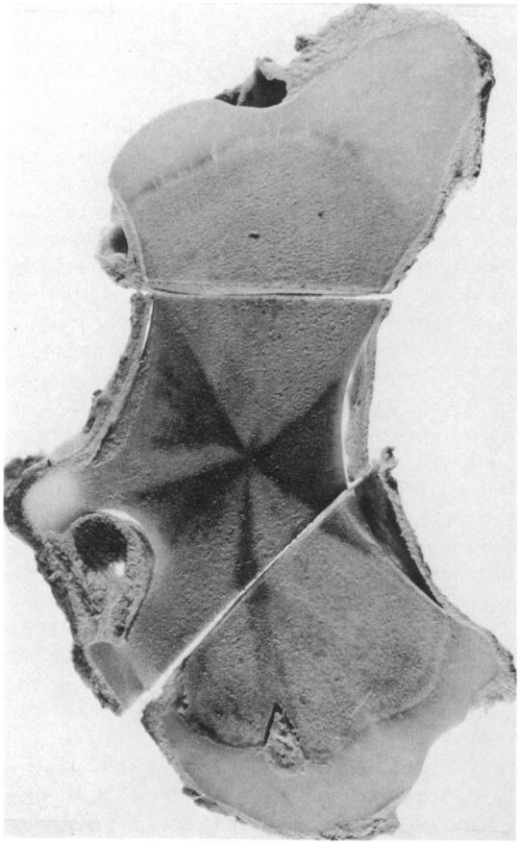

Fig. 9. Longitudinal section of adult *Dermochelys coriacea* (135 cm carapace length) humerus (Rhodin et al., 1981). Light-colored endochondral bone cones are separated by dark-colored periosteal bone (see text for details).

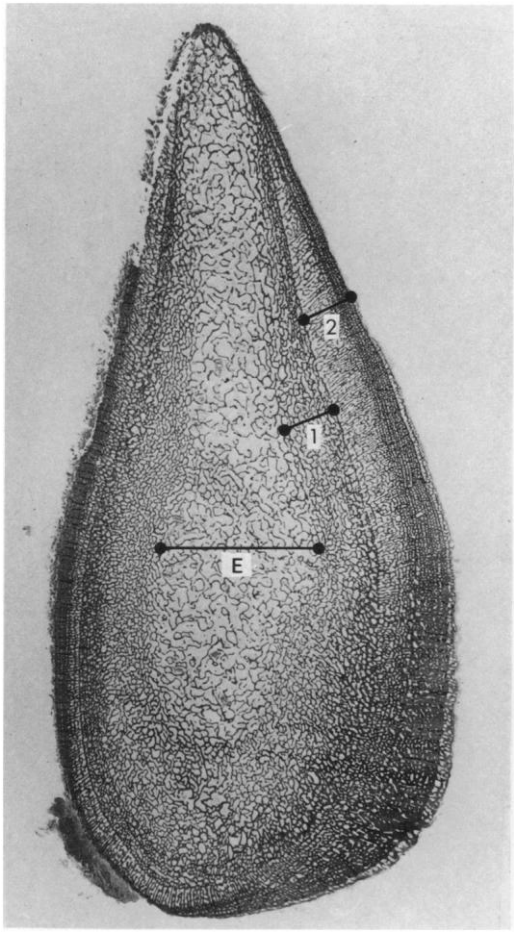

Fig. 10. Histologic cross-section (ca 1.5×) of adult *Dermochelys coriacea* (135 cm carapace length) humerus, just proximal to mid-diaphysis. E, endochondral medullary bone; 1 and 2, growth rings in well vascularized periosteal bone (see text for details).

cm) also had transphyseally vascularized chondroepiphyses. Comparison of the subchondral physeal bone surface in dried leatherback bones and well preserved fossil *Archelon* bones demonstrates an identical pattern of transphyseal vascular channels (Fig. 11). Also, on ground histologic cross-sections of *Archelon* bones the pattern of cancellous bone merging gradually into vascular compact bone is nearly identical to the pattern in the leatherback.

A review of the literature, with careful examination of published figures, indicates that certain other extinct marine turtles probably also had similar patterns of transphyseally vascularized chondroepiphyses with roughened, fenestrated subchondral bone surfaces and poorly defined articular surfaces. Turtles with similar patterns appear to be: *Psephophorus scaldii* (Dollo, 1888), *Eosphargis breineri* (Nielsen, 1963), *Pneumatoarthrus peloreus* (Baird, 1978) and *Corsochelys haliniches* (Zangerl, 1960).

Most extinct marine turtles, however, probably resembled the typical Recent cheloniid species with avascular epiphyseal cartilage, smooth subchondral physeal bone surfaces, and well defined articular surfaces (Rhodin et al., 1981). Examination of fossil bones of the extinct Cretaceous desmatochelyid marine turtle *Rhinochelys pulchriceps* demonstrates this smooth subchondral surface. A review of the literature with careful examination of published figures indicates that the following marine turtle species

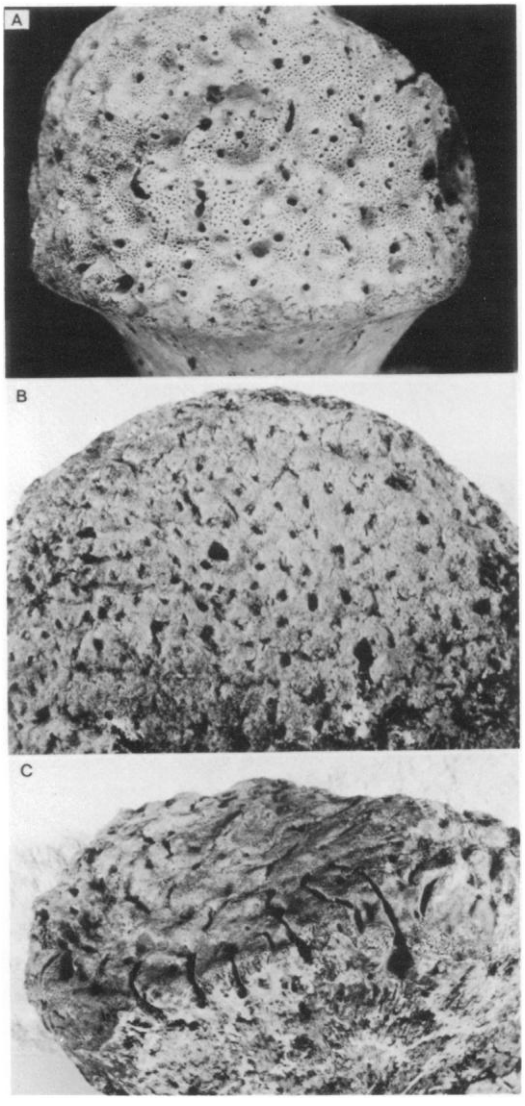

Fig. 11. Subchondral physeal bone surfaces of specialized marine turtles showing large transphyseal vascular channels leading to epiphyseal cartilage canals and smaller metaphyseal vascular foramina involved in endochondral ossification. A. *Dermochelys coriacea* adult proximal humeral epiphysis. B. *Archelon ischyros* adult proximal metacarpal epiphysis. C. *Archelon ischyros* adult distal pisiform joint surface (at top) and outer surface of metaphyseal periosteal bone (at bottom) with transphyseal and circumphyseal vascular channels penetrating into epiphysis.

probably also had typical avascular epiphyseal cartilage: *Desmatochelys lowi* (Zangerl and Sloan, 1960), *Syllomus aegyptiacus* (Weems, 1974), *Procolpochelys grandaeva* (Weems, 1974), *Eochelone brabantica* (Zangerl, 1980), *Allopleuron hofmanni* (Winkler, 1869), *Osteopygis emarginatus* (Zangerl, 1953), *Ctenochelys tenuitesta* (Zangerl, 1953) and *Toxochelys latiremis* (Case, 1898).

Since both *Dermochelys* (carapace length up to 180 cm) and *Archelon* (carapace length ca 190 cm) are giant marine turtles, and *Psephophorus, Eosphargis, Pneumatoarthrus* and *Corsochelys* are also evidently quite large, the question arises whether their pattern of vascularily mediated cartilage growth is related primarily to their large body size. Several cases apparently falsify this hypothesis. The Recent cheloniid green sea turtle, *Chelonia mydas,* can reach carapace lengths of 100–140 cm, yet careful examination of its bones reveals typical chelonian articular surfaces without transphyseal vascularization. More importantly, examination of the fossil bones of the largest turtle that ever lived, the giant Tertiary pelomedusid *Stupendemys geographicus* (carapace length ca 220 cm) (Wood, 1976) also reveals well-defined articular surfaces with a smooth subchondral physeal bone surface without transphyseal vascular channels. Recent pelomedusid turtles are much smaller than the giant *Stupendemys,* but *Podocnemis expansa* can reach carapace lengths of almost 90 cm, and gross examination of its bones as well as histologic examination of the bones of its smaller congener *P. unifilis* (carapace length up to ca 50 cm) reveals typical chelonian patterns of avascular cartilage. In addition, histologic examination of the bones of the relatively large Galapagos tortoise (*Geochelone elephantopus*) and the alligator snapping turtle (*Macroclemys temmincki*) also reveals typical chelonian avascular cartilage.

Based, then, on my review of living and fossil turtles, there appear to be two basic mechanisms of chondro-osseous development among chelonians. These mechanisms are schematically represented in Fig. 12. The typical, generalized, and presumably primitive pattern characterized by avascular cartilage, subphyseal plates, and isolated cartilage cones apparently occurs in all freshwater and terrestrial chelonians as well as many marine species. The atypical, specialized, and presumably derived pattern characterized by vascularized cartilage and mammalian-like growth without subphyseal plates or isolated cartilage cones apparently occurs only in certain large marine species.

The presence of the two kinds of bone growth among living and extinct marine turtles corresponds relatively well with one of the current

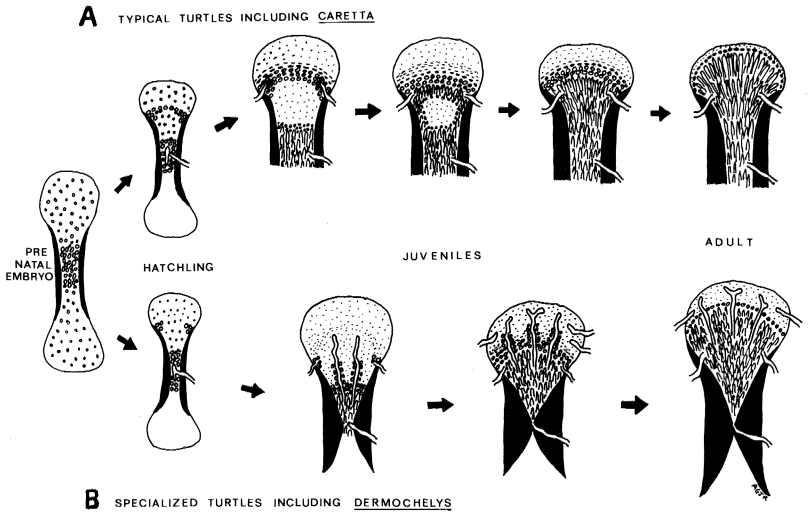

Fig. 12. Schematic representation of the two basic longitudinal chondro-osseous growth patterns occurring in chelonians. Most turtles, including modern cheloniid marine turtles, follow pattern A; a few specialized ones including *Dermochelys* and *Archelon* follow pattern B. See text for details. Solid black represents periosteal bone, inverted V's medullary endochondral bone, large circles hypertrophied cartilage, dots and dashes resting and proliferating cartilage. Areas of vascular ingrowth indicated by schematic blood vessels.

concepts of phylogenetic hypotheses of marine turtles (Fig. 13). However, the presumed presence of vascularized cartilage in the cheloniid *Corsochelys* (based on examination of figures by Zangerl, 1960), as well as the absence of vascularized cartilage among desmatochelyine turtles sheds some doubt on the phylogenetic reconstruction presented. Either the derived condition of vascularized cartilage arose independently in some early cheloniids as well as in some unknown pre-dermochelyid, pre-protostegine ancestor, or vascularized cartilage arose only once and represents a shared derived character, requiring that the relationships of *Corsochelys* with the protostegid-dermochelyid lineage be re-examined.

Given that turtles have developed two different mechanisms of skeletal growth, and that the difference is not due solely to differences in body size (see discussion of *Archelon* vs *Stupendemys* above), what then is the physiologic basis for the difference? In other words, why vascularize a cartilaginous epiphysis? Based on extensive work on the form and function of vascular cartilage canals in mammals and birds (Levene, 1964; Lutfi, 1970; Wilsman and Van Sickle, 1970, 1972; Kugler et al., 1979; Ogden, 1980; Kuettner and Pauli, 1983), it appears that they fulfill four different functions. Cartilage canals are: 1) nutritive to cartilage when the cartilage is too thick to derive nutrition by direct diffusion from the joint surface; 2) a source of prechondral mesenchymal cells for continued interstitial cartilage expansion in rapidly growing cartilage (Fig. 7C); 3) structurally supportive in thick cartilage, especially when surrounded by narrow sleeves of hypertrophying and calcifying cartilage; and 4) usually accompanied by eventual formation of a secondary ossification center.

Based on this, it appears that the presence of vascularized cartilage may be related to rapid growth to a large size, where the metabolic requirements of the large, fast-growing cartilage require the presence of vascularity. Large, but presumably slow-growing chelonians, such as *Stupendemys* and most cheloniid sea turtles, do not require vascularized cartilage. The presence of vascular cartilage in *Archelon* and *Dermochelys*, on the other hand, suggest that they are very rapidly growing animals in addition to being large.

How rapidly does *Dermochelys* grow? Unfortunately, there are very few data available regarding its rate of growth; no studies in the wild have been undertaken, and no captive growth to maturity has ever been recorded. However, a few data on captive growth of juveniles is available, and they support the hypothesis that the leatherback grows much more rapidly than che-

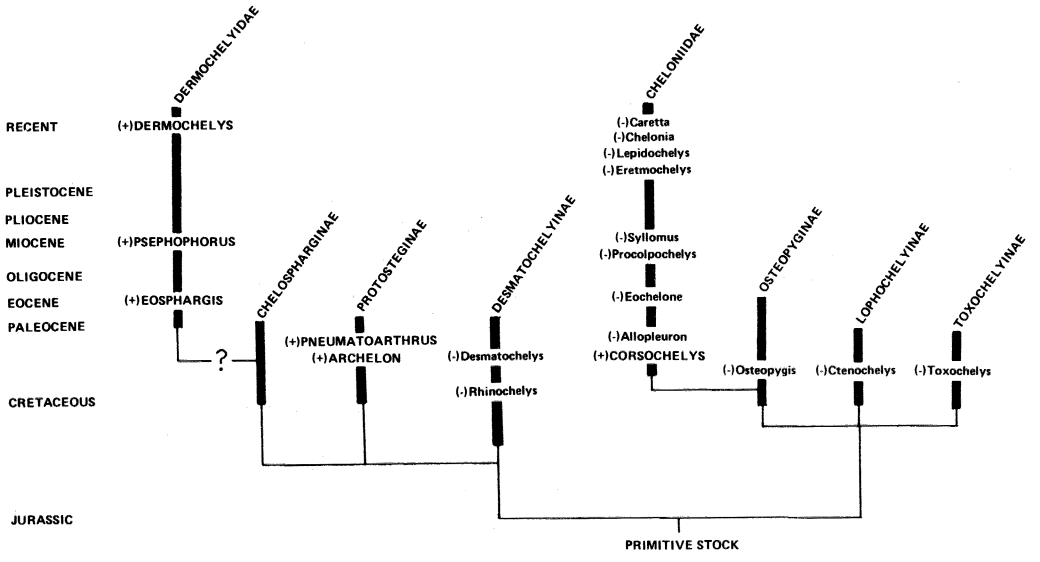

Fig. 13. Hypothetical phylogenetic relationships of marine turtles, following Pritchard, 1979. Refer also to Zangerl (1980) for alternate reconstruction. Genera marked with a (+) have vascularized chondroepiphyses, those with a (−) have avascular epiphyseal cartilages (see text for details).

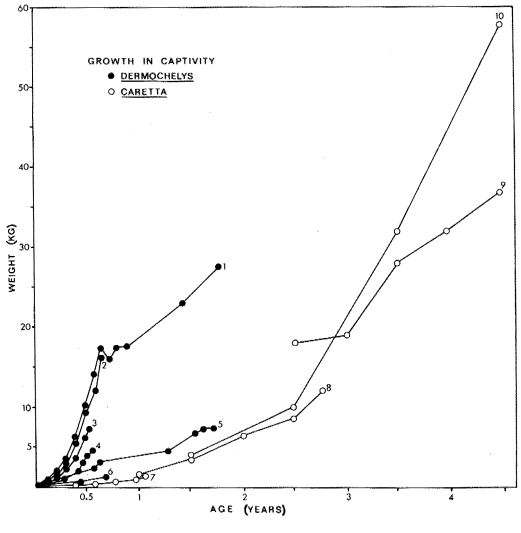

Fig. 14. Plot of known age in years vs body weight in kg of *Dermochelys coriacea* and *Caretta caretta* raised in captivity. Sharp decrease in curve no. 1 at about 8 months related to morbidity associated with skin lesion on head resulting eventually in septicemia and death. Data from: 1–3) Witham, 1977; 4) Birkenmeier, 1971; 5) Deraniyagala, 1936; 6) Phillips, 1977; 7) Witham and Futch, 1977; 8–9) Parker, 1929; and 10) Uchida, 1967. Data for *Caretta* also discussed and analyzed by Frazer (1982), who unfortunately misinterpreted Uchida's curve, shifting it 1.5 years further to the left on his graph than it should be. This error was apparently due to Frazer not noting that Uchida set his theoretical age of zero equal to an actual age of 1.5 years. As a result, Frazer's equations and calculations may need to be reworked.

loniid sea turtles (Fig. 14). From this graph it is clear that the leatherback initially grows at a much faster rate than the loggerhead. How does this early growth rate in captivity extrapolate to overall growth rate and age at sexual maturity? Very few data are available on length-weight relationships of leatherbacks, but if we plot a graph of the few actual measurements obtained over the years (Fig. 15), a relatively smooth curve results. There is an apparent point of inflection at sexual maturity, which occurs at a carapace length of about 135–140 cm and weight of about 250 kg (Pritchard, 1971; Fretey, 1978). The size of six-month-old captive-raised leatherbacks is indicated on the growth curve. Though the curve does not relate size to age other than for the six-month-old captive-raised animals, it appears possible from these data that sexual maturity might be obtained in a relatively short time. Unless growth slows considerably after the age of six months, I predict that the leatherback may reach sexual maturity in as little as two or three years. Such possibly

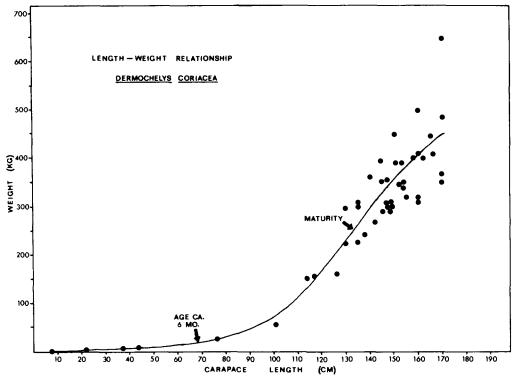

Fig. 15. Plot of carapace length in cm vs body weight in kg for *Dermochelys coriacea*. Data points represent only measured as opposed to estimated weights. Data from: Mitchill, 1812; Ford, 1879; Deraniyagala, 1936, 1939; Dunlap, 1955; Lowe and Norris, 1955; Ray and Coates, 1958; Bleakney, 1965; Pritchard, 1969, 1971; Hirth and Carr, 1970; Birkenmeier, 1971; Hughes, 1971; Brongersma, 1972; Phillips, 1977; Duguy and Duron, 1981; Duguy, 1983; and Ehrhart, pers. comm.

rapid growth in overall size is strongly supported by the observed histological evidence presented above of the extremely rapid growth of the leatherback's bone and cartilage. Also supporting this hypothesis is the observation that the humeral cross section of a 135 cm mature female appears to have two growth rings (see above and Fig. 10). Whether the growth rings in this young female represent annual cycles is not known. They may well be related to the cyclical migratory movements by leatherbacks into boreal waters (Lazell, 1980; Rhodin and Schoelkopf, 1982), just as similar growth rings in beluga whales represent migratory patterns in and out of boreal waters (Felts and Spurrell, 1965, 1966). It is possible that the narrow zone of slowed periosteal bone growth in the leatherback represents the period of maximal energy expenditure and minimal energy intake associated with the rapid migration from southerly to boreal waters, and that the wider zone of rapid periosteal bone growth represents the highly anabolic period of maximal energy intake as the leatherbacks slowly migrate southward while following and feeding on large accumulations of jellyfish. In larger mature females with prior nesting experience, cyclical patterns might also reflect decreased bone growth due to the energy requirements of the reproductive effort, including body mobilization of calcium for the production of eggshells (Edgren, 1960; Simkiss, 1962).

Despite these considerations, we are left without any definite evidence as to age at sexual maturity for the leatherback. However, two previous researchers have reached the same conclusion that *Dermochelys* apparently matures at an age of 2–3 yr (Deraniyagala, 1953; Birkenmeier, 1971). Both of these conclusions were based on captive growth, and caution must be exercised in extrapolating to free-living animals. Growth studies in loggerheads and green turtles demonstrate the discrepancy between captive and wild growth rates. Caldwell (1962) and Uchida (1967) predicted age at sexual maturity in captive *C. caretta* at 6–7 yr, whereas Mendonça (1981) predicted 10–15 yr in free-living animals, Zug et al. (1983) predicted 14–19 yr and Limpus (1979) concluded that maturity in natural populations was reached in about 30 yr. Similarly, some captive *C. mydas*

TABLE 1. POST-NATAL GROWTH RATES IN LARGE REPTILES.

Species	Hatchling weight	Weight at maturity	Age at maturity	Growth rate
Caretta caretta	22 gm	110,000 gm	if 6 yr	50 gm/d
Caretta caretta	22 gm	110,000 gm	if 10 yr	30 gm/d
Caretta caretta	22 gm	110,000 gm	if 15 yr	20 gm/d
Dermochelys coriacea	33 gm	250,000 gm	if 3 yr	228 gm/d
Dermochelys coriacea	33 gm	250,000 gm	if 6 yr	114 gm/d
Chelonia mydas				16 gm/d**
Geochelone elephantopus				47 gm/d*
Alligator mississippiensis				27 gm/d*
Alligator mississippiensis				36 gm/d**
Python reticulatus				18 gm/d*
Varanus komodoensis				12 gm/d***

* Data from Case (1978), ** Andrews (1982), and *** Auffenberg (1981).

have been found to mature in as little as 8–9 yr (Wood and Wood, 1980), whereas free-living animals apparently take much longer, with Limpus and Walter (1980) predicting 10–30 yr, and Balazs (1982) predicting 9–48 yr to reach sexual maturity.

Even if the 2–3 yr estimate for sexual maturity in the leatherback is incorrect by the same order of magnitude as the discrepancy between captive and free-living growth studies in other marine turtles, then we would still predict maturity for the leatherback within about six years. This is an incredibly short maturation period for an animal of such a large body size. In fact, if we compare the postnatal growth rates for various large reptiles (Table 1), we see that the leatherback exhibits by far the fastest growth, even if its age at maturity is six years rather than three. No other living reptile even comes close, and the growth rate of the leatherback is paralleled only by that of larger mammals (Case, 1978).

The histological investigations on chondro-osseous development presented in this paper support the hypothesis that the leatherback has developed the physiological mechanisms required to support incredibly rapid growth to a large body size. Confirmatory and elaborative studies of the associated life-cycle patterns now need to be pursued through appropriate ecological investigations, correlating known ages and life-cycle stages with observed chondro-osseous patterns. For example, growth rings need to be correlated with chronologic, migratory, and reproductive parameters, and skeletal changes associated with onset of sexual maturity need to be outlined. On a more basic level, the failure of formation of secondary ossification centers in the face of vascularized chondro-epiphyses needs to be investigated.

In summary, we have in the leatherback turtle a unique life form. Chelonian in derivation, reptilian in ancestry, it has reached a degree of biologic specialization unparalleled by other living turtles or reptiles, and appears to be converging on the biological regulatory mechanisms utilized by mammals. How far the similarities to mammals extend, and where the important differences lie, await future research.

Material examined.—Collection acronyms as follows: MCZ = Museum of Comparative Zoology, Harvard University; YOS = Yale Orthopaedic Surgery (to be accessioned to MCZ); YPM = Yale Peabody Museum; FMNH = Field Museum of Natural History; SDNHM = San Diego Natural History Museum. *Caretta caretta*: YOS C509, MCZ 1412, 13416, 156988, 157130; *Lepidochelys kempi*: MCZ Z08022; *Dermochelys coriacea*: YOS C414, MCZ 59030, 59033, 67781, SDNHM 49851, FMNH 190307; *Carettochelys insculpta*: MCZ 20964, 53770, 138103, 140905-6, 153916; *Geochelone elephantopus*: MCZ 29052; *Macroclemys temmincki*: MCZ 1420; *Podocnemis unifilis*: MCZ 4470; *Archelon ischyros*: YPM 2431, 2434, 2898; *Stupendemys geographicus*: MCZ 4376-8; *Rhinochelys pulchriceps*: MCZ 2435; other recent marine turtle species and non-marine genera: all from MCZ skeletal collection.

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On a personal note, I dedicate this paper to

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Renal and Extra-renal Mechanisms of Salt and Water Regulation of Sea Turtles: A Speculative Review

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Sea turtles can regulate levels of the majority of the solutes (the monovalent ions) in their body fluids via the secretions of the post-orbital salt glands. The concentration of these secretions can be twice that of sea water. In some cases, the osmotic concentration of the urine may be greater than that of the plasma but this concentration is probably more important for waste removal than for osmoregulation.

An examination of the salt and water regulation of sea turtles provides an opportunity to consider other more fundamental of our notions about vertebrate regulation and adaptation. (1) Although both marine and desert environments may be described as desiccating, the physiological adaptations required by these environments are completely different. (2) The inference from mammals that the kidney is the primary organ of osmoregulation is not supported in the cases of other vertebrate classes. (3) The capacity for accurate regulation of body water and solute levels does not necessarily imply that such homeostatic regulation occurs.

IT is not uncommon that the role of the comparative approach to physiology is to bring to light misconceptions in our understanding of animal function. These misunderstandings often arise from application of our concept of the adaptations of one animal or group of animals to a different group without sufficiently careful consideration of the particular abilities and limitations of the second group. I believe some aspects of the conventional wisdom regarding the adaptations for osmotic and ionic regulation of marine reptiles represent such a case.

It is my intent to review the means by which sea turtles control the salt and water content of their bodies with an eye towards three notions which I think are either incorrect or lead us to consider the phenomenon of such regulation incorrectly. These notions are (1) that the marine environment is similar to a desert in that water loss to a desiccating environment is the major physiological challenge in both; (2) that ionic and osmotic regulation is the primary role of the vertebrate kidney and (3) that the physiological capacity for accurate regulation implies the existence of precise regulation (homeostasis).

The information upon which this review is based comes from the literature on reptilian excretion and ionic and osmotic regulation which has been extensively reviewed by Bentley (1976), Dantzler (1976) and Dunson (1976) and from my own research, some of which is published here for the first time. It is not the purpose of this paper to duplicate the efforts of the above-named reviewers in the narrower context of sea turtles. Rather, I would like to use the information available on sea turtles to address the means by which we can understand more thoroughly "how animals work."

The nature of the marine environment.—Is the sea a desert? For humans, the ocean may seem to be a desert: "Water, water, every where, Nor any drop to drink" (Coleridge). It is without