

Age Determination of Loggerhead  
Sea Turtles, *Caretta caretta*,  
by Incremental Growth  
Marks in the Skeleton

GEORGE R. ZUG, ADDISON H. WYNN,  
and CAROL RUCKDESCHEL

## SERIES PUBLICATIONS OF THE SMITHSONIAN INSTITUTION

Emphasis upon publication as a means of "diffusing knowledge" was expressed by the first Secretary of the Smithsonian. In his formal plan for the Institution, Joseph Henry outlined a program that included the following statement: "It is proposed to publish a series of reports, giving an account of the new discoveries in science, and of the changes made from year to year in all branches of knowledge." This theme of basic research has been adhered to through the years by thousands of titles issued in series publications under the Smithsonian imprint, commencing with *Smithsonian Contributions to Knowledge* in 1848 and continuing with the following active series:

*Smithsonian Contributions to Anthropology*  
*Smithsonian Contributions to Astrophysics*  
*Smithsonian Contributions to Botany*  
*Smithsonian Contributions to the Earth Sciences*  
*Smithsonian Contributions to the Marine Sciences*  
*Smithsonian Contributions to Paleobiology*  
*Smithsonian Contributions to Zoology*  
*Smithsonian Folklife Studies*  
*Smithsonian Studies in Air and Space*  
*Smithsonian Studies in History and Technology*

In these series, the Institution publishes small papers and full-scale monographs that report the research and collections of its various museums and bureaux or of professional colleagues in the world of science and scholarship. The publications are distributed by mailing lists to libraries, universities, and similar institutions throughout the world.

Papers or monographs submitted for series publication are received by the Smithsonian Institution Press, subject to its own review for format and style, only through departments of the various Smithsonian museums or bureaux, where the manuscripts are given substantive review. Press requirements for manuscript and art preparation are outlined on the inside back cover.

Robert McC. Adams  
*Secretary*  
Smithsonian Institution

SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY • NUMBER 427

Age Determination of Loggerhead  
Sea Turtles, *Caretta caretta*,  
by Incremental Growth  
Marks in the Skeleton

*George R. Zug, Addison H. Wynn,  
and Carol Ruckdeschel*



SMITHSONIAN INSTITUTION PRESS

City of Washington

1986

## ABSTRACT

Zug, George R., Addison H. Wynn, and Carol Ruckdeschel. Age Determination of Loggerhead Sea Turtles, *Caretta caretta*, by Incremental Growth Marks in the Skeleton. *Smithsonian Contributions to Zoology*, number 427, 34 pages, 9 figures, 6 tables, 1 appendix, 1986.—Periosteal growth in the skeleton of *Caretta caretta* is cyclic and produces a record of distinct bony layers (growth marks). These layers are most apparent in the long bones, particularly the humerus and femur. Correlative evidence supports the production of one layer (i.e., growth increment) each year in some reptiles, and the annual nature of each bony layer is an explicit assumption in our estimation of ages of *Caretta* from Cumberland Island, Georgia. Sections from the shafts of humeri were prepared with standard histological techniques, and the marks of skeletal growth were counted and measured. Owing to resorption of the early periosteal layers, determination of number of growth marks and, hence, age requires an extrapolation from the remaining marks to total growth marks produced during the life of the turtle. Various age estimates are possible; the most reliable are derived from the narrowest axis of the humerus sections and suggest that, on the average, Georgia *Caretta* attain sexual maturity in their thirteenth to fifteenth years, with some individuals possibly maturing as early as six years and others as late as their twenty-fifth year. Since the average age of maturity agrees with the results of a mark-recapture study in a neighboring Florida population, the value of the skeletochronological technique and its assumptions are confirmed. The technique is not advocated as a method for the age determination of individual sea turtles, but does provide statistical age estimates for different size classes of turtles.

OFFICIAL PUBLICATION DATE is handstamped in a limited number of initial copies and is recorded in the Institution's annual report, *Smithsonian Year*. SERIES COVER DESIGN: The coral *Montastrea cavernosa* Linnaeus.

---

Library of Congress Cataloging in Publication Data

Zug, George R., Addison H. Wynn, and Carol Ruckdeschel

Age determination of loggerhead sea turtles, *Caretta caretta*, by incremental growth marks in the skeleton

(Smithsonian contributions to zoology ; no. 427)

Bibliography: p.

Supt. of Docs. no. : SI 1.27:427

1. Loggerhead turtle—Age determination. 2. Skeleton—Growth. 3. Reptiles—Age determination. I. Wynn, Addison H., 1955- . II. Ruckdeschel, Carol. III. Title. IV. Series. QL1.S54 no. 427 591s [597.92] 85-600229 [QL666.C536]

# Contents

|   | <i>Page</i> |
|---|-------------|
| Introduction . . . . .                      | 1           |
| Acknowledgments . . . . .                   | 2           |
| Materials, Methods, and Rationale . . . . . | 3           |
| Turtles . . . . .                           | 3           |
| Selection of Bone . . . . .                 | 3           |
| Preparation of Bone . . . . .               | 3           |
| Measurements and Counts . . . . .           | 4           |
| Anatomy of the Humerus . . . . .            | 5           |
| Gross Morphology . . . . .                  | 5           |
| Morphometrics . . . . .                     | 8           |
| Tissue Organization . . . . .               | 9           |
| Estimation of Age . . . . .                 | 10          |
| Assumptions and Difficulties . . . . .      | 10          |
| Data Analysis . . . . .                     | 13          |
| Life History Implications . . . . .         | 18          |
| Summary . . . . .                           | 22          |
| Appendix . . . . .                          | 24          |
| Literature Cited . . . . .                  | 31          |

**Dedicated to the memory of Chuck Ossola, a friend and outstanding scientific administrator. Chuck served as executive officer for the National Museum of Natural History from 1977 to 1982.**

# Age Determination of Loggerhead Sea Turtles, *Caretta caretta*, by Incremental Growth Marks in the Skeleton

*George R. Zug, Addison H. Wynn,  
and Carol Ruckdeschel*

## Introduction

The "lost year" of sea turtles is much discussed. Upon entering the sea, what happens to the tiny hatchling sea turtles until they are seen again as half-grown juveniles? Where do they go, what do they do, and, most importantly, for how long are they absent? The intense and voluminous research efforts of the last decade and a half have slowly begun to answer these questions and have revealed many unanticipated and fascinating features of sea turtle biology, behavior, and ecology.

Of particular interest to us are growth rates, age at sexual maturity, and other aspects of aging. These aspects are critical in the development of demographic profiles for the different sea turtle species and populations, hence their conservation and management. Mark and recapture studies, such as those of Balazs (1980), Limpus and Walter (1980), and Mendonca (1981), are the ideal means for obtaining the most accurate age determinations. Such studies are, however,

labor intensive, time demanding in the short and long term, and frequently logistically difficult and expensive. Captive-rearing, as done by Witham and Futch (1977) and Wood and Wood (1980), is similarly costly in time, labor, and equipment. Furthermore, captive rearing gives unnatural results, because these turtles grow faster and reach maturity sooner than wild ones (Balazs, 1979).

The research activities of the Université de Paris "Equipe de Recherche 'Formation squelettiques'" and particularly the investigations of Castanet into skeletochronology suggested an alternative approach that might convert the numerous strandings of dead sea turtles into potentially valuable research specimens. They (Castanet et al., 1970; Castanet, Meunier, and Ricqlès, 1977) provided a convincing argument that ectothermic vertebrates possess cyclic bone growth and that the cycles are annual. Other authors have offered varied opinions upon annual cyclic growth of bone in turtles. Mattox (1936) was the first to recognize the potential of bone growth rings or marks as a means of aging turtles; he noted that, in *Chrysemys picta*, smaller/younger turtles had fewer rings than did larger/older turtles. Peabody (1961) was a strong advocate of

---

*George R. Zug and Addison H. Wynn, Department of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560. Carol Ruckdeschel, The Settlement, Cumberland Island, P.O. Box 796, St. Marys, GA 31558.*

age determination through the use of these bony growth rings and he assumed, although he never tested, the annual nature of the rings. He observed these growth marks in *Chelydra serpentina*, but provided no estimate of age. Suzuki (1963) studied osteogenesis in *Trachemys scripta elegans*. He accepted the presence of annual growth layers in the long bones; however, he adamantly rejected the use of these growth marks for age determination owing to the extensive resorption and remodeling that occurs throughout growth. In contrast, Hammer (1969) suggested the use of the bony rings for aging, since he found a high correlation ( $r = 0.94$ ) of number of rings to carapace length. Dobie (1971) found no such correlation in *Macrochelys temminckii*. He examined sections of vertebrae and mandibles, whereas Hammer used a variety of skeletal material, but found the growth marks most evident in long bones of *Chelydra*. Castanet and Cheylan (1979) found concordance between the number of rings and the known age of a *Testudo hermanni* and high correlations ( $r = 0.89$ ) for ring number and carapace length (also scute annuli) in *T. graeca* and *T. hermanni*. Hohn and Frazier (1979) also noted a positive relationship between number of bone layers and carapace length in several species of sea turtles. Castanet (1982) proposed that skeletochronology was promising for most turtles with the exception of sea turtles owing to the extensive remodeling in their long bones.

A number of amphibian and reptile species match age in years with number of bony growth layers. Hemelaar and van Gelder (1980) found that more than 90% of toads (*Bufo bufo*) recaptured showed an increase in number of marks of skeletal growth (MSGs) equal to the difference in years between capture and recapture. This concordance in a wild population is one of the strongest confirmations for the annual production of one growth layer in ectothermic tetrapods. Several studies by the Université de Paris research group (Castanet, Cheylan, de Buffrenil, Gasc, Meunier, Naulleau, and Pilorge) confirm the one-layer/one-year hypothesis. De Buffrenil (1980) showed that a 4-yr-old captive *Crocodylus*

*siamensis* possessed three complete growth layers and was forming a fourth one at the time of its death. Castanet and Naulleau (1974) found that only 10% of their *Vipera aspis* born in captivity and raised under constant conditions match age and number of growth layers; in contrast, captive vipers exposed to seasonal conditions produced one growth layer per year. Pilorge and Castanet (1981, table 2) demonstrated complete agreement between actual age and number of growth layers. Minakami (1979) demonstrated that the growth period (deposition of a single zone) of *Trimeresurus okinavensis* occurred from June to September. His results derive from in vivo staining of snakes maintained in the laboratory. Similarly, Castanet (1982) showed with fluorescent labelling that one layer was deposited each year in *Lacerta viridis*. Studies of *Iguana iguana* (Zug, Rand, Wynn, and Bock, 1983) revealed that the number of growth layers closely match the known age of marked and recaptured animals.

Although numerous studies in turtles have confirmed the concordance of epidermal scute annuli with age in years, there is only one study with turtles of known ages that confirms the concordance of bone layer number with age in years. Castanet (1982) raised *Emys orbicularis* in seminatural conditions and with fluorescent labelling showed a one-to-one relationship between number of bone layers and years. Castanet and Cheylan (1979) demonstrated a concordance of epidermal scute annulus number with bony growth layers in *Testudo graeca* and *T. hermanni*; they also demonstrated a high positive correlation of skeletochronological age estimates and carapace length. Others (e.g., Hammer, 1969) have also observed a high correlation between carapace length and age estimates. The data confirming the production of one bone layer each year is largely circumstantial, but convincing. Herein, we summarize our successes and failures for age determination in the loggerhead sea turtle through the use of skeletochronology.

ACKNOWLEDGMENTS.—This research project had its beginning in a series of coincidences largely linked through Charles W. Potter.



Shortly after G. Zug had read Castanet, Meunier, and Ricqlès (1977), C. Potter introduced him to Aleta Hohn and her spinner dolphin aging research. Then after some tentative histological preparations of sea turtle bone proved successful, C. Potter introduced G. Zug to C. Ruckdeschel, thereby permitting the collection (Endangered Species Permit: PRT 2-2381) and eventual examination of a large, yet geographically restricted sample of sea turtles. C. Potter has our thanks for providing the initial linkage and stimulation for the research reported herein. The initial histological preparations were made by Margaret M. Barber; however, the histology for the research sample derives entirely from the skilled hands of Helen F. Wimer. Discussions on skeletochronology with Jack Frazier encouraged our research in the early stages. Nat Frazer and Terry Henwood most generously shared with us their current ideas and research data on *Caretta* growth and age determination.

The manuscript has benefitted by the reviews of Jacques Castanet, C. Kenneth Dodd, Jr., Nat B. Frazer, J. Whitfield Gibbons, Tyrell A. Henwood, W. Ronald Heyer, Peter C.H. Pritchard, and Anders G.J. Rhodin. We appreciate their valuable advice, but remain totally responsible for the interpretations of the data.

This project was supported by the Smithsonian's Fluid Research Fund, NMNH Director's Fund, and the Department of Vertebrate Zoology. Without their support, this research would have been impossible.

### Materials, Methods, and Rationale

**TURTLES.**—During 1979 and 1980, C.R. measured and collected a skeletal voucher specimen from each sea turtle stranded on the oceanic beach of Cumberland Island, Camden County, Georgia. A total of 187 *Caretta caretta* were stranded in 1979 (Ruckdeschel and Zug, 1980) and 222 in 1980 (Ruckdeschel and Zug, 1981). The preferred skeletal voucher was the complete cranial and right forelimb skeletons for each specimen. Many specimens, however, lacked ap-

pendages, head, or some combination thereof owing to butchery by original captors, sharks, or beachcombing souvenir hunters. Thus, our research samples are less than the total number of stranded turtles. The humeral morphometric set consists of 137 humeri, and the histological (age determination) set represents 119 humeri, in 81 of which MSGs could be measured. These sets derive almost entirely from the 1979 strandings.

**SELECTION OF BONE.**—Growth increments (= layers or marks) are observed most consistently in the long bones of turtles (see, e.g., Mattox, 1936; Hammer, 1969). Our preliminary histological examination included a third peripheral bone from the carapace, the dentary (a section adjacent to the symphysis and one in the middle of the ramus), a centrum of a cervical vertebrae, a penultimate phalanx of forefoot, an ulna, and a humerus. Regular periosteal layers were evident in the ulna and humerus. In the dentary, growth layers were present, but owing to the spongy nature of this bone, the layers were too irregularly arranged to permit accurate and repeatable counts and measurements. The peripheral bone, centrum, and phalanx showed no discernible pattern of incremental growth of periosteal bone, and the ulna possessed only a weak pattern. Growth marks were clearly evident in the shaft of the humerus and, thus, the humerus was selected for further examination. The femur also shows a strong pattern of incremental periosteal growth (Frazier, 1982) and is likely as well suited for age estimation in sea turtles as the humerus.

**PREPARATION OF BONE.**—The entire forelimb, usually the right, was removed, macerated in water, washed, and air-dried. Prior to sectioning, each humerus was weighed and measured (measurements are described in the following section). A transverse section of bone approximately 5–7 mm thick was cut with a bandsaw from the humerus just distal to the deltopectoral ridge. The section was stored in a 4% formalin solution for at least 24 hrs prior to decalcification.

Histological preparation began with decalcification. Several decalcification solutions were

tried. RDO (a commercial decalcification solution) was fast and effective; however, its speed and the unequal thickness of our bone sections resulted in over-decalcification. A formic-citric acid solution was very slow and resulted in uneven decalcification. A solution of equal parts of 8% formic acid and 8% hydrochloric acid gave good results. Decalcification in the formic-hydrochloric acid solution required 4–8 days, depending upon the thickness of the bone and its porosity. Complete decalcification was determined by X-ray.

The decalcified bone was rinsed in tap water and processed in a Fisher Histomatic Tissue Processor as follows: (1) 95% ethanol for 24 hrs, three changes of alcohol, the last 12 hrs under a vacuum; (2) 100% ethanol for 30 hrs, four changes of alcohol, the last 18 hrs under a vacuum; (3) xylene for 12 hrs, three changes of xylene, all under a vacuum; (4) paraffin (paraplast) for 6 hrs, two changes, both under a vacuum. The paraffin-impregnated bone was mounted in a block of paraffin and transversely sectioned (6  $\mu$ m) on a standard microtome. The bone was periodically soaked with water (cut surface of block covered with dripping wet gauze pad) to obtain the best results during sectioning. All sections were stained with Harris hematoxylin and eosin and normally differentiated.

**MEASUREMENTS AND COUNTS.**—When a dead sea turtle washed ashore on Cumberland Island, a series of shell and soft part measurements was collected. Only one measurement is reported here: curved carapace length (cCL), the midline distance from anterior edge of cervical scute to tips of thirteenth marginal scutes measured over the curve. Over-the-curve measurements are potentially more accurate for bloated carcasses than straight-line measurements (e.g., sCL), owing to shape changes; the measurement error increases in both types as maceration and gaseous swelling begin to separate the articular surfaces within the shell of stranded sea turtles. In spite of the potential error, these shell measurements can serve as size class designators for comparison with

the nesting female loggerhead population of the Georgia coastal islands and with populations of marked-and-recaptured loggerheads from other areas.

Prior to removal of the bone section, a series of 12 straight-line distance measurements was recorded from each humerus, as well as its air dried weight. The measurements are: (1) maximum length (ML), distance from proximal-most tip of ulnar process to distal articular surface; (2) longitudinal length (LL), distance from proximal surface of head to distal articular surface, parallel to longitudinal axis of humerus; (3) ulnar process length (UPL), distance from proximal tip of ulnar process to juncture of head and process; (4) proximal length (PL), distance from proximal surface of head to distal edge of radial process, parallel to longitudinal axis; (5) proximal width (PW), distance from preaxial surface of head to postaxial surface of ulnar process, perpendicular to longitudinal axis; (6) radial process length (RPL), distance from pre- to postaxial edges of process, diagonal to longitudinal axis; (7) width at deltopectoral crest (DpCW), transverse distance of shaft from pre- to postaxial surfaces at deltopectoral crest; (8) medial width (MW), transverse distance from pre- to postaxial surfaces at point of minimum width; (9) distal width (DW), transverse distance from pre- to postaxial surfaces at juncture of articular condyles with shaft; (10) maximum head diameter (MaxHD); (11) minimum head diameter (MinHD); (12) thickness (T), minimum depth in middle of shaft, approximately in vicinity of MW, perpendicular to longitudinal and transverse axes.

The histological sections were measured grossly and microscopically. The length and width of bone sections were measured with a caliper to 0.1 mm. The periosteal layers were measured to 1.0  $\mu$ m with a Wild micrometer and counted at 60  $\times$  magnification on a transmitted light microscope. The counts and measurements of the layers were made along two perpendicular axes, the long (pre-postaxial) and short (dorso-ventral) axes, of the bone section.

**Anatomy of the Humerus**

**GROSS MORPHOLOGY.**—The humerus of the sea turtles (Cheloniidae and Dermochelyidae) differs from that of all other extant turtles in several respects. Presumably, the differences are related to a structural reorganization of the forelimb for aquatic flight. The sea-turtle humerus,

specifically that of *Caretta caretta* (Figure 1), is flattened in cross-section as well as in the proximodistal plane. Cross-sections through most regions of the diaphysis (shaft) have elliptical outlines. The head lies at an approximately 45° angle from the diaphysis in contrast to the nearly perpendicular orientation in other turtles. The articular surface retains the 180° arc, thereby

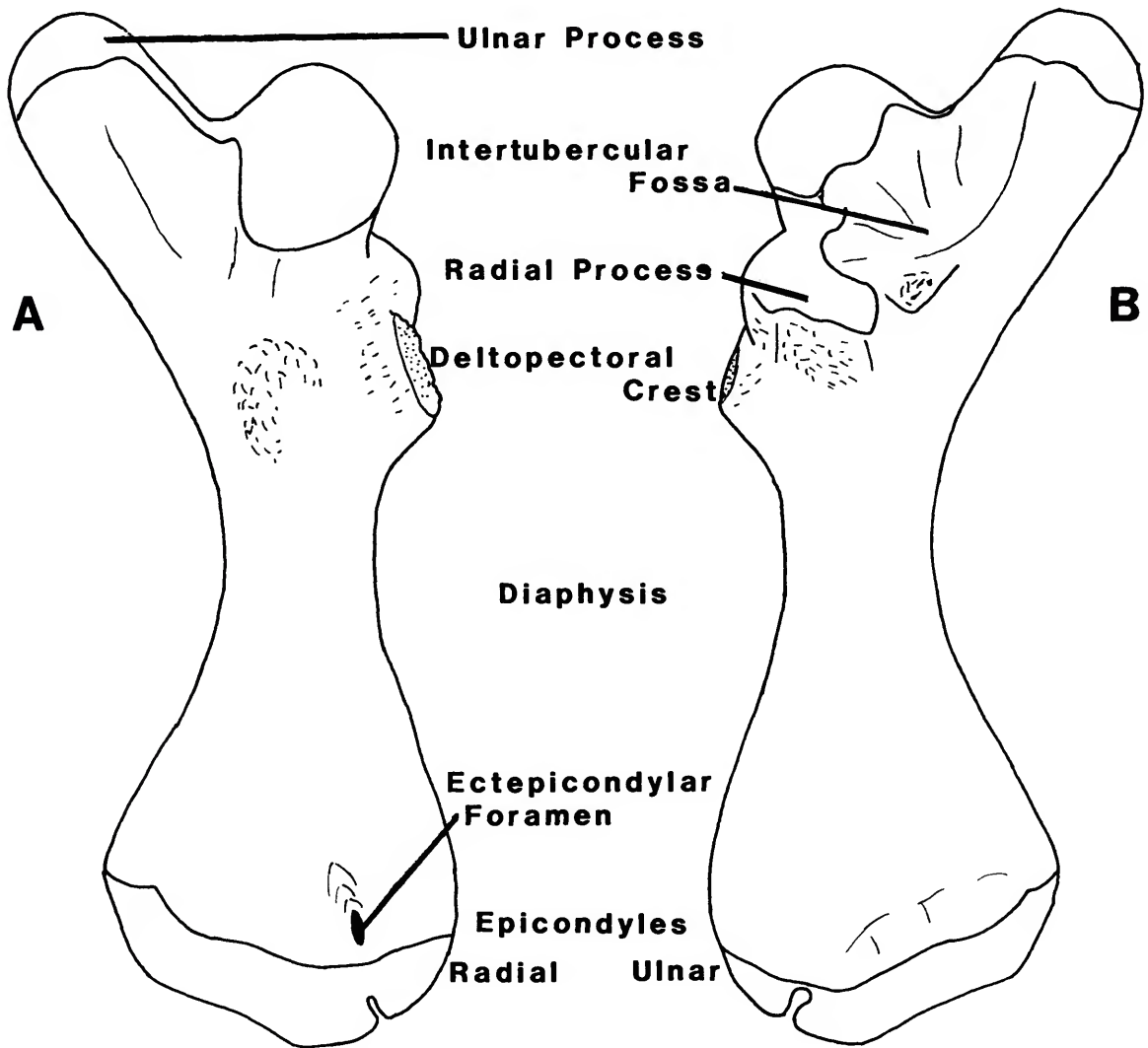


FIGURE 1.—Entire right humerus: A, dorsal view; B, ventral view.

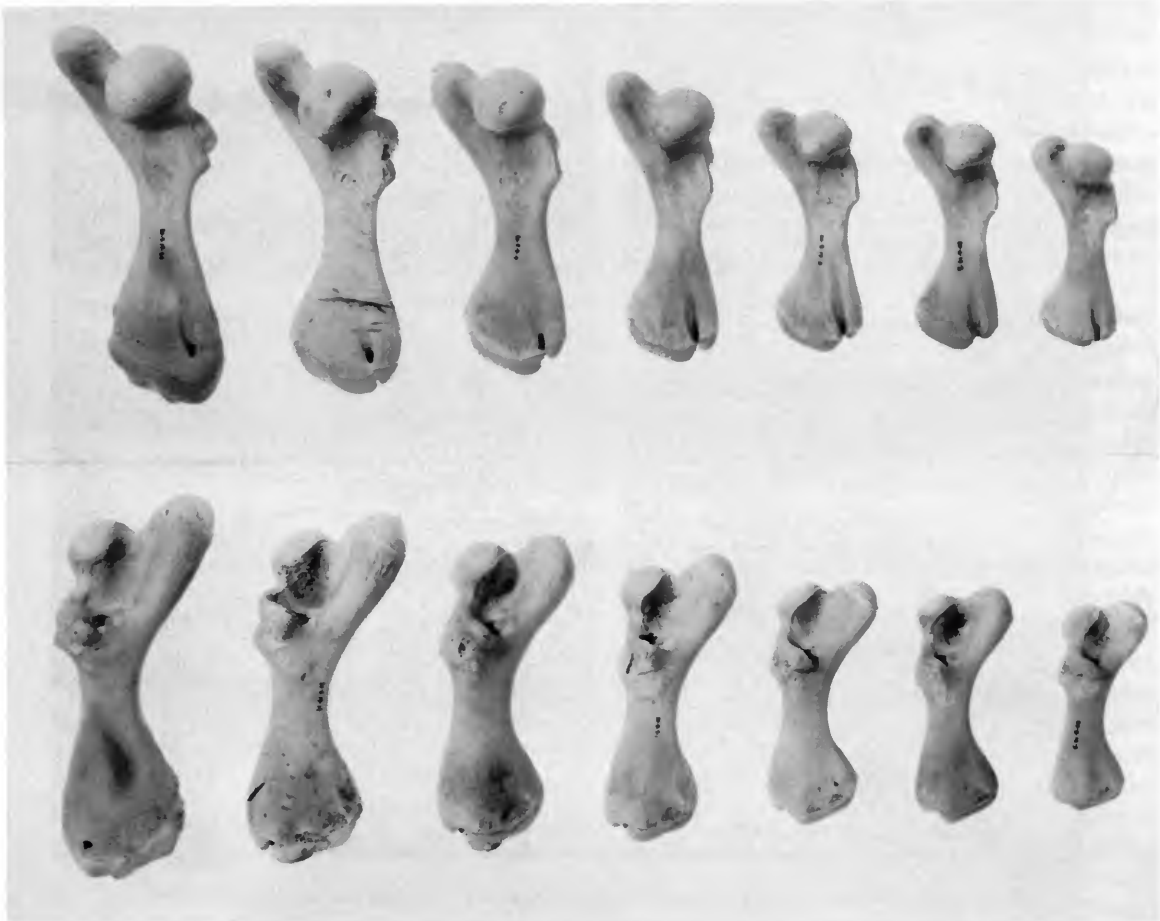


FIGURE 2.—Growth series of humeri showing the closure of the ectepicondylar foramen through growth. Curved carapace lengths of specimens (left to right): 995, 965, 890, 815, 720, 660, and 590 mm.

giving the articulation a limited ventral aspect as well as medial and dorsal ones. In general appearance, the articular surface is egg-shaped, with the blunter end ventral and the long axis dorsoventral. The anterior articular shoulder or flange, so characteristic of the humeral head of other turtles, is absent; there is no hint of its former presence. The ulnar (medial) process (or tuberosity) is narrow and elongate, extending posteromedial at approximately a  $25^\circ$  angle from the shaft; the medial tip of the process is strongly proximal to the humeral head. The

radial (or lateral) process lies distal to the head and ventrally on the preaxial edge of the diaphysis. The radial process is often stated (Romer, 1956:355) to have shifted distally on the shaft, yet a comparison of its position and its orientation in other turtles suggests that the change in head orientation and the elongation of the ulnar process result in a change in the radial process's relative, but not actual position on the shaft. Another process arises on the preaxial border contiguously with the radial process. This process is suitably called the deltopectoral crest owing to

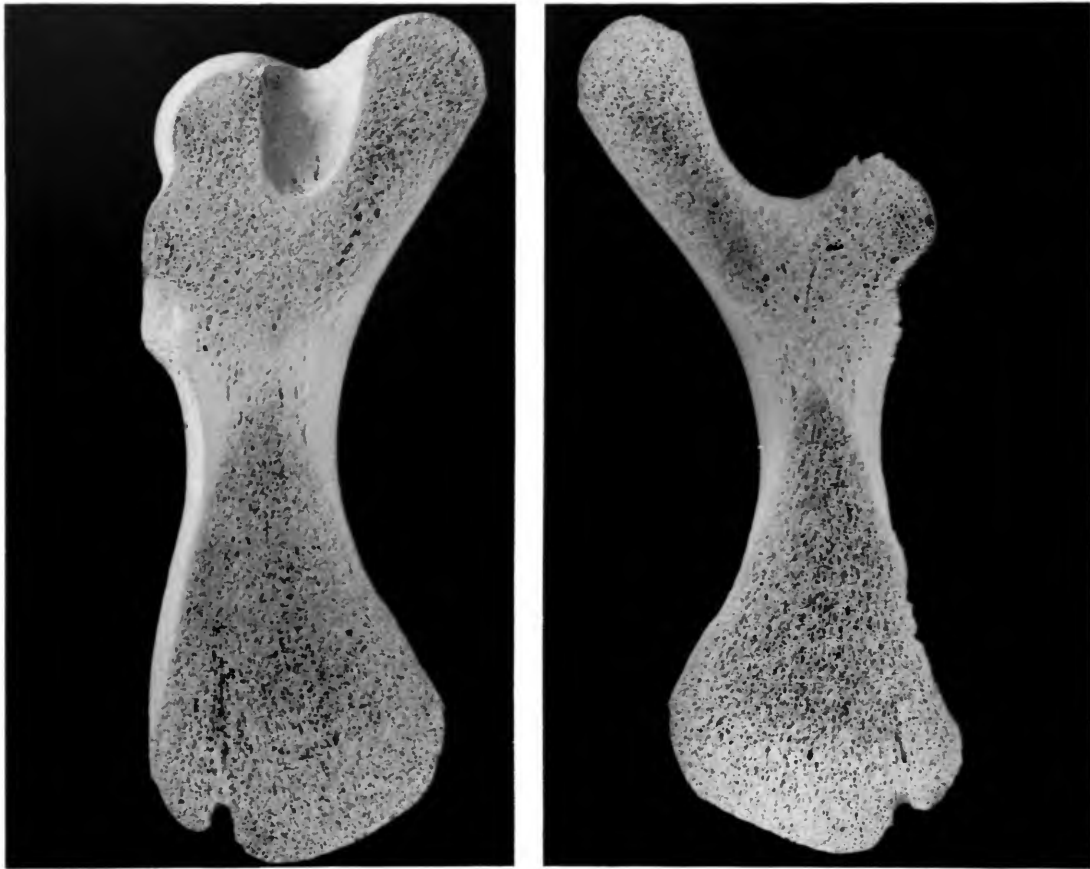


FIGURE 3.—Frontal section of the humerus: dorsal half on left, ventral half on right; 660 mm cCL.

its location in the center of the insertions of the deltoid and pectoral muscles; however, this name is used by others, such as Romer (1956), as a synonym of the radial or medial process. In sea turtles, they are clearly two distinct processes and shall be so treated in the subsequent discussion.

Immediately distal to these two processes, the diaphysis narrows and then gradually widens (along the pre-postaxial axis) distally toward the epicondyles. The epicondylar surface is smooth with only a slight medial concavity to separate the radial and ulnar epicondyles. The radial epicondyle is notched in subadults and juveniles by the ectepicondylar groove. The groove gradually closes with age as the epicondylar area grows

beyond and around the radial nerve and blood vessels (Figure 2).

Externally, the humerus bears a smooth, dense bony surface except for the articular surfaces and a few of the major muscle insertions. The humeral head, the ulnar, radial and deltopectoral processes, and the epicondyles possess smooth porous surfaces. The head region of the inter-tubercular fossa, the region between the radial and deltopectoral process, and the dorsal surface of the diaphysis adjacent to the head are commonly rugose; other regions develop ridges or rugosities in larger (presumably older) turtles. Internally (Figures 3 and 4), the humerus consists of a narrow shell of dense compact bone and a

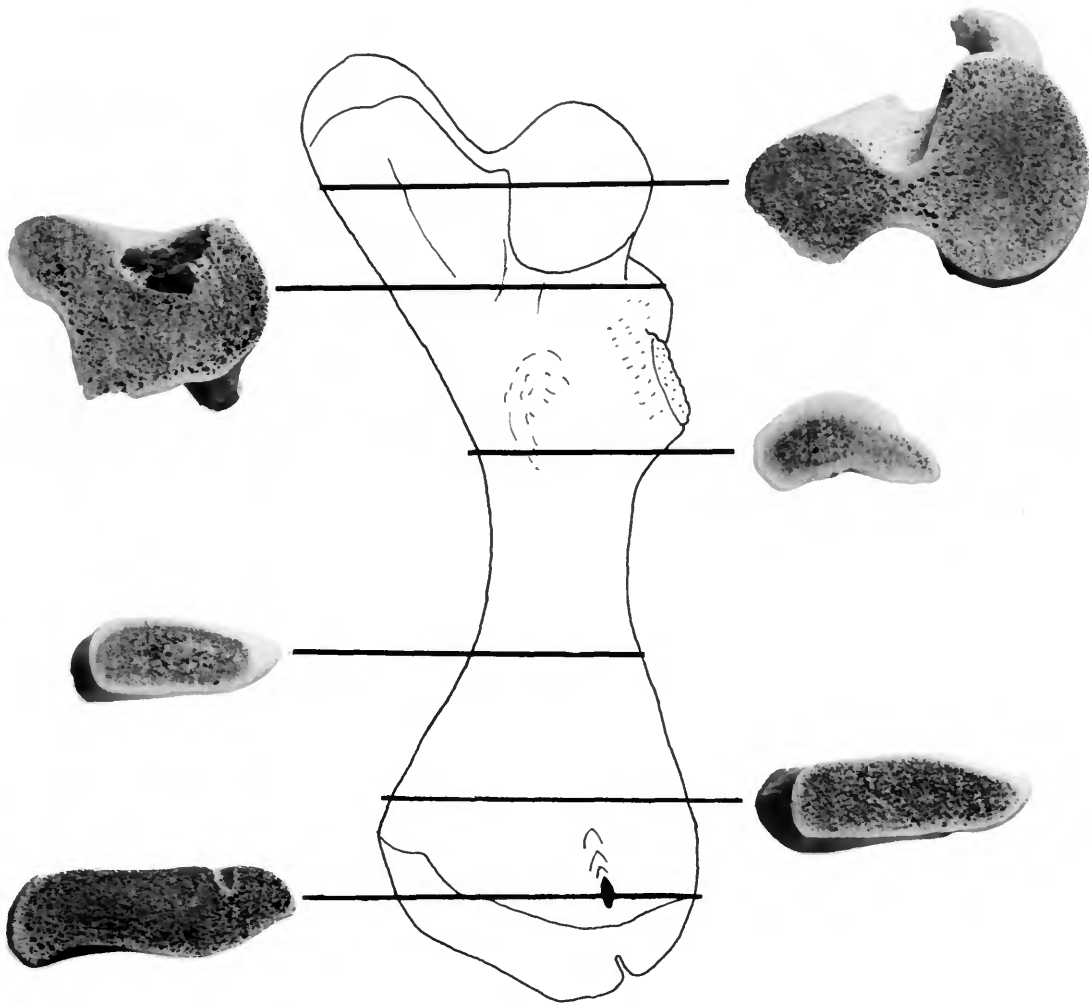


FIGURE 4.—Representative cross-sections of the humerus. The photographs show the proximal surface of each section, except for the distal-most section, which shows the distal surface.

core of spongy cancellous bone. The dense bone contains the periosteal growth layers; the spongy bone is the endosteal, remodeled periosteal, and perhaps endochondral bone. There is no marrow cavity, although the center of the bone is more porous owing to the concentration of blood vessels.

**MORPHOMETRICS.**—The change of the ectepicondylar groove to a foramen suggests differential or asymmetrical growth of the humerus.

Comparison of a hatchling's (48 mm cCL) humerus with that of a juvenile (565 mm cCL) does show proportional changes in humerus shape (Figure 5). The present sample permits an examination of shape changes from half grown juveniles (560 mm cCL) to reproductively active adults (>900 mm cCL); however, the sample does not permit segregation by sex. We examine only a subset ( $N = 80$ ) of the data to address the relative growth of humerus length to body length

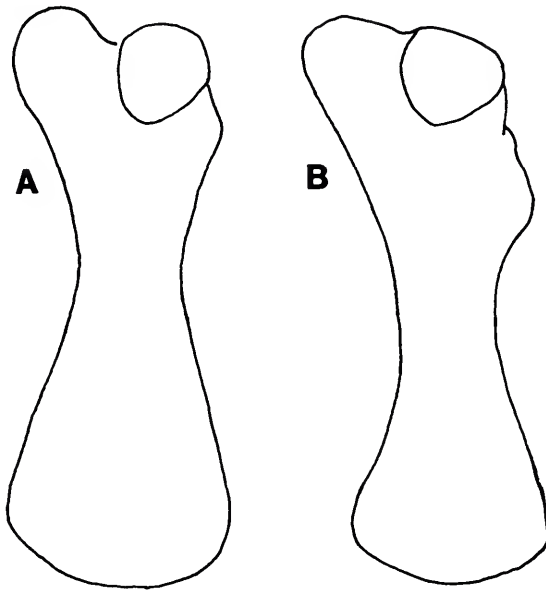


FIGURE 5.—Comparison of humerus shape in a hatchling (A; cCL = 48 mm), and an old juvenile (B; cCL = 565 mm).

and differential longitudinal growth of the humerus and some of its processes (Figure 6).

Not surprisingly, both measures of humeral length—maximum (ML) and longitudinal length (LL)—are strongly correlated to carapace length (cCL); for example, the correlation coefficient of LL/cCL is 0.98 ( $LL = -13.25 + 0.2033 \text{ cCL}$ ). Similarly, other humeral measurements are strongly correlated with carapace and humeral length. The two length measurements possess a nearly isometric growth pattern ( $ML = -6.97 + 1.1077 \text{ LL}$ ;  $r = 0.996$ ). The regression slope is greater than 1.0, however, and suggests that the ulnar process grows slightly faster than the major axis of the humerus (i.e., the ulnar process length is contained within the ML measurement, but not within the LL measurement). The ulnar process (UPL) grows faster than the radial process (RPL), as demonstrated by a UPL/LL slope of 0.24 and a RPL/LL slope of 0.19. Although the differences in growth rate are slight, they tend to confirm the production of the peculiar configuration of the proximal end of the sea

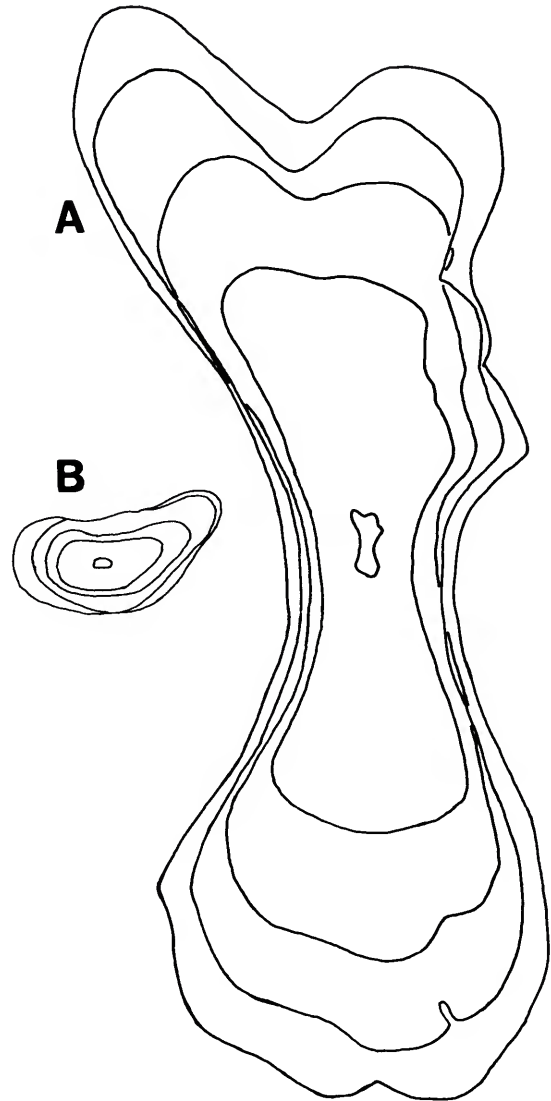


FIGURE 6.—Growth changes in humerus: A, whole bone; B, cross-section through the middle of diaphysis. The lines represent outlines from actual specimens.

turtle humerus through differential growth of the processes.

**TISSUE ORGANIZATION.**—The following description is based on bone that has been macerated, air dried, and hydrated in formalin prior to histological preparation; thus, only the min-

eralized framework of the bone remains. Further, the description is based entirely on transverse sections through the diaphysis immediately distal to the deltopectoral crest, and of individuals with cCL greater than 55 cm.

The cortex and medulla are composed of cellular, vascular bone (terminology from Enlow, 1969). Both the cortex and medulla are formed by periosteal deposition. The layers are distinct in the cortex, but strongly modified in the medulla by enlargement of the blood vessels through resorption and endosteal layering of these vascular canals. The layers appear to consist entirely of non-lamellar (parallel-fibered) bone. The remodeling of the vascular canals in the cortex results in one to several layers of endosteal bone on the wall of the canal; however, we are reluctant to label the resulting structure as secondary osteones (Haversian systems), owing to the irregular spacing of the osteocyte lacunae. The endosteal layers appear to be non-lamellar bone.

The bony layers of the cortex are the growth layers used in skeletochronology. Each growth layer consists of a light-staining area and dark-staining area. The light area represents an area of rapid growth, the dark area slow or no growth. Together, an adjacent light and a dark area represent one complete cycle of growth; hence their pivotal importance in skeletochronology. Castanet (1982; Castanet and Naulleau, 1974; Castanet and Cheylan, 1979) has established a formal terminology for the layers and their subunits; his terminology is used here and translated into English where necessary. Each growth layer is called a mark of skeletal growth (MSG; = MSC of Castanet) and consists of a zone (broad, light-staining region) and a line of arrested growth (LAG; = LAC of Castanet; narrow, dark-staining region).

### Estimation of Age

**ASSUMPTIONS AND DIFFICULTIES.**—Our primary assumption is that each MSG represents one year of growth. Tests of this assumption/

hypothesis have produced conflicting conclusions, i.e., both for confirmation and falsification. Our results favor the acceptance of this hypothesis, although, as we noted earlier in the introduction, some authors (e.g., Dobie, 1971), reject this hypothesis. Hohn and Frazier (1979) recognized the presence of growth layers (MSGs) in *Eretmochelys* and the positive correlation of MSG number to shell size. To test this correlation further, Frazier (1982) examined sections of humeri and femora in five species of sea turtles. His conclusions were that (1) bone sections of *Dermochelys* and *Lepidochelys* are difficult to interpret and other sea turtles, particularly *Eretmochelys*, have readable growth layers; (2) the interpretation of growth layers in sea turtle bones is not simple, owing to endosteal resorption, unequal lamellar accretion rates, and variable visibility and routes of arrested growth lines (LAGs); (3) width of adjacent MSGs shows no predictable relationship; and (4) known-aged *Chelonia mydas* (14 mo, 18 mo, and 42 mo old turtles) from Cayman Turtle Farm, Ltd. often possess more growth layers than their age in years, but fewer layers than their age in months. Thus, Frazier's results suggest a falsification of the one-MSG/one-year hypothesis and his remarks (1982) echo those of Suzuki (1963) and Dobie (1971) in largely dismissing bone layers for age determination.

Our study of *Caretta* humeri reveals the same difficulties in MSG recognition and other ones as well; however, recognition of distinct MSGs is possible in the majority of specimens. Within *Caretta*, the major problem areas are as follows:

- Resorption and redeposition. Loss of MSGs, usually the earlier ones; appearance of endosteal layers.
- Accessory LAGs. The occasional presence of duplicate arrested growth lines (Figure 7B).
- Absence of LAGs. Bone with homogeneous appearance, no apparent layering (Figure 7C).
- Discontinuous LAGs. Arrested growth lines that do not completely encircle the circumference of the bone or lines which converge and cannot be differentiated (Figure 7D).
- Irregular MSGs and LAGs. Occurrence of adjacent MSGs of strikingly different thickness and/or wavy or



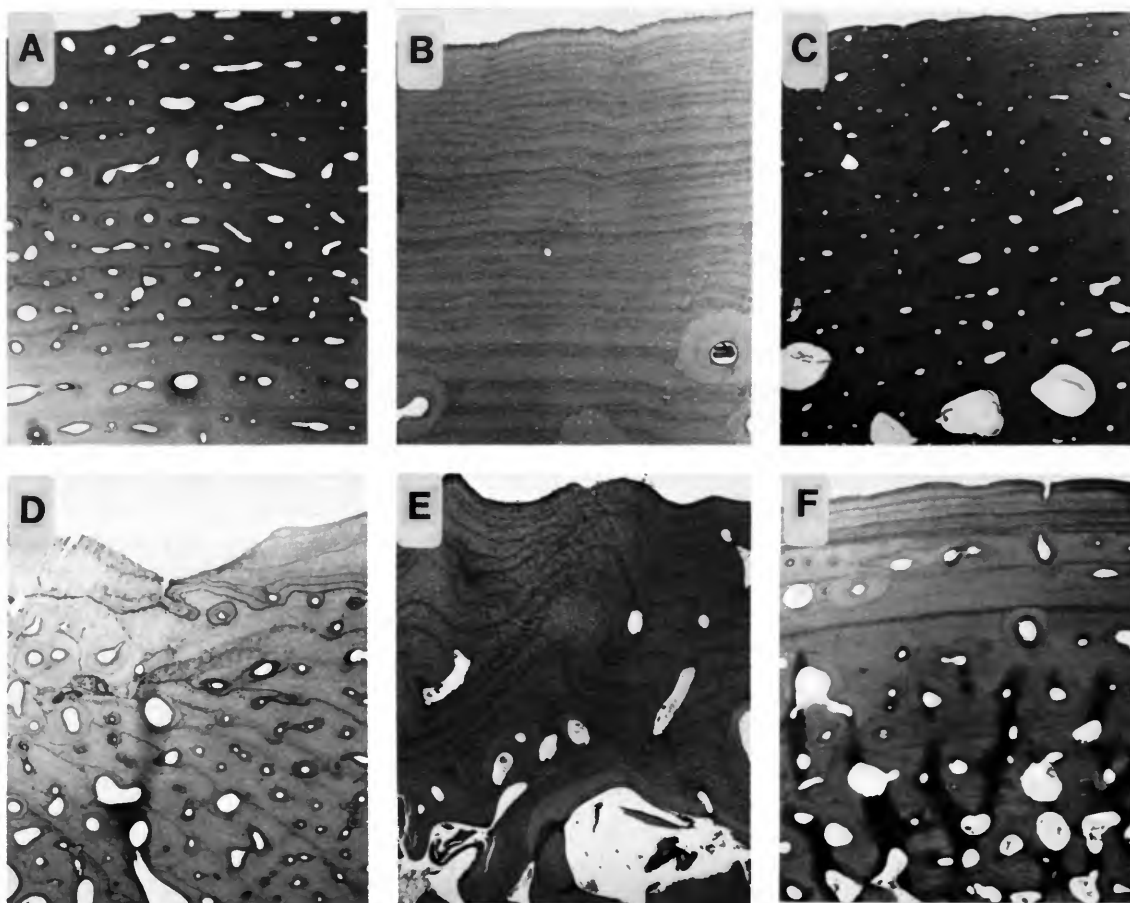


FIGURE 7.—Histological cross-sections of humeri demonstrating the various states of the marks of skeletal growth (MSGs): A, distinct MSGs bordering area of resorption; B, accessory lines of arrested growth; C, no lines of arrested growth (LAG); D, discontinuous LAGs; E, irregular growth layers; F, compaction of MSGs.

interrupted, non-contiguous arrested growth lines (Figure 7E).

Compaction of MSGs. Adjacent arrest lines so close to one another as to prevent differentiation of the individual growth layers (Figure 7F).

Resorption and redeposition of the periosteal layers is extensive in the *Caretta* humerus, because its cross-sectional diameter (narrowest axis) increases tenfold from hatching to adulthood. In addition, there are changes in proportions and in orientation of the longitudinal

axis (Figure 6), thus the original humerus and the early periosteal layers are entirely replaced by remodeling and endosteal growth. The loss of the earlier periosteal layers, i.e., the MSGs, requires an extrapolation from the width of the extant MSGs in order to estimate the number of lost MSGs.

Accessory LAGs are lines probably resulting from nonseasonal retardation or cessation of growth, caused by such events as injury, illness, or short-term reduction in food supply. Often

the accessory LAGs can be discerned from the "true" LAGs by less intense or more diffuse staining or by incompleteness of the line. Accessory LAGs potentially cause an over-estimate of age, since their development violates the one-MSG/one-year assumption.

The absence of LAGs prevents the estimation of age. The cause of this condition is unknown. Continuous, more or less uniform growth would produce this condition, although such a growth pattern seems unlikely for members of the Georgia *Caretta* population, unless some individuals migrate to warmer waters in the winter.

Discontinuous LAGs and compacted MSGs increase the difficulties of recognition of MSGs and increase the likelihood of sampling errors. They do not, however, prevent the estimation of age. Compaction is most prevalent in large turtles and may result from a reduction in growth rate following the attainment of sexual maturity (Carr and Goodman, 1970). Discontinuous MSGs may reflect a growth pattern where one region of the periosteum slowed its rate of deposition while an adjacent region did not. The process is analogous to the differential rates of deposition whereby a bone alters its shape by producing a thicker MSG (i.e., periosteal layer) on one surface than on another surface (see Figure 6 for shape changes owing to differential growth).

These problem areas cause difficulties in counting and measuring MSGs and in the estimation of age from the MSG data. These difficulties are not insurmountable, but they do require care of interpretation and impose narrow limits upon the amount of extrapolation from the age estimates. We are not proposing that we can precisely age every individual turtle. Although our age estimates may be accurate for individual turtles, our goal is to provide age estimates for various classes of turtles, e.g., immatures of 500–600 mm cCL or adults >1000 mm cCL, and most specifically to provide an accurate estimate of the age of sexual maturity for the Georgia *Caretta* popu-

lation. (We assume that the juveniles living adjacent to the Georgia coastal islands become the adults breeding on these islands.) Thus, our analysis and interpretation depend upon a large sample of turtles, not on individual specimens.

We believe that such an approach overcomes the six problem areas mentioned above. First, the large sample eliminates the dependency of interpretation upon individual specimens and permits the removal of specimens with anomalous or peculiar growth patterns which would likely cause erroneous age estimates. The large sample further provides an overview of bone growth and remodeling, so that the counting and measuring of MSGs is standardized and objective. This standardization is important, because data collection is always more efficient and consistent when the collector knows the subject area well, particularly its variability, and collects the data within a limited and uninterrupted time period. The *Caretta* data set was collected by A. Wynn during a single time period (3 mo), and upon completion of the entire set, the earlier specimens and randomly selected later specimens were re-examined to confirm the consistency of the entire data set. In this latter respect, re-examination at lower magnification (10–20 X) was useful in the confirmation of number of MSGs, although not their widths.

Such problems as accessory LAGs and irregular growth layers illustrate that periosteal growth has periods of slow and rapid growth, thereby emphasizing the cyclic nature of MSGs. Nonetheless, their presence only clouds the question of whether or not the cycle is an annual one. Our data on *Caretta* cannot address this question. Further, the inability to locate MSGs in all individuals of a sample or in all skeletal elements within a single individual is inadequate grounds to falsify the one-MSG/one-year hypothesis. We accept the annual production of one mark of skeletal growth (MSG) on several lines of circumstantial evidence.

Our second assumption in the application of skeletochronology is that the number of MSGs lost through bone resorption/remodeling can be estimated from the number and size of the remaining MSGs. Our method depends upon using the average width of extant MSGs to estimate the total numbers of MSGs formed from hatching to death. The estimate derives from the number of times that the average MSG width occurs in half the diameter of the sample bone. The formula is

$$TM = \frac{(0.5 \text{ BD}) - \text{HD}}{\text{AW}},$$

where TM is the total number of MSGs; BD is the cross-sectional diameter of the sample bone; HD is the average cross-sectional diameter of hatchling *Caretta* humerus (HD = 1.5063 mm); and AW is average width of extant MSGs. HD is subtracted, because it represents bone diameter at age zero; only the subsequent growth marks represent years of growth. BD is halved, because the average MSG width derives from only one side of the bone.

The estimate of total number of MSGs is equivalent to age in years if we accept a cyclic growth pattern of one MSG per year and that the average width of extant MSGs accurately reflects the average width of lost and extant MSGs.

**DATA ANALYSIS.**—In our preliminary analysis (Zug, Wynn, and Ruckdeschel, 1983), we demonstrated a strong positive correlation of humerus length to carapace length (over-the-curve, cCL) as well as significant positive correlations of humerus length to estimated age and of carapace length to age. Those analyses are reproduced in Part 1 of the Appendix, because they provide the analytical base for our present discussion and may be unavailable to many readers of this report. Although the basic data are the same, the analytical procedure differs.

Herein, each age estimate is rounded to the nearest whole number, in contrast to the near-

est hundredths in the preliminary analysis. The regression analyses examine the data in three overlapping sets: (1) IMMATURES, all specimens less than 860 mm cCL, except for individuals with excessively high estimates of age; (2) IMMATURES AND ADULTS, all specimens, except for individuals with excessively high estimates of age; (3) ALL, all specimens. The data are reproduced in Part 2 of the Appendix.

Our preliminary analysis (see Appendix, Part 1) used age as the dependent variable, because carapace and humerus length were directly measurable variables and age was estimated. That manner of presentation caused some confusion or was less easily read owing to the reversal of the axes as commonly presented for the analysis of growth. An argument can be given for each manner of presentation; hence we provide both. Importantly, the analysis of estimated age as a dependent variable provides regression equations that more accurately predict size at hatching.

A comparison of the preliminary analysis with the current analysis shows a striking difference in regression equations and correlations. (For both analyses, all correlation coefficients are statistically significant at 0.01 probability level.) The linear regression equations for both analyses (Table 1, 2L1.2; Appendix, Part 1,  $N = 75^*$ ) give unrealistic carapace lengths (407.8 and 580.5 mm, current and preliminary analyses, respectively) for hatchlings; the power or allometric equations for the same data sets (2P1.2;  $N = 75^+$ ) predict more realistic lengths (33.0 and 71.1 mm, respectively). Actual carapace lengths (38–50 mm; Baldwin and Lofton, 1959:342) of hatchling *Caretta* lie between these two allometric equation predictions and are somewhat closer to the current data set's prediction. The point is not that one data set is better than the other; rather that the analysis of age estimates as whole numbers versus that using decimal numbers does not alter the general results.

The age estimates derive from two axes of the humeral section. The results are usually

TABLE 1.—Regression statistics for age estimates (long axis) and carapace length. A model code is assigned to each regression to facilitate discussion within the text. Models 1L1 and 1P1 include all specimens with cCL <860 mm except those with excessive age estimates; models 1L2 and 1P2, all specimens except those with excessive ages. Data from Part 2 of Appendix. (Abbreviations: A, Y-intercept; B, slope of regression curve; N, sample size; r, correlation coefficient.)

| (X, Y)                         | N  | A                    | B     | r    | Range   |         | Model |
|--------------------------------|----|----------------------|-------|------|---------|---------|-------|
|                                |    |                      |       |      | X       | Y       |       |
| Linear Regression $Y = A + BX$ |    |                      |       |      |         |         |       |
| Age, cCL                       | 38 | 576.966              | 5.163 | 0.55 | 11–40   | 565–855 | 1L1.1 |
| cCL, Age                       | 38 | -17.561              | 0.059 | 0.55 | 565–855 | 11–40   | 1L1.2 |
| Age, cCL                       | 44 | 615.845              | 3.808 | 0.75 | 11–111  | 565–960 | 1L2.1 |
| cCL, Age                       | 44 | -77.325              | 0.147 | 0.75 | 565–960 | 11–111  | 1L2.2 |
| Power Regression $Y = AX^B$    |    |                      |       |      |         |         |       |
| Age, cCL                       | 38 | 402.524              | 0.176 | 0.59 | 11–40   | 565–855 | 1P1.1 |
| cCL, Age                       | 38 | $5.7 \times 10^{-5}$ | 1.966 | 0.59 | 565–855 | 11–40   | 1P1.2 |
| Age, cCL                       | 44 | 365.485              | 0.210 | 0.78 | 11–111  | 565–960 | 1P2.1 |
| cCL, Age                       | 44 | $1.6 \times 10^{-7}$ | 2.870 | 0.78 | 565–960 | 11–111  | 1P2.2 |

strikingly different, with the long axis yielding estimates typically two or more times those of the short axis (see Appendix, Part 2). These differences arise not from a greater number of MSGs, but from fewer MSGs of the same or narrower widths than those of the short axis. Hence, the narrower average MSG width and the greater bone diameter of the long axis result in the estimation of a greater number of MSGs, which convert to older age estimates. Because the number of MSGs seems unreasonably high and because the number of sections showing measurable MSGs on the long axis is approximately half the sample size of the short axis, the long axis data will not be emphasized.

The short axis data possess a greater uniformity of estimates, although disparate age estimates do occur between similar sized individuals and seemingly high estimates occur for other individuals. As defined earlier, the data are analyzed in three overlapping sets. The first set (IMMATURES, cCL <860 mm) contains immature turtles and is a particularly valuable set for determining the age of sexual maturity. The second set (IMMATURES AND ADULTS) includes all the turtles of the previous set and the mature turtles (cCL >860 mm). The selec-

tion of a size for classifying loggerheads as immature or mature is arbitrary, because individuals of the same sex obtain maturity at different sizes and males and females presumably mature at different average sizes. Nonetheless, a selection is useful for analysis and the 860 mm cCL should accurately sort most of the turtles in our sample. The choice of this value derives from the range of nesting-female carapace lengths, not from mean lengths which are characteristically greater than 900 mm cCL (e.g., Ehrhart and Yoder, 1978; Stoneburner, 1980). For the U.S. Atlantic coast, ranges are 845–1029 mm cCL (Cape Romain, SC; Baldwin and Lofton, 1959), 800–1150 mm cCL (Jekyll Island, Ga.; Caldwell, Carr, and Owen, 1959), 892–1186 mm cCL (Little Cumberland Isl., Ga.; Ruckdeschel unpubl. data), 830–1240 mm cCL (Merritt Isl., Fla.; Ehrhart and Yoder 1978), 775–1067 mm cCL (Hutchinson Isl., Fla.; Gallagher et al., 1972), and 749–1092 mm sCL (Melbourne Beach, Fla.; Bjorndal et al., 1983).

A comparison of age estimates from the long and the short axis samples (Tables 1 and 2) shows that the long axis sample possesses higher correlation coefficients than the short

TABLE 2.—Regression statistics for age estimates (short axis) and carapace length. Data from Part 2 of Appendix. (Abbreviations and explanations same as in Table 1.)

| (X, Y)                          | N  | A                    | B     | r    | Range    |          | Model |
|---------------------------------|----|----------------------|-------|------|----------|----------|-------|
|                                 |    |                      |       |      | X        | Y        |       |
| Linear Regression, $Y = A + BX$ |    |                      |       |      |          |          |       |
| Age, cCL                        | 68 | 631.009              | 7.460 | 0.49 | 3-25     | 565-855  | 2L1.1 |
| cCL, Age                        | 68 | -13.454              | 0.033 | 0.49 | 565-855  | 3-25     | 2L1.2 |
| Age, cCL                        | 76 | 657.848              | 5.656 | 0.63 | 3-74     | 565-1010 | 2L2.1 |
| cCL, Age                        | 76 | -38.976              | 0.070 | 0.63 | 565-1010 | 3-74     | 2L2.2 |
| Age, cCL                        | 81 | 699.103              | 2.149 | 0.60 | 3-175    | 565-1090 | 2L3.1 |
| Power Regression, $Y = AX^B$    |    |                      |       |      |          |          |       |
| Age, cCL                        | 68 | 529.673              | 0.130 | 0.58 | 3-25     | 565-855  | 2P1.1 |
| cCL, Age                        | 68 | $3.1 \times 10^{-7}$ | 2.616 | 0.58 | 565-855  | 3-25     | 2P1.2 |
| Age, cCL                        | 76 | 511.863              | 0.151 | 0.70 | 3-74     | 565-1010 | 2P2.1 |
| cCL, Age                        | 76 | $1.0 \times 10^{-8}$ | 3.239 | 0.70 | 565-1010 | 3-74     | 2P2.2 |
| Age, cCL                        | 81 | 537.579              | 0.128 | 0.74 | 3-175    | 565-1090 | 2P3.1 |

TABLE 3.—Regression statistics for age estimates (short axis) and carapace length. Age estimates used herein were based on the maximum number of MSGs, either observed or estimated; data from Part 2 of Appendix. (Abbreviations and explanations same as in Table 1.)

| (X, Y)                         | N  | A                    | B     | r    | Range    |          | Model |
|--------------------------------|----|----------------------|-------|------|----------|----------|-------|
|                                |    |                      |       |      | X        | Y        |       |
| Linear Regression $Y = A + BX$ |    |                      |       |      |          |          |       |
| Age, cCL                       | 68 | 628.010              | 7.553 | 0.49 | 4-25     | 565-855  | 3L1.1 |
| cCL, Age                       | 68 | -12.550              | 0.032 | 0.49 | 565-855  | 4-25     | 3L1.2 |
| Age, cCL                       | 76 | 655.892              | 5.693 | 0.63 | 4-74     | 565-1010 | 3L2.1 |
| cCL, Age                       | 76 | -38.087              | 0.070 | 0.63 | 565-1010 | 4-74     | 3L2.2 |
| Age, cCL                       | 81 | 698.549              | 2.150 | 0.60 | 4-175    | 565-1090 | 3L3.1 |
| Power Regression $Y = AX^B$    |    |                      |       |      |          |          |       |
| Age, cCL                       | 68 | 519.381              | 0.136 | 0.57 | 4-25     | 565-855  | 3P1.1 |
| cCL, Age                       | 68 | $1.8 \times 10^{-6}$ | 2.349 | 0.57 | 565-855  | 4-25     | 3P1.2 |
| Age, cCL                       | 76 | 500.267              | 0.159 | 0.70 | 4-74     | 565-1010 | 3P2.1 |
| cCL, Age                       | 76 | $2.0 \times 10^{-7}$ | 3.044 | 0.70 | 565-1010 | 4-74     | 3P2.2 |
| Age, cCL                       | 81 | 530.481              | 0.132 | 0.73 | 4-175    | 565-1090 | 3P3.1 |

axis sample. This difference is especially noticeable in the linear regression analysis.

In calculating the number of MSGs for each specimen, the resulting MSG estimate was occasionally less than the number of MSGs observed. Potentially, these differences might reduce the predictability of the regression equations which were determined strictly from the MSG/age estimate data. The low frequency of higher observed MSG counts versus estimated MSG counts and the slight difference between

the two when they are different have no major effect on the regression equations (Tables 2 and 3) and their curves (Figure 8C,D). The differences are sufficiently minor that the mixed data set (observed and estimated, Table 3) can be ignored.

The estimated data (Figure 8A,B) yield five estimated MSGs/ages that are clearly outside the main cluster of points. These outliers were removed from the analysis (Table 4, Figure 8E,F). Their removal results in a striking im-

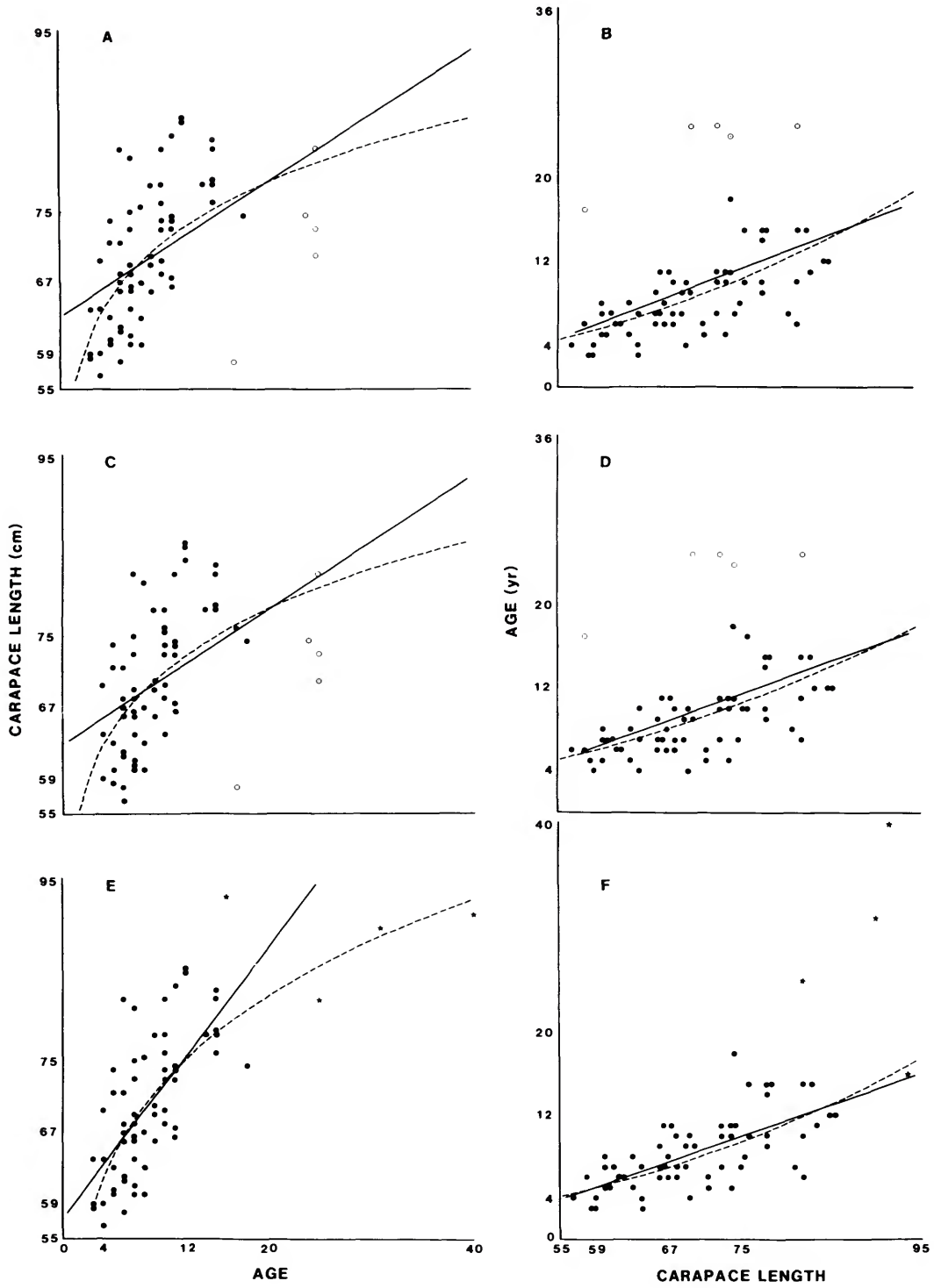


TABLE 4.—Regression statistics for age estimates (short axis) and carapace length; same data set as in Table 2 with the removal of outliers (shown as open circles in Figure 8A,B). Data from Part 2 of Appendix. (Abbreviations and explanations same as in Table 1.)

| (X, Y)                         | N  | A                     | B      | r    | Range    |          | Model |
|--------------------------------|----|-----------------------|--------|------|----------|----------|-------|
|                                |    |                       |        |      | X        | Y        |       |
| Linear Regression $Y = A + BX$ |    |                       |        |      |          |          |       |
| Age, cCL                       | 63 | 572.778               | 15.178 | 0.68 | 3-18     | 565-855  | 4L1.1 |
| cCL, Age                       | 63 | -12.741               | 0.030  | 0.68 | 565-855  | 3-18     | 4L1.2 |
| Age, cCL                       | 71 | 656.076               | 5.647  | 0.76 | 3-81     | 565-1060 | 4L2.1 |
| cCL, Age                       | 71 | -61.204               | 0.102  | 0.76 | 565-1060 | 3-81     | 4L2.2 |
| Power Regression $Y = AX^B$    |    |                       |        |      |          |          |       |
| Age, cCL                       | 63 | 484.290               | 0.178  | 0.68 | 3-18     | 565-855  | 4P1.1 |
| cCL, Age                       | 63 | $2.8 \times 10^{-7}$  | 2.617  | 0.68 | 565-855  | 3-18     | 4P1.2 |
| Age, cCL                       | 71 | 491.263               | 0.171  | 0.82 | 3-81     | 565-1060 | 4P2.1 |
| cCL, Age                       | 71 | $4.3 \times 10^{-11}$ | 3.972  | 0.82 | 565-1060 | 3-81     | 4P2.2 |

provement of the correlation coefficients and a better fit of the regression curves to the cluster of points. The outliers share no features that might explain their isolation from the other data points. They do not derive from similar-sized turtles, they do not have exceptionally high numbers of observed MSGs, and they do not have narrow average MSG widths.

The linear regressions and correlation coefficients (Tables 1, 2, and 4; Figure 8) provide reasonably good fits to the data clusters for the immature turtles (cCL <860 mm). The addition of the adult specimens to the samples (models 2L2 and 4L2) improves the correlation of carapace length with age; however, the addition of specimens with very high age estimates (e.g., model 2L3) suppresses the correlation coefficients, but not below that of the immature turtles. The same summary remarks

apply to the power regressions and correlation coefficients; however, the fit is better for the power equations in all cases. Owing to the better fit and higher coefficients, subsequent extrapolation to determine body size at sexual maturity and hatching will be based on power equations. The inability of the linear regression equations to predict accurately hatchling size is apparent from the following calculations derived from the values in Table 2 where cCL(mm) and age (yr, 1 day = 0.003). For example, sizes are 631.0 mm ( $Y = 631.009 + 7.46(0.003)$  for model 2L1.1), 407.8 mm ( $0.003 = -13.454 + 0.033X$  for model 2L1.2), 657.9 (2L2.1), 556.8 mm (2L2.2), and 699.1 mm (2L3). Such predictions are far in excess of the 38-50 mm range for *Caretta* hatchlings (Baldwin and Lofton, 1959).

Prediction of hatchling size is improved by using the power equations. The comparable size predictions are: 248.9 mm (2P1.1), 33.4 mm (2P1.2), 212.9 mm (2P2.1) 49.1 mm (2P2.2), and 255.6 mm (2P3) from Table 2. The predictions, however, are biologically realistic only for power equations where Y equals age, which is the reverse of the typical presentation for growth. Technically, regression is appropriate only for independent variables measured without error. The age data do not meet this criterion and, statistically, are ana-

FIGURE 8.—The relationship of estimated age to carapace length. Age is an independent variable in the left column of graphs and a dependent variable in the right column of graphs. The top row of graphs (A,B) contains the ages (of immature turtles, <860 mm cCL) derived entirely from estimated MSGs (Table 2, models 2L1 and 2P1; outliers shown as open circles). The middle row (C,D) contains the ages (of immature turtles) derived from the highest number of MSGs, either observed or estimated (Table 3, models 3L1 and 3P1; outliers shown as open circles). The lower row (E,F) shows the same age data as the top row with the removal of the five outliers (Table 4, models 4L1 and 4P1).

lyzed correctly as dependent variables. Visually, the graphs (Figure 8) show that the power curve for age as a dependent variable matches better the longitudinal axis of the data cluster for immature turtles. The better fit to the data cluster and accurate prediction also recommend the use of the power equations with age as the dependent variable.

In the determination of age at sexual maturity, linear regression and power equations show the same general pattern as observed in the hatchling-size predictions. Those equations with age as the independent variable always predict an older age than the equations with age as a dependent variable (Table 5). The skeletochronological age estimates for specimens between 801 and 900 mm cCL (Appendix, Part 2 and Figure 9) range from 6 to 31 yrs with a mean of 14.5 yrs ( $s = 7.4614$ ,  $N = 11$ ). These data would again recommend the use of equations with age as the dependent variable. Furthermore, the equations (both linear and power) with the closest similarity to actual data are those derived from the IMMATURE data set. Importantly, the equations  $Y = (3.1 \times 10^{-7}) \times 2.616$  (Table 2, 2P1.2;  $Y$  age,  $X$  cCL)  $Y = (2.8 \times 10^{-7}) \times 2.617$  (Table 4, 4P1.2),  $Y = (1.0 \times 10^{-8}) \times 3.239$  (Table 2, 2P2.2) yield realistic, although small estimates of hatchling size (33.4 mm, 34.7 mm, and 32.0 mm cCL, respectively). The equations  $Y = 365.485 \times 0.21$  (Table 1, 1P2.1;  $Y$  cCL,  $\times$  age) and  $Y =$

$529.673 \times 0.13$  (Table 2, 2P2.2) give hatchling carapace lengths of 58.8 and 41.6 mm, respectively; these predictions are within the size range of hatchling *Caretta*. The corresponding age estimates for sexual maturity from the preceding five equations are 14.7, 13.4, 32, 58.8, and 41.6 yrs, respectively.

The mean age estimate for different size classes (Figure 9) shows a gradual increase in mean age from 6 yrs for the immature turtles (550–600 mm cCL) to 13 yrs for those nearing sexual maturity. The ages for the mature size classes (>850 mm) are from 20 to 50 yrs. Although the latter estimates seem biologically reasonable, the small samples for each class suggest that the data be treated with caution. This caution is also advocated by the wide range of estimates and the large standard deviations of the mature turtles. The small samples reflect not only the fewer number of adults stranding on Cumberland Island (Ruckdeschel and Zug, 1980), but also the difficulty of obtaining skeletochronological data from mature specimens. These difficulties encompass the entire spectrum from major remodeling with no MSGs to compaction of MSGs. It is the latter condition which results in the excessively high age estimates, e.g., 81 yrs for 1060 mm cCL, 142 yrs for 1000 mm cCL, 140 yrs for 975 mm cCL. These specimens have very narrow mean MSG widths, which overestimate the total number of MSGs.

TABLE 5.—Age (years) at sexual maturity calculated using linear and power equations of preceding tables and an 860 mm cCL.

| Data      | X = Age |       | Y = Age |       |
|-----------|---------|-------|---------|-------|
|           | Linear  | Power | Linear  | Power |
| Table 1   |         |       |         |       |
| 1L2 & 1P2 | 64.1    | 58.8  | 49.1    | 42.3  |
| Table 2   |         |       |         |       |
| 2L1 & 2P1 | 30.7    | 41.6  | 14.9    | 14.7  |
| 2L2 & 2P2 | 35.7    | 31.1  | 21.2    | 32.0  |
| Table 4   |         |       |         |       |
| 4L1 & 4P1 | 18.9    | 25.2  | 13.1    | 13.4  |
| 4L2 & 4P2 | 40.2    | 26.4  | 26.5    | 19.5  |

### Life History Implications

The preceding data center the attainment of sexual maturity on the ages of 13–15 yrs (Table 5 and Figure 9). This result matches Mendonca's (1981) estimate of 10–15 yrs for Merritt Island loggerheads remarkably well. Mendonca derived her estimates from the growth rates of recaptured wild *Caretta* with straight-line carapace lengths (sCL) of 440–925 mm. The average annual growth rate for her sample is 59 mm/yr, which yields an estimate of 13 years to reach 800 mm sCL, i.e., sexual maturity. The concordance



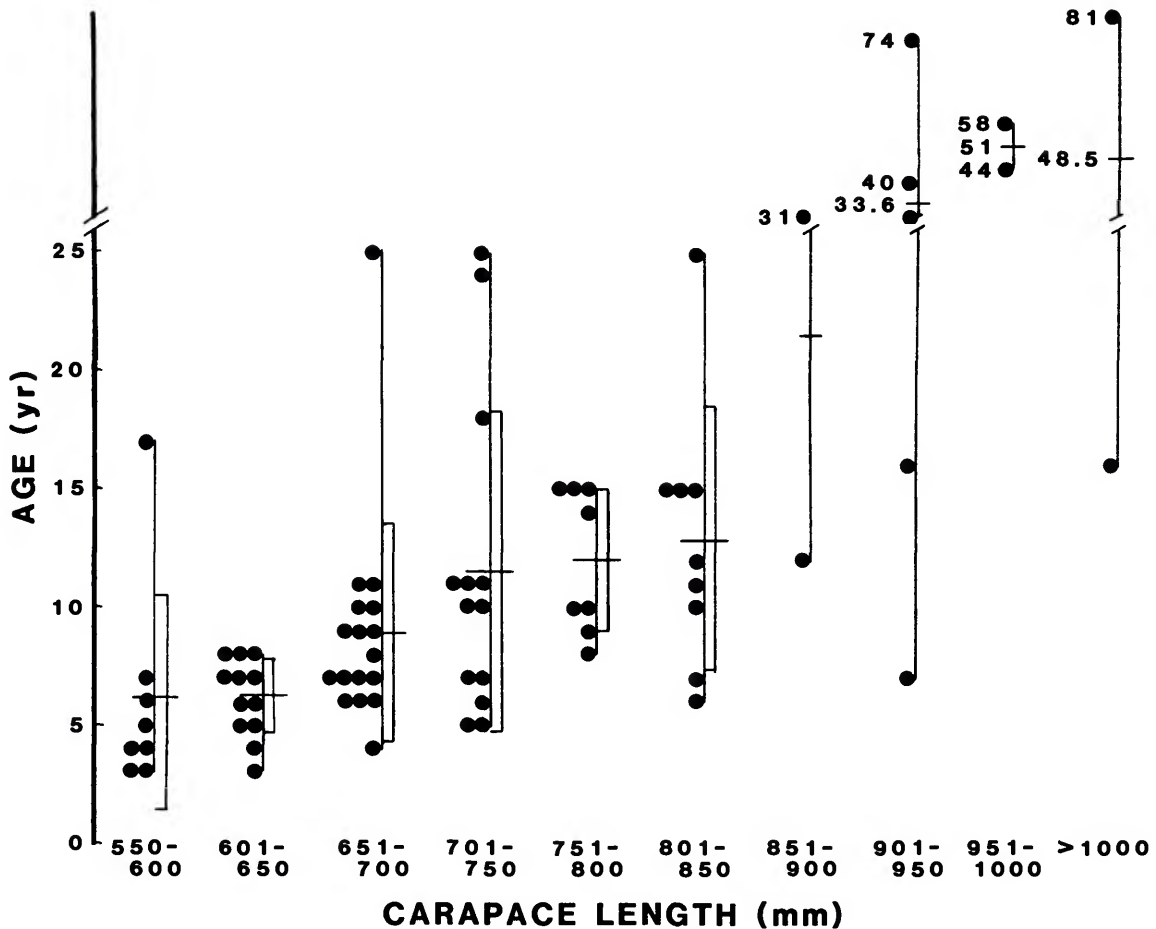


FIGURE 9.—The distributions of age estimates for sequential size classes of the 1979 Cumberland Island sample of loggerhead sea turtles. Vertical line = range; horizontal bar = mean; open box =  $\pm 1$  standard deviation of mean; each dot represents one individual.

of Mendonca's and our age estimates of sexual maturity is important in that the estimates were obtained by two strikingly different techniques; hence the concordance supports the acceptance of 15 years as an "average" age for sexual maturity of southeastern U.S. *Caretta*. Frazer and Ehrhart (1985) suggest an older "average" age for maturing loggerheads at Merritt Island. Their results derive from the Mendonca data set expanded by the inclusion of growth rates from females nesting in successive years and predict a range of 12-30 yrs for maturation. The two

predictions differ for several reasons (Frazer and Ehrhart, 1985), but primarily because Mendonca used a smaller body size for determining age of maturation and a linear model (in contrast to the von Bertalanffy model) with only the faster juvenile growth rates. As noted earlier, the mean CL of nesting females is more than 900 mm. Mendonca's linear model will predict 16 yrs at this length, and our allometric equations yield ages of 16 yrs (2P1.2) and 15 yrs (4P1.2). These latter predictions are like Mendonca's, because they are derived from the IMMATURE data. Using

the combined IMMATURE AND ADULT set, age at 900 mm cCL is 37 yrs (2P2.2) and 23 yrs (4P2.2); these latter estimates are more in agreement with those of Frazer and Ehrhart (1985). Henwood (in prep.) also uses a von Bertalanffy model and juvenile and adult growth data to predict maturation in the mid-twenties for western Atlantic loggerheads.

An earlier estimate of maturity for the Georgia *Caretta* population was 6–7 yrs (Caldwell, 1962) and was based on the growth rates of captive-reared hatchlings. The growth rate of well-fed captive sea turtles is typically two or more times faster than that of wild ones (Appendix, Part 3), and it is becoming increasingly apparent that age extrapolations from captive growth rates must be used cautiously. The average captive growth rate (from data in Appendix) is 136.6 mm/yr ( $s = 35.28$ ,  $N = 8$ ) for loggerheads. This rate would convert a 42 mm hatchling into an adult in 6 yrs as Caldwell (1962) and Uchida (1967) predicted. Use of captive growth rates ignores two aspects of natural growth, however. It assumes a constancy of growth rate in all growth stages, and even captive rearing of different size classes of sea turtles demonstrates the fallacy of this assumption (e.g., Frazer, 1982; Limpus, 1979; Parker, 1926, 1929; Uchida, 1967; Witham and Futch, 1977; Witzell, 1980). Furthermore, observations from captive rearing programs typically record growth from hatching to one year of age, occasionally for a second year, when growth is maximal. Second, the diet of captives is high in mass and protein and low in undigestible components (reported captive diets usually consisted of chopped fish and/or shrimp). Wild turtles probably obtain such a high quality meal rarely and probably do not approach the same mass of food on a monthly or yearly basis. Nuitja and Uchida (1982) have shown that growth rates in *Caretta* are directly linked to diet; more food produces faster growth. Third, wild turtles expend more energy in food gathering, so the net energy available for growth is presumably much less than that for captive turtles.

A striking exception to the preceding exposi-

tion are the growth data of two *Caretta* raised in captivity from hatching to 14 yrs. As they reached 14 yrs, the turtles were beginning to develop secondary sexual characteristics. If they continued their growth pattern, they would reach 860 mm cCL at 16–17 yrs and 920 mm at 19–20 yrs. Since they fed year round, although at a reduced level in the winter, an “average” age of maturation for wild loggerheads from the U.S. Atlantic coast would likely fall in the mid-twenties as postulated by Frazer and Ehrhart (1985) and Henwood (in prep.).

Most captive growth experiments demonstrate only that sea turtles are capable of rapid growth when given abundant food resources, not that they do so in the wild. The reproductive data on captive reared green sea turtles suggests, however, that the attainment of “mature” size and the production of gametes may occur prior to the animals being fully mature (Witham, 1971; Wood and Wood, 1980), because nesting frequency and clutch size of captive-reared females are well below normal. In addition, hatching success (? = fertility of eggs) is extremely low the first nesting season and increases gradually thereafter (Wood and Wood, 1980). A side, but related aspect to the preceding observations is the lack of concordance between age and marks of skeletal growth (MSGs) in *Chelonia mydas* at the Cayman Turtle Farm (Frazier, 1982). Since the growth rates are abnormally high in captive turtles and this rapid growth affects the physiology of reproduction (as outlined above), the normal pattern of bone growth may be similarly disrupted; hence, captive-reared known-aged turtles are a poor basis on which to confirm or falsify the one-MSG equals one-year hypothesis.

Maturity does not occur in all *Caretta* populations at the same age. Loggerheads from the Great Barrier Reef may require more than 30 yrs (Limpus, 1979), because growth rates of the older juveniles (>500 mm CL) are only 10–20 mm/yr. Such slow growth presumably reflects the quality and quantity of the food available to these turtles rather than a genetically determined growth potential. The rapid growth response of

all sea turtle species to abundant food in captivity illustrates the plasticity of sea turtle growth. This plasticity is evident in the differential response of turtles in adjacent populations to differences in food quality and quantity. For example, *Chelonia mydas* populations in the Hawaiian Archipelago show growth rates ranging from 10 to 53 mm/yr (Appendix, Part 3), and these rates are directly correlated with food supply (Balazs, 1979, 1980, 1982; see also Gibbons, 1967; Hulse, 1976; and Parmenter, 1980 for the influence of food quality and abundance on growth in populations of freshwater turtles). *Caretta* populations may respond similarly, but the growth rates of wild populations are known for so few that such patterns cannot be discerned at present.

Growth rates and ages of maturity are not identical for all members of a population even though they may have access to the same food resources and experience the same environmental conditions. Beginning with hatching, siblings show a range of body sizes. With growth, the range/variation of body sizes increases (e.g., see Bourke, Balazs, and Shallenberger, 1977, fig. 1, for captive-reared *Chelonia mydas*). Such differential growth probably occurs throughout the juvenile stage, and Carr and Goodman (1970) have hypothesized that the variability of body size in nesting female *Chelonia* is more strongly affected by the different sizes (i.e., differential growth) attained at maturity than by differences in postmaturity growth; Hildebrand (1932) found that maturation age may differ as much as four years in sibling *Malaclemys terrapin* from the same clutch of eggs. *Caretta* should show similar variation in size and age at maturation.

Although our data cannot directly address this individuality of growth and maturity, the high variation of age estimates within size classes (Figure 9) indicates its presence. The smallest size class (550–660 mm cCL) has a range of 3–17 yrs and, excluding the 17-yr estimate, an average age of 4.6 yrs (standard deviation,  $s = 1.51$ ). This average age closely matches the median and modal ages for this size class. With the above exclusion, this size class and the next largest

(601–650 mm cCL) have the lowest variation. Age variation is noticeably higher in the larger juvenile size classes and several magnitudes higher in the adult classes (>851 mm cCL), although the sample size of the latter is too small to attribute any statistical significance to the increase in variation at maturity. The increase in variation is principally caused by the adult classes containing the full spectrum of mature individuals from those nesting for the first time to those in their fifth or later nesting season. Secondly, the range of ages at maturity is broad, and this phenomenon is probably common to all populations of sea turtles. Even though our data are few in the mature age classes, they strongly suggest that most of the mature *Caretta* (>900 mm cCL) are old (>30 yrs). Furthermore, our data show one individual with 6 estimated MSGs and another with 25 MSGs, suggesting a potential age range of 19 yrs in maturing Georgia *Caretta*.

Our age estimates can provide estimates of growth rates in the same manner as growth rates can be used to estimate maturity. In this case, we estimate the growth by subtracting average hatchling size (45 mm) from the carapace length of each specimen and then dividing by its estimated age (short axis estimate; Appendix, Part 2). The range for the total sample is 4.2–198.3 mm/yr (Table 6) and this is equivalent to actual growth rates observed in captive and wild loggerheads (Appendix, Part 3). More important, however, is the lack of agreement with Mendonca's data (1981: table 1). Our estimates are 20–30 mm/yr faster than her observed rates. We suspect that this difference is partially explained by our inability to eliminate the earlier rapid growth from our estimates. Mendonca's data measured growth during an interval of late juvenile life; our estimates measure growth from hatching to the animal's death and include the rapid growth of posthatchlings so the average is higher. Nonetheless, the mean growth rates (Table 6) show the anticipated pattern of slowing growth with increasing size (and age). In addition, the data suggest a relatively homogeneous growth in the 650–850 mm size classes and then

TABLE 6.—Growth rate estimates (mm/yr) for sequential size classes of loggerhead sea turtles. Sexual maturation is assumed to occur in the 851–900 mm cCL size class.

| Size Class<br>(cCL) | N* | Mean  | Standard<br>Deviation | Range      |
|---------------------|----|-------|-----------------------|------------|
| 550–600             | 8  | 117.4 | 51.04                 | 79.3–181.7 |
| 601–650             | 12 | 102.8 | 37.69                 | 69.4–198.3 |
| 651–700             | 17 | 82.0  | 29.18                 | 26.2–162.5 |
| 701–750             | 13 | 77.4  | 36.74                 | 27.4–139.0 |
| 751–800             | 8  | 64.2  | 16.51                 | 47.7–88.7  |
| 801–850             | 9  | 71.4  | 30.79                 | 31.0–129.2 |
| 851–900             | 2  | 47.6  | –                     | 27.6–67.5  |
| 901–950             | 5  | 48.0  | 44.92                 | 12.0–122.9 |
| 951–1000            | 2  | 18.4  | –                     | 15.8–21.1  |
| > 1000              | 2  | 36.4  | –                     | 12.5–60.3  |

\* Four specimens with extraordinary age estimates are not included in this table; their estimates are (cCL, mm/yr): 735, 4.2; 975, 6.6; 1000, 6.7; 1090, 5.9.

a sharp drop in growth with maturity (>850 mm).

In comparison to North American freshwater and terrestrial turtles (Appendix, Part 4), *Caretta caretta* appears to mature sooner than would be expected by extrapolation from ages and sizes at maturation of the smaller turtle species. The larger emydines (*Pseudemys* and *Trachemys*) and *Chelydra* typically require a minimum of 6 yrs to attain a 200 mm CL. Simple linear extrapolation would suggest a minimum of 24 yrs for maturity at 800 mm CL. The relationship between turtle species' size and their age at maturity is not linear, however, because smaller species (e.g., *Clemmys*, *Kinosternon*, and *Sternotherus* mature in 4–7 yrs at 100 mm CL or less) possess ages of maturity equivalent to those of their bigger brethren. Clearly one aspect which biases our expectation of delayed maturity is that the majority of turtles studied derive from cooler aquatic environments with shorter growing seasons than the sea turtles studied. Turtles in warmer waters do grow faster (Cagle, 1954; Gibbons et al., 1981; Thornhill, 1982), and where examined closely (Gibbons et al., 1981; Parmenter, 1980), this faster growth results from two factors: primarily, owing to the availability of more and higher quality food and, secondarily, by higher ingestion rates (likely higher assimila-

tion rates as well) and a longer growing season. Thus, relative to the growth and maturation in these turtle populations, the growth and maturation of the Georgia *Caretta* do not deviate from the expected. Furthermore, the range of wild growth rates in sea turtles (Appendix, Part 3) and the high captive growth rates suggest that there are no real intrinsic differences in growth physiology between cheloniid sea turtles and the smaller-bodied freshwater turtles. Likewise, the larger-bodied freshwater and terrestrial turtles show similar growth rates or maturation ages as sea turtles (Appendix, Part 4). This similarity is most apparent in the giant tortoises (*Geochelone*), which have estimates of 16 to more than 30 yrs to attain sexual maturity.

### Summary

The humeri of *Caretta caretta* show distinct bony layers, and these marks of skeletal growth (MSGs) are assumed to be annual records of growth. The use of the skeletochronological technique is not without difficulties, such as absence of MSGs; irregular, interrupted, or accessory arrested growth lines; loss of MSGs by bone remodeling. Consequently, we use large samples and treat each age determination as an estimate.

Two age estimates were made from each bone section removed from the diaphysis just distal to the deltopectoral ridge. One estimate derived from the long axis of the section and the other from the short axis. Remodeling occurred in all humeri and required an extrapolation from existing MSGs to estimate the total number of MSGs formed during the life of the turtle. The estimate was obtained by dividing half of the humerus diameter by the average width of the extant MSGs. Since the basic assumption is that one MSG forms each year, the total number of MSGs equals the turtle's age in years. Age estimates derived from the long axis are usually 10 or more yrs higher than those from the short axis. Also linear and curvilinear regression equations derived from short-axis age estimates and carapace lengths calculations provide the best estimates of carapace lengths at hatching. Hence,

short-axis age estimates are considered the most reliable.

Sexual maturity in Cumberland Island *Caretta* occurs most commonly between 13 and 15 yrs from hatching. These values derive both from the average of the age estimates for the 800–900 mm cCL size class and from the regression equa-

tions for 860 mm cCL turtles, i.e., an arbitrary minimum size for *Caretta* nesting on the U.S. Atlantic coast. This age estimate for maturity matches one estimate proposed for a Florida *Caretta* population and is 5–10 yrs less for two other estimates that use 900–920 mm sCL as the size at maturity.

# Appendix

## Part 1

Table and figure from our preliminary analysis of age estimates in *Caretta* (Zug, Wynn, and Ruckdeschel, 1983) in the *Marine Turtle Newsletter*. They are reproduced to permit ready comparison with the results of the present analysis.

Age estimates, carapace lengths, and humerus lengths. Data for linear regression ( $Y = A + BX$ )\* and power ( $Y = AX^B$ )† equations. Other abbreviations are: cCL, carapace length over the curve; HL, humerus length;  $N$ , sample size;  $r$ , correlation coefficient. Lengths are given in mm, age in yrs.

| (X, Y)   | $N$ | A                     | B     | $r$  | X           | Y         |
|----------|-----|-----------------------|-------|------|-------------|-----------|
| HL, cCL  | 78* | -26.759               | 0.230 | 0.97 | 105.5-200.8 | 565-1060  |
|          | 78† | 0.078                 | 1.136 | 0.97 |             |           |
| HL, Age  | 76* | -45.738               | 0.416 | 0.75 | 105.5-200.8 | 3.0-80.9  |
|          | 76† | $8.8 \times 10^{-7}$  | 3.286 | 0.80 |             |           |
| cCL, Age | 75* | -51.081               | 0.088 | 0.69 | 565-1060    | 3.0-80.9  |
|          | 75† | $1.0 \times 10^{-9}$  | 3.498 | 0.73 |             |           |
| cCL, Age | 78* | -108.40               | 0.171 | 0.69 | 565-1060    | 3.0-175.3 |
|          | 78† | $0.6 \times 10^{-11}$ | 4.279 | 0.78 |             |           |

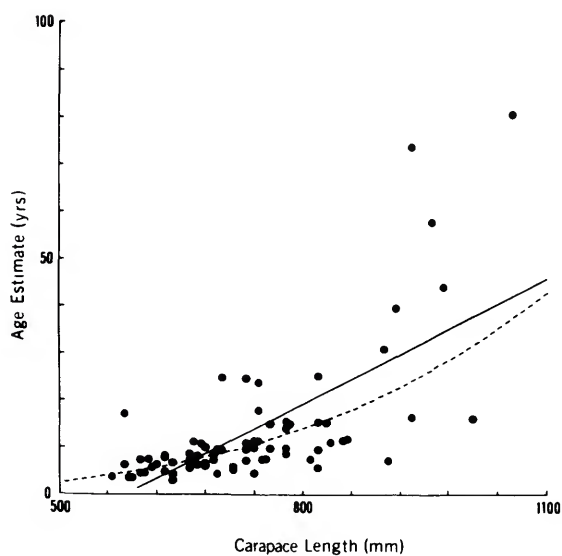


FIGURE A1.—The relation of curved carapace length to age estimates derived from periosteal annuli in *Caretta* humeri. Both the straight (linear regression) and curved (power) lines are based on 75 individuals; the three individuals with age estimates greater than 50 years were excluded from the calculations for these lines.

## Part 2

Data summary for the skeletochronological sample of *Caretta caretta* from Cumberland Island, Georgia. Age estimates were made from measurements of MSGs along the anteroposterior (long) axis and the dorsoventral (short) axis of the humerus section. Abbreviations and symbols: AW, mean width of MSGs along a single axis; cCL, carapace length over the curve; growth rate, estimated average annual cCL growth from hatching to death using estimated MSGs (short axis) as age at death; ML, maximum humerus length; †, an outlier value; \*, an excessively high age estimate. The 235000 series specimen numbers are from the USNM series, from collections deposited in the National Museum of Natural History, Smithsonian Institution; the 79.0.0.0 series are field numbers assigned by the collector.

| Specimen Number | Long axis |       |           |             | Short axis |      |             | Growth rate (mm/yr) |
|-----------------|-----------|-------|-----------|-------------|------------|------|-------------|---------------------|
|                 | cCL       | ML    | Obs. MSGs | Estim. MSGs | Obs. MSGs  | AW   | Estim. MSGs |                     |
| 235284          | 695       | 123.5 | -         | -           | 4          | 0.76 | 4           | 162.5               |
| 235286          | 690       | 143.1 | -         | -           | 7          | 0.45 | 9           | 71.7                |
| 235287          | 960       | 200.8 | 8         | 111         | 7          | 0.10 | 58          | 15.8                |
| 235291          | 630       | 121.8 | -         | -           | 4          | 0.39 | 8           | 73.1                |
| 235292          | 935       | 198.0 | -         | -           | 9          | 0.10 | 74          | 12.0                |
| 235293          | 670       | 129.4 | -         | -           | 4          | 0.50 | 8           | 78.0                |
| 235294          | 665       | 138.0 | 4         | 35          | 4          | 0.46 | 11          | 56.4                |
| 235295          | 745†      | 146.6 | 11        | 40          | 17         | 0.20 | 24          | 29.2                |
| 235296          | 975       | 193.0 | 19        | 94          | 14         | 0.14 | 44          | 21.1                |
| 79.5.4.9        | 695       | 134.8 | 6         | 35          | 7          | 0.48 | 10          | 65.0                |
| 79.5.4.10       | 745       | 143.6 | -         | -           | 4          | 0.20 | 18          | 38.9                |
| 235297          | 700†      | 135.4 | 5         | 25          | 6          | 0.16 | 25          | 26.2                |
| 235298          | 780       | 154.7 | -         | -           | 4          | 0.42 | 9           | 81.7                |
| 235301          | 905       | 168.0 | 8         | 30          | 8          | 0.54 | 7           | 122.9               |
| 235302          | 740       | 152.4 | -         | -           | 6          | 0.23 | 11          | 63.2                |
| 235303          | 730†      | 144.9 | 4         | 30          | 9          | 0.20 | 25          | 27.4                |
| 235305          | 735*      | 143.5 | 27        | 343         | 30         | 0.03 | 164         | 4.2                 |
| 235306          | 935       | 189.0 | 7         | 59          | 7          | 0.29 | 16          | 55.6                |
| 235310          | 820†      | 161.7 | -         | -           | 4          | 0.43 | 25          | 31.0                |
| 235314          | 1090*     | 250.0 | 23        | 638         | 41         | 0.04 | 175         | 6.0                 |
| 235315          | 760       | 145.4 | -         | -           | 5          | 0.46 | 10          | 71.5                |
| 235316          | 1060*     | 224.0 | 10        | 169         | 18         | 0.10 | 81          | 12.5                |
| 235318          | 600       | 112.0 | -         | -           | 5          | 0.44 | 8           | 69.4                |
| 235319          | 820       | 162.1 | -         | -           | 4          | 0.34 | 15          | 51.7                |
| 235320          | 715       | 139.1 | -         | -           | 4          | 0.81 | 5           | 134.0               |
| 79.5.18.8       | 820       | 151.4 | -         | -           | 7          | 0.81 | 6           | 129.2               |
| 235324          | 900       | 176.6 | 10        | 89          | 11         | 0.19 | 31          | 27.6                |
| 235325          | 590       | 112.0 | -         | -           | 4          | 0.71 | 3           | 181.7               |
| 235327          | 670       | 132.7 | -         | -           | 4          | 0.58 | 6           | 104.2               |
| 235328          | 630       | 125.2 | 4         | 23          | 4          | 0.44 | 8           | 73.1                |
| 235330          | 850       | 170.3 | -         | -           | 5          | 0.43 | 12          | 67.1                |

## Part 2.—Continued.

| Specimen Number |       |       | Long axis |             | Short axis |      |             | Growth rate (mm/yr) |
|-----------------|-------|-------|-----------|-------------|------------|------|-------------|---------------------|
|                 | cCL   | ML    | Obs. MSGs | Estim. MSGs | Obs. MSGs  | AW   | Estim. MSGs |                     |
| 235332          | 660   | 130.8 | 5         | 20          | 5          | 0.56 | 7           | 87.9                |
| 235333          | 615   | 119.1 | 6         | 12          | 6          | 0.79 | 6           | 95.0                |
| 235334          | 680   | 142.0 | 6         | 23          | 6          | 0.47 | 10          | 63.5                |
| 235336          | 820   | 145.6 | 11        | 24          | 11         | 0.49 | 10          | 77.5                |
| 235337          | 585   | 113.3 | —         | —           | 5          | 0.98 | 3           | 180.0               |
| 235338          | 855   | 157.9 | 9         | 25          | 9          | 0.50 | 12          | 67.5                |
| 235340          | 620   | 115.4 | 8         | 18          | 8          | 0.54 | 6           | 95.8                |
| 235341          | 640   | 116.2 | 4         | 12          | 4          | 1.40 | 3           | 198.3               |
| 235343          | 780   | 146.4 | —         | —           | 4          | 0.33 | 15          | 49.0                |
| 235344          | 830   | 159.1 | 7         | 37          | 6          | 0.35 | 15          | 52.3                |
| 235345          | 1010  | 210.0 | —         | —           | 4          | 0.42 | 16          | 60.3                |
| 235346          | 680   | 121.7 | 5         | 22          | 5          | 0.54 | 6           | 105.8               |
| 79.6.17.5       | 1000* | 217.0 | 11        | 420         | 9          | 0.06 | 142         | 6.7                 |
| 235348          | 755   | 141.4 | 11        | 19          | 10         | 0.50 | 8           | 88.7                |
| 235349          | 665   | 123.0 | 5         | 17          | 5          | 0.45 | 7           | 88.6                |
| 79.6.17.8       | 580   | —     | 4         | 18          | 4          | 0.42 | 6           | 89.2                |
| 235350          | 835   | 170.2 | 11        | 35          | 12         | 0.41 | 11          | 71.8                |
| 79.7.5.1        | 975*  | 195.0 | 13        | 339         | 30         | 0.05 | 140         | 6.6                 |
| 235356          | 730   | 144.4 | —         | —           | 10         | 0.03 | 10          | 68.5                |
| 235357          | 630   | 121.8 | —         | —           | 4          | 0.68 | 5           | 117.0               |
| 235358          | 675   | 129.4 | 5         | 27          | 5          | 0.35 | 11          | 57.3                |
| 235362          | 680   | 122.8 | 6         | 19          | 6          | 0.55 | 7           | 90.7                |
| 235363          | 730   | 139.9 | 4         | 20          | 7          | 0.63 | 7           | 97.8                |
| 235365          | 565   | 105.5 | 4         | 12          | 6          | 0.73 | 4           | 130.0               |
| 235366          | 600   | 123.7 | —         | —           | 6          | 0.50 | 7           | 79.3                |
| 235367          | 745   | 144.2 | —         | —           | 4          | 0.38 | 11          | 63.6                |
| 235371          | 660   | 120.0 | —         | —           | 4          | 0.68 | 6           | 102.5               |
| 235375          | 780   | 146.0 | 8         | 28          | 7          | 0.43 | 10          | 73.5                |
| 235378          | 640   | 131.4 | 6         | 15          | 7          | 0.66 | 7           | 85.0                |
| 235380          | 750   | 134.4 | —         | —           | 7          | 0.63 | 7           | 100.7               |
| 235381          | 915   | 173.5 | 10        | 43          | 8          | 0.16 | 40          | 21.7                |
| 235383          | 640   | 118.4 | 4         | 22          | 10         | 0.52 | 7           | 85.0                |
| 235388          | 810   | 156.0 | 5         | 22          | 8          | 0.73 | 7           | 109.3               |
| 235389          | 600   | 117.2 | 4         | 13          | 4          | 0.77 | 5           | 111.0               |
| 235390          | 830   | 155.5 | —         | —           | 4          | 0.34 | 15          | 52.3                |
| 235391          | 590   | 107.9 | —         | —           | 4          | 0.82 | 4           | 136.3               |
| 235392          | 785   | 147.3 | 4         | 36          | 5          | 0.35 | 15          | 49.3                |
| 235393          | 760   | 141.1 | 10        | 32          | 17         | 0.31 | 15          | 47.7                |
| 235394          | 730   | 146.0 | 8         | 23          | 9          | 0.42 | 11          | 62.3                |
| 235395          | 740   | 143.3 | 4         | 24          | 6          | 0.49 | 10          | 69.5                |
| 235397          | 640   | 119.5 | —         | —           | 4          | 1.02 | 4           | 148.7               |
| 235398          | 580†  | 116.3 | —         | —           | 8          | 0.18 | 17          | 31.5                |
| 235399          | 660   | 128.1 | 7         | 36          | 7          | 0.42 | 9           | 68.3                |
| 235400          | 700   | 124.7 | 4         | 22          | 4          | 0.45 | 9           | 72.8                |
| 235401          | 780   | 149.9 | —         | —           | 5          | 0.31 | 14          | 52.5                |
| 235407          | 715   | 130.0 | 5         | 13          | 5          | 0.77 | 6           | 111.7               |
| 235415          | 610   | 113.5 | 4         | 26          | 7          | 0.58 | 7           | 80.7                |
| 235417          | 740   | 133.6 | —         | —           | 5          | 0.87 | 5           | 139.0               |
| 235418          | 690   | 123.7 | 7         | 18          | 7          | 0.60 | 7           | 92.1                |
| 235419          | 605   | 106.5 | 4         | 11          | 7          | 0.74 | 5           | 112.0               |



### Part 3

Summary of selected references on growth rates and age estimates of sexual maturity in cheloniid sea turtles. The data listed below may not match the values listed in the text for these references, because we often summarized the original data; the data could not be standardized to a single method of carapace measurement. (Abbreviations: C, data from captive raised turtles; W, mark and recapture data from wild turtles; dash, no data; ?, questionable data.)

| Species<br>Locality    | Sample<br>size | Exper.<br>cond. | Growth<br>rate<br>(mm/yr) | Age at<br>maturity<br>(estim.<br>yrs) | Reference                   |
|------------------------|----------------|-----------------|---------------------------|---------------------------------------|-----------------------------|
| <i>Caretta caretta</i> |                |                 |                           |                                       |                             |
| Florida                | 67             | W               | 57.0                      | -                                     | Bjorndal et al., 1983       |
| Florida                | 2              | C               | 82.1                      | -                                     | Caldwell et al., 1955       |
| Georgia                | 5              | C               | 131.4                     | 6-7                                   | Caldwell, 1962              |
| North Carolina         | 2              | C               | 110.3                     | -                                     | Hildebrand and Hatsel, 1927 |
| Colombia               | 9              | C               | 176.8                     | -                                     | Kaufmann, 1972              |
| Colombia               | 13             | C               | 111.4                     | -                                     | Kaufmann, 1972              |
| Great Barrier Reef     | -              | W               | -                         | >30                                   | Limpus, 1979                |
| Florida                | 13             | W               | 59.0                      | 10-15                                 | Mendonca, 1981              |
| Florida                | 1              | C               | 161.7                     | -                                     | Parker, 1926                |
| Florida                | 8              | C               | 182.9                     | -                                     | Rebel, 1974                 |
| Florida                | 25             | C               | 136.4                     | -                                     | Witham and Futch, 1977      |
| <i>Chelonia mydas</i>  |                |                 |                           |                                       |                             |
| Hawaii                 | 4              | W               | 52.8                      | 11                                    | Balazs, 1979, 1982          |
| Oahu                   | 2              | W               | 24.0                      | 24                                    | Balazs, 1980, 1982          |
| Necker                 | 1              | W               | 16.8                      | 34                                    | Balazs, 1980, 1982          |
| French Frigate         | 19             | W               | 9.6                       | 59                                    | Balazs, 1980, 1982          |
| Lisianski              | 3              | W               | 15.6                      | 36                                    | Balazs, 1980, 1982          |
| Midway                 | 8              | W               | 10.8                      | 53                                    | Balazs, 1980, 1982          |
| Kure                   | 2              | W               | 9.6                       | 59                                    | Balazs, 1980, 1982          |
| hatchlings             | 4              | C               | 210.3                     | -                                     | Balazs, 1980                |
| immatures              | 6              | C               | 60.1                      | -                                     | Balazs, 1980                |
| adults                 | 8              | C               | 0.24                      | -                                     | Balazs, 1980                |
| U.S. Virgin Islands    | 35             | W               | 50.4                      | -                                     | Boulon, 1983                |
| Florida                | 4              | C               | 110.0                     | 8-13                                  | Caldwell, 1962              |
| Tortuguero             | 141            | W               | 5.8                       | -                                     | Carr and Goodman, 1970      |
| Sarawak                | -              | C               | 104.0                     | 4-6                                   | Hendrickson, 1958           |
| Colombia               | 4              | C               | 148.9                     | -                                     | Kaufmann, 1972              |
| Torres Strait          | 8              | W               | 17.4                      | -                                     | Kowarsky and Capelle, 1979  |
| Great Barrier Reef     | 40             | W               | 13.2                      | >30                                   | Limpus, 1979                |
| Great Barrier Reef     | 12             | W               | 1.4                       | -                                     | Limpus, 1979                |
| Heron Island           | 40             | W               | 13.5                      | >30                                   | Limpus and Walter, 1980     |
| Florida                | 12             | W               | 35.4                      | 25-30                                 | Mendonca, 1981              |
| Heron Island           | 2              | C               | 120.9                     | -                                     | Moorhouse, 1933             |

## Part 3.—Continued.

| Species<br>Locality           | Sample<br>size | Exper.<br>cond. | Growth<br>rate<br>(mm/yr) | Age at<br>maturity<br>(estim.<br>yrs) | Reference                  |
|-------------------------------|----------------|-----------------|---------------------------|---------------------------------------|----------------------------|
| St. Thomas                    | 9              | W               | 51.1                      | —                                     | Schmidt, 1916              |
| Mauritania                    | —              | C,W             | —                         | 5.5                                   | Toquin et al., 1980        |
| Florida                       | 12             | C               | 166.9                     | —                                     | Witham and Futch, 1977     |
| Grand Cayman                  | 22             | C               | —                         | 8–10                                  | Wood and Wood, 1980        |
| <i>Eretmochelys imbricata</i> |                |                 |                           |                                       |                            |
| U.S. Virgin Islands           | 15             | W               | 33.6                      | —                                     | Boulon, 1983               |
| Jamaica                       | ?              | C               | 50.3                      | —                                     | Brown et al., 1982         |
| Jamaica                       | ?              | C               | 23.3                      | —                                     | Brown et al., 1982         |
| Florida                       | 9              | C               | 86.8                      | —                                     | Caldwell, 1962             |
| Sri Lanka                     | 1              | C               | 247.2                     | —                                     | Deraniyagala, 1939         |
| Sri Lanka                     | 1              | C               | 93.0                      | —                                     | Deraniyagala, 1939         |
| Seychelles                    | 10             | C               | 170.5                     | —                                     | Diamond, 1976              |
| Sarawak                       | 3              | C               | 113.4                     | 4                                     | Harrisson, 1963            |
| Sarawak                       | 4              | C               | 132.1                     | —                                     | Harrisson, 1963            |
| Colombia                      | 7              | C               | 174.2                     | —                                     | Kaufmann, 1972             |
| Torres Strait                 | 2              | W               | 90.6                      | —                                     | Kowarsky and Capelle, 1979 |
| St. Thomas                    | 3              | C               | 192.8                     | —                                     | Schmidt, 1916              |
| Samoa                         | 6              | C               | 172.3                     | 3.5                                   | Witzell, 1980              |
| <i>Lepidochelys kempii</i>    |                |                 |                           |                                       |                            |
| Florida                       | 2              | C               | 42.0                      | —                                     | Caldwell, 1962             |
| Mexico                        | —              | C               | 105.0                     | —                                     | Marquez, 1972              |
| juveniles                     | —              | C               | 105.0                     | —                                     | Marquez, 1972              |
| adult females                 | >10            | W               | 35.0                      | 5.5                                   | Marquez, 1972              |
| <i>Lepidochelys olivacea</i>  |                |                 |                           |                                       |                            |
| India                         | 15             | C               | 125.2                     | —                                     | Rajagopalan, 1984          |
| India                         | 19             | C               | 143.3                     | —                                     | Rajagopalan, 1984          |
| Sri Lanka                     | 3              | C               | 52.7                      | —                                     | Deraniyagala, 1939         |
| Sri Lanka                     | 1              | C               | 188.4                     | —                                     | Deraniyagala, 1939         |

## Part 4

Summary of selected references on minimum size and estimated ages at sexual maturity in miscellaneous freshwater and terrestrial turtles. The data listed below may not match the values listed in the references, because we may have abstracted the original data or extracted the data from graphs or figures. (Abbreviation: PL, body size given as plastron length rather than as carapace length.)

| Species<br>Locality            | Minimum size<br>at maturity<br>(CL, mm) | Age of<br>maturity (yrs) | Reference                   |
|--------------------------------|---|--------------------------|-----------------------------|
| <i>Chelydra serpentina</i>     |   |                          |                             |
| Iowa ♀♀                        | 210                                     | 6-10                     | Christiansen & Burken, 1979 |
| Iowa ♂♂                        | 190                                     | 4-5                      | Christiansen & Burken, 1979 |
| Quebec ♀♀                      | 200                                     | -                        | Mosimann & Bider, 1960      |
| Tennessee                      | 145                                     | -                        | White & Murphy, 1973        |
| <i>Chrysemys picta</i>         |   |                          |                             |
| All ♀♀                         | 120-130 (PL)                            | -                        | Cagle, 1954                 |
| Michigan ♂♂                    | 90 (PL)                                 | 3-4                      | Cagle, 1954                 |
| Illinois ♂♂                    | 70 (PL)                                 | 2-3                      | Cagle, 1954                 |
| Louisiana ♂♂                   | 50-60 (PL)                              | 1                        | Cagle, 1954                 |
| Pennsylvania ♀♀                | 110 (PL)                                | 5-6                      | Ernst, 1971                 |
| Pennsylvania ♂♂                | 80-90 (PL)                              | 4-5                      | Ernst, 1971                 |
| Michigan ♀♀                    | 120-130                                 | 6-7                      | Wilbur, 1975                |
| Michigan ♂♂                    | 90-105                                  | 4-5                      | Wilbur, 1975                |
| <i>Clemmys guttata</i>         |   |                          |                             |
| Pennsylvania ♀♀, ♂♂            | 80-90 (PL)                              | 7-10                     | Ernst, 1975                 |
| <i>Emydoidea blandingii</i>    |   |                          |                             |
| Massachusetts ♂♂               | 180-190                                 | 9-11                     | Graham & Doyle, 1977        |
| <i>Geochelone elephantopus</i> |   |                          |                             |
| <i>hoodensis</i> ♀♀            | 550                                     | >30                      | MacFarland et al., 1974     |
| <i>hoodensis</i> ♂♂            | 700                                     | >30                      | MacFarland et al., 1974     |
| <i>porteri</i> ♀♀              | 800                                     | >30                      | MacFarland et al., 1974     |
| <i>porteri</i> ♂♂              | 950                                     | >30                      | MacFarland et al., 1974     |
| <i>Geochelone gigantea</i>     |   |                          |                             |
| Malabar ♀♀                     | -                                       | 16-18                    | Swingland & Coe, 1978       |
| Grand Terre ♀♀                 | -                                       | 22-24                    | Swingland & Coe, 1978       |
| <i>Kinosternon flavescens</i>  |   |                          |                             |
| Oklahoma                       | 80                                      | 5-6                      | Mahmoud, 1967               |
| <i>Kinosternon subrubrum</i>   |   |                          |                             |
| Florida                        | 80                                      | 6-7                      | Ernst et al., 1973          |
| Oklahoma                       | 80                                      | 5-6                      | Mahmoud, 1967               |
| <i>Macroclemys temminckii</i>  |   |                          |                             |
| Louisiana                      | 340-400                                 | 11-13                    | Dobie, 1971                 |
| <i>Malaclemys terrapin</i>     |   |                          |                             |
| N. Carolina captive ♀♀         | 120-140                                 | 5-9                      | Hildebrand, 1932            |
| N. Carolina captive ♂♂         | 80-90                                   | 2-6                      | Hildebrand, 1932            |

Part 4.—*Continued.*

| Species<br>Locality           | Minimum size<br>at maturity<br>(CL, mm) | Age of<br>maturity (yrs) | Reference             |
|-------------------------------|---|--------------------------|-----------------------|
| <i>Pseudemys floridana</i>    |   |                          |                       |
| S. Carolina ♀♀                | 200–240 (PL)                            | 6–7                      | Gibbons & Coker, 1977 |
| S. Carolina ♂♂                | 100–120 (PL)                            | 3–4                      | Gibbons & Coker, 1977 |
| <i>Sternotherus carinatus</i> |   |                          |                       |
| Oklahoma                      | 80                                      | 4                        | Mahmoud, 1967         |
| <i>Sternotherus odoratus</i>  |   |                          |                       |
| Oklahoma                      | 65                                      | 5–6                      | Mahmoud, 1967         |
| <i>Terrapene ornata</i>       |   |                          |                       |
| Kansas ♀♀                     | 110–120                                 | 6–11                     | Legler, 1960          |
| Kansas ♂♂                     | 100–110                                 | 4–9                      | Legler, 1960          |
| <i>Trachemys scripta</i>      |   |                          |                       |
| S. Carolina: Ellent. Bay ♀♀   | 160–170 (PL)                            | 7                        | Gibbons et al., 1981  |
| S. Carolina: Ellent. Bay ♂    | 80–100 (PL)                             | 4                        | Gibbons et al., 1981  |
| S. Carolina: Par Pond ♀♀      | 200–210 (PL)                            | 7                        | Gibbons et al., 1981  |
| S. Carolina: Par Pond ♂♂      | 80–100 (PL)                             | 3                        | Gibbons et al., 1981  |
| Illinois natural ♀♀           | 170–195                                 | 4–5                      | Thornhill, 1982       |
| Illinois: heated ♂♂           | 185–190                                 | 3–4                      | Thornhill, 1982       |

## Literature Cited

- Balazs, George H.  
1979. Growth, Food Sources and Migrations of Immature Hawaiian *Chelonia*. *Marine Turtle Newsletter*, (10):1-3.  
1980. Synopsis of Biological Data on the Green Turtle in the Hawaiian Islands. *NOAA Technical Memorandum NMFS*, 141 pages.  
1982. Growth Rates of Immature Green Turtles in the Hawaiian Archipelago. In Karen A. Bjorndal, editor, *Biology and Conservation of Sea Turtles*, pages 117-125. Washington, D.C.: Smithsonian Institution Press.
- Baldwin, William P., Jr., and John P. Lofton, Jr.  
1959. The Loggerhead Turtles of Cape Romain, South Carolina. *Bulletin of the Florida State Museum, Biological Sciences*, 4(10):319-448.
- Bjorndal, Karen A., Anne B. Meylan, and Billy J. Turner  
1983. Sea Turtles Nesting at Melbourne Beach, Florida, I: Size, Growth and Reproductive Biology. *Biological Conservation*, 26:65-77.
- Boulon, Ralf H., Jr.  
1983. *Some Notes on the Population Biology of Green (Chelonia mydas) and Hawksbill (Eretmochelys imbricata) Turtles in Northern U.S. Virgin Islands: 1981-83*. 18 pages. [Report to National Marine Fisheries Service, NA 82-GA-A-00044.]
- Bourke, R.E., G. Balazs, and E.W. Shallenberger  
1977. Breeding of the Sea Turtle (*Chelonia mydas*) at Sea Life Park, Hawaii. *Drum and Croaker*, 17(2):4-9.
- Brown, Robert A., Guy C. McN. Harvey, and Lesley A. Wilkins  
1982. Growth of Jamaican Hawksbill Turtles (*Eretmochelys imbricata*) Reared in Captivity. *British Journal of Herpetology*, 6(7):233-236.
- Cagle, Fred R.  
1954. Observations on the Life Cycles of Painted Turtles (Genus *Chrysemys*). *American Midland Naturalist*, 52(1):225-235.
- Caldwell, David K.  
1962. Growth Measurements of Young Captive Atlantic Sea Turtles in Temperate Waters. *Los Angeles County Museum, Contributions in Science*, (50):1-8.
- Caldwell, David K., Archie Carr, and Thomas R. Hellier, Jr.  
1955. Natural History Notes on the Atlantic Loggerhead Turtle, *Caretta caretta caretta*. *Quarterly Journal of the Florida Academy of Science*, 18(4):292-302.
- Caldwell, David K., Archie Carr, and Larry H. Ogren  
1959. Nesting and Migration of the Atlantic Loggerhead Turtle. *Bulletin of the Florida State Museum, Biological Sciences*, 4(10):295-308.
- Carr, Archie, and Donald Goodman  
1970. Ecological Implications of Size and Growth in *Chelonia*. *Copeia*, 1970(4):783-786.
- Castanet, Jacques  
1982. Recherches sur la Croissance du Tissu Osseux des Reptiles. Application: La Methode Squeletto-chronologique. Doctoral dissertation, University of Paris, VII, 191 pages.
- Castanet, Jacques, and Marc Cheylan  
1979. Les marques de croissance des os et des ecailles comme indicateur de l'âge chez *Testudo hermanni* et *Testudo graeca* (Reptilia, Chelonia, Testudini-dae). *Canadian Journal of Zoology*, 57(8):1649-1665.
- Castanet, Jacques, Jean-Pierre Gasc, François Meunier, and Armand de Ricqlès  
1970. Calcium et nature des zones de croissance cyclique dans l'os des vertebres poikilothermes. *Compte Rendu Academie de Science Paris, series D*, 270:2853-2856.
- Castanet, Jacques, F.J. Meunier, and A. de Ricqlès  
1977. L'enregistrement de la croissance cyclique par le tissu osseux chez les vertebres poikilothermes: donnees comparatives et essai de synthese. *Bulletin Biologique de la France et de la Belgique*, 111(2):183-202.
- Castanet, Jacques, and Guy Naulleau  
1974. Données expérimentales sur la valeur des marques squelettiques comme indicateur de l'âge chez *Vipera aspis* (L.) (Ophidia, Viperidae). *Zoologica Scripta*, 3(2):201-208.
- Christiansen, James L., and Russell R. Burken  
1979. Growth and Maturity of the Snapping Turtle (*Chelydra serpentina*) in Iowa. *Herpetologica*, 35(3):261-266.
- de Buffrenil, Vivian  
1980. Mise en évidence de l'incidence des conditions de milieu sur la croissance de *Crocodylus siamensis* (Schneider, 1801) et valeur des marques de croissance squelettiques pour l'évaluation de l'âge individuel. *Archives de Zoologie experimentale et generale*, 121(1):63-76.

- Deraniyagala, P.E.P.  
1939. *The Tetrapod Reptiles of Ceylon*. Volume 1, Testudines and Crocodylians. Colombo: Colombo Museum.
- Diamond, A.W.  
1976. Breeding Biology and Conservation of Hawksbill Turtles, *Eretmochelys imbricata* L., on Cousin Island, Seychelles. *Biological Conservation*, 9(3):199-215.
- Dobie, James L.  
1971. Reproduction and Growth in the Alligator Snapping Turtle, *Macrochelys temmincki* (Troost). *Copeia*, 1971(4):645-658.
- Ehrhart, L.M., and R.G. Yoder  
1978. Marine Turtles of Merritt Island National Wildlife Refuge, Kennedy Space Center, Florida. In G.E. Henderson, editor, Proceedings of the Florida and Interrregional Conference on Sea Turtles, 24-25 July 1976. *Florida Marine Research Publication*, 33:25-30. Jensen Beach, Florida.
- Enlow, Donald H.  
1969. The Bones of Reptiles. In C. Gans, T.S. Parsons, and A. d'A. Bellairs, editors, *Biology of the Reptilia*, volume 1:45-80. London: Academic Press.
- Ernst, Carl H.  
1971. Sexual Cycles and Maturity of the Turtle *Chrysemys picta*. *Biological Bulletin*, 140(2):191-200.  
1975. Growth of the Spotted Turtle, *Clemmys guttata*. *Journal of Herpetology*, 9(3):313-318.
- Ernst, Carl H., Roger W. Barbour, Evelyn M. Ernst, and James R. Butler  
1973. Growth of the Mud Turtle, *Kinosternon subrubrum*, in Florida. *Herpetologica*, 29(3):247-250.
- Frazer, Nat B.  
1982. Growth and Age at Maturity of Loggerhead Sea Turtles: Review and Prospectus. *Marine Turtle Newsletter*, 22:5-8.
- Frazer, Nat B., and Llewellyn M. Ehrhart  
1985. Preliminary Growth Models for Green, *Chelonia mydas*, and Loggerhead, *Caretta caretta*, Turtles in the Wild. *Copeia*, 1985(1):73-79.
- Frazer, Nat B., and Frank J. Schwartz  
1984. Growth Curves for Captive Loggerhead Turtles, *Caretta caretta*, in North Carolina, USA. *Bulletin of Marine Science*, 34(4):485-489.
- Frazier, John  
1982. *Aging Studies of Sea Turtles*. 133 pages. [Report to the National Marine Fisheries Service, NA 81-GA-C-00018, and the U.S. Fish and Wildlife Service, NA 81-GF-A-184.]
- Gallagher, Robert M., Malcolm L. Hollinger, Robert M. Ingle, and Charles R. Futch  
1972. Marine Turtle Nesting on Hutchinson Island, Florida, in 1971. *Florida Department of Natural Resources, Marine Research Laboratory Special Report*, (37):1-11.
- Gibbons, J. Whitfield  
1967. Variation in Growth Rates in Three Populations of the Painted Turtle, *Chrysemys picta*. *Herpetologica*, 23(4):296-303.
- Gibbons, J. Whitfield, and John W. Coker  
1977. Ecological and Life History Aspects of the Cooter, *Chrysemys floridana* (Le Conte). *Herpetologica*, 33(1):29-33.
- Gibbons, J. Whitfield, Raymond D. Semlitsch, Judith L. Greene, and Joseph P. Schubauer  
1981. Variation in Age and Size at Maturity of the Slider Turtle (*Pseudemys scripta*). *American Naturalist*, 117:841-845.
- Graham, Terry E., and Timothy S. Doyle  
1977. Growth and Population Characteristics of Blanding's Turtle, *Emydoidea blandingii*, in Massachusetts. *Herpetologica*, 33(4):410-414.
- Hammer, Donald A.  
1969. Parameters of a Marsh Snapping Turtle Population, Lacreek Refuge, South Dakota. *Journal of Wildlife Management*, 33(4):995-1005.
- Harrison, Tom  
1963. Notes on Marine Turtles: 13—Growth Rate of the Hawksbill. *The Sarawak Museum Journal*, 11(21, 22):302-303.
- Hemelaar, A.S.M., and J.J. van Gelder  
1980. Annual Growth Rings in Phalanges of *Bufo bufo* (Anura, Amphibia) from the Netherlands and Their Use for Age Determination. *Netherlands Journal of Zoology*, 30(1):129-135.
- Hendrickson, John R.  
1958. The Green Sea Turtle, *Chelonia mydas* (Linn.), in Malaya and Sarawak. *Proceedings of the Zoological Society of London*, 130(4):455-535.
- Henwood, T.  
In prep. Age, Growth, and Survival in Loggerhead Sea Turtles, *Caretta caretta*.
- Hildebrand, Samuel F.  
1932. Growth of Diamond-back Terrapins, Size Attained, Sex Ratio and Longevity. *Zoologica*, 9(15):551-563.
- Hildebrand, Samuel F., and Charles Hatsel  
1927. On the Growth, Care and Behavior of Loggerhead Turtles in Captivity. *Proceedings of the National Academy of Sciences*, 13(6):374-377.
- Hohn, A., and J. Frazier  
1979. Growth Layers in Bones and Scutes of Sea Turtles: A Possible Aging Method [abstract]. *American Zoologist*, 19(3):953.
- Hulse, Arthur C.  
1976. Growth and Morphometrics of *Kinosternon sonoriense* (Reptilia, Testudines, Kinosternidae). *Jour-*

- nal of Herpetology*, 10(4):341–348.
- Kaufmann, Reinhard  
1972. Wachstumsraten in Gefangenschaft gehaltener Meeresschildkroten, II. *Instituto Colombo-Aleman, Investigaciones Cientificas*, 6:105–112.
- Kowarsky, John, and Mikael Capelle  
1979. Returns of Pond-reared Juvenile Green Turtles Tagged and Released in Torres Strait, Northern Australia. *Biological Conservation*, 15(3):207–214.
- Legler, John M.  
1960. Natural History of the Ornate Box Turtle, *Terrapene ornata ornata* Agassiz. *University of Kansas Publications, Museum of Natural History*, 11(10):527–669.
- Limpus, Colin  
1979. Notes on Growth Rates of Wild Turtles. *Marine Turtle Newsletter*, (10):3–5.
- Limpus, Colin, and David G. Walter  
1980. The Growth of Immature Green Turtles (*Chelonia mydas*) under Natural Conditions. *Herpetologica*, 36(2):162–165.
- MacFarland, Craig G., José Villa, and Basilio Toro  
1974. The Galapagos Giant Tortoises (*Geochelone elephantopus*), Part I: Status of Surviving Populations. *Biological Conservation*, 6(2):118–133.
- Mahmoud, I.Y.  
1967. Courtship Behavior and Sexual Maturity in Four Species of Kinosternid Turtles. *Copeia*, 1967(2):314–319.
- Márquez, René  
1972. Resultados preliminares sobre edad y crecimiento de la tortuga lora, *Lepidochelys kempi* (Garman). In *Memorias IV Congreso Nacional de Oceanografía, Mexico, D.F., 17–19 Noviembre 1969*, pages 419–427.
- Mattox, Norman T.  
1936. Annular Rings in the Long Bones of Turtles and Their Correlation with Size. *Transactions of the Illinois State Academy of Science*, [1935] 28(2):255–256.
- Mendonca, Mary T.  
1981. Comparative Growth Rates of Wild Immature *Chelonia mydas* and *Caretta caretta* in Florida. *Journal of Herpetology*, 15(4):447–451.
- Minakami, Korebumi  
1979. An Estimation of Age and Life Span of the Genus *Trimeresurus* (Reptilia, Serpentes, Viperidae) on Amani Oshima Island, Japan. *Journal of Herpetology*, 13(2):147–152.
- Moorhouse, F.W.  
1933. Notes on the Green Turtle (*Chelonia mydas*). *Report of the Great Barrier Reef Committee*, 4(1):1–22.
- Mosimann, James E., and J. Roger Bider  
1960. Variation, Sexual Dimorphism, and Maturity in a Quebec Population of the Common Snapping Turtle, *Chelydra serpentina*. *Canadian Journal of Zoology*, 38(1):19–38.
- Nuitja, I. Njoman S., and I. Uchida  
1982. Preliminary Studies on the Growth and Food Consumption of the Juvenile Loggerhead Turtle (*Caretta caretta* L.) in Captivity. *Aquaculture*, 27(2):157–160.
- Parmenter, Robert R.  
1980. Effects of Food Availability and Water Temperature on the Feeding Ecology of Pond Sliders (*Chrysemys s. scripta*). *Copeia*, 1980(3):503–514.
- Parker, G.H.  
1926. The Growth of Turtles. *Proceedings of the National Academy of Science*, 12(7):422–424.  
1929. The Growth of the Loggerhead Turtle in Captivity. *American Naturalist*, 63(687):367–373.
- Peabody, Frank E.  
1961. Annual Growth Zones in Living and Fossil Vertebrates. *Journal of Morphology*, 108(1):11–62.
- Pilorge, Thierry, and Jacques Castanet  
1981. Détermination l'âge dans une population naturelle du lézard vivipare (*Lacerta vivipara* Jacquin 1787). *Acta OEcologica/OEcologia Generalis*, 2(1):3–16.
- Rajagopalan, M.  
1984. Studies on the Growth of Olive Ridley *Lepidochelys olivacea* in Captivity. *Central Marine Fisheries Research Institute (India)*, 35:49–54.
- Rebel, Thomas P.  
1974. *Sea Turtles and the Turtle Industry of the West Indies, Florida, and the Gulf of Mexico*. 250 pages, Coral Gables, Florida: University of Miami Press.
- Rhodin, Anders G.J.  
1985. Comparative Chondro-osseous Development and Growth of Marine Turtles. *Copeia*, 1985(3):752–771.
- Rhodin, Anders G.J., John A. Ogden and Gerald J. Conlogue  
1981. Chondro-osseous Morphology of *Dermochelys coriacea*, a Marine Reptile with Mammalian Skeletal Features. *Nature*, 290(5803):244–246.
- Romer, Alfred Sherwood  
1956. *Osteology of the Reptiles*. 772 pages. Chicago: University of Chicago Press.
- Ruckdeschel, Carol, and George R. Zug  
1980. Marine Turtles [1979 Strandings on Cumberland Island]. *SEAN Bulletin*, 5(2):14–16.  
1981. 1980 Marine Turtle Stranding Survey Cumberland Island, Georgia. *SEAN Bulletin*, 6(2):20–21.
- Schmidt, Johs.  
1916. Marking Experiments with Turtles in the Danish West Indies. *Meddelser fra Kommissionen for Havundersogelser, Serie Fiskeri*, 5(1):1–26.

- Stickney, Robert R., David B. White, and Daniel Perlmutter  
1973. Growth of Green and Loggerhead Sea Turtles in Georgia on Natural and Artificial Diets. *Bulletin of the Georgia Academy of Science*, 31:37-44.
- Stoneburner, D.L.  
1980. Body Depth: An Indicator of Morphological Variation among Nesting Groups of Adult Loggerhead Sea Turtles (*Caretta caretta*). *Journal of Herpetology*, 14(2):205-206.
- Suzuki, Howard K.  
1963. Studies on the Osseous System of the Slider Turtle. *Annals of the New York Academy of Sciences*, 109(1):351-410.
- Swingland, Ian R., and Malcolm Coe  
1978. The Natural Regulation of Giant Tortoises Populations on Aldabra Atoll: Reproduction. *Journal of Zoology, London*, 186:285-309.
- Thornhill, Gary M.  
1982. Comparative Reproduction of the Turtle, *Chrysemys scripta elegans*, in Heated and Natural Lakes. *Journal of Herpetology*, 16(4):347-353.
- Toquin, A. Le., E. Gamel, and J. Trotignon  
1980. Morphologie, croissance individuelle et dynamique des populations de la tortue verte (*Chelonia mydas* L.) au Banc d'Arguin (Republique Islamique de Mauritanie). *Revue d'Ecologie, Terre et Vie*, 34:271-302.
- Uchida, Itaru  
1967. On the Growth of the Loggerhead Turtle, *Caretta caretta*, under Rearing Conditions. *Bulletin of the Japanese Society of Scientific Fisheries*, 33(6):497-507.
- White, James B., and George G. Murphy  
1973. The Reproductive Cycle and Sexual Dimorphism of the Common Snapping Turtle, *Chelydra serpentina serpentina*. *Herpetologica*, 29(3):240-246.
- Wilbur, Henry M.  
1975. The Evolutionary and Mathematical Demography of the Turtle *Chrysemys picta*. *Ecology*, 56(1):64-77.
- Witham, Ross  
1971. Breeding of a Pair of Pen-reared Green Turtles. *Quarterly Journal of the Florida Academy of Science* [1970], 33(4):288-290.
- Witham, R., and C. Futch  
1977. Early Growth and Oceanic Survival of Pen-reared Sea Turtles. *Herpetologica*, 33(4):404-409.
- Witzell, W.N.  
1980. Growth of Captive Hawksbill Turtles, *Eretmochelys imbricata*, in Western Samoa. *Bulletin of Marine Science*, 30(4):909-912.
- Wood, James R., and Fern E. Wood  
1980. Reproductive Biology of Captive Green Sea Turtles *Chelonia mydas*. *American Zoologist*, 20(3):499-505.
1981. Growth and Digestibility for the Green Turtle (*Chelonia mydas*) Fed Diets Containing Varying Protein Levels. *Aquaculture*, 25:269-274.
- Zug, G.R., A.S. Rand, A.H. Wynn, and B. Bock  
1983. Skeletochronology of Panamanian *Iguana iguana*: A Test of Annual Periosteal Growth [abstract]. Program of Twenty-sixth Annual Meeting (SSAR) and Thirty-first Annual Meeting, HL, page 100.
- Zug, George R., Addison Wynn, and Carol Ruckdeschel  
1983. Age Estimates of Cumberland Island Loggerhead Sea Turtles. *Marine Turtle Newsletter*, (25):9-11.







## REQUIREMENTS FOR SMITHSONIAN SERIES PUBLICATION

**Manuscripts** intended for series publication receive substantive review (conducted by their originating Smithsonian museums or offices) and are submitted to the Smithsonian Institution Press with Form SI-36, which must show the approval of the appropriate authority designated by the sponsoring organizational unit. Requests for special treatment—use of color, foldouts, case-bound covers, etc.—require, on the same form, the added approval of the sponsoring authority.

**Review** of manuscripts and art by the Press for requirements of series format and style, completeness and clarity of copy, and arrangement of all material, as outlined below, will govern, within the judgment of the Press, acceptance or rejection of manuscripts and art.

**Copy** must be prepared on typewriter or word processor, double-spaced, on one side of standard white bond paper (not erasable), with 1¼" margins, submitted as ribbon copy (not carbon or xerox), in loose sheets (not stapled or bound), and accompanied by original art. Minimum acceptable length is 30 pages.

**Front matter** (preceding the text) should include: **title page** with only title and author and no other information, **abstract** page with author, title, series, etc., following the established format; table of **contents** with indents reflecting the hierarchy of heads in the paper; also, **foreword** and/or **preface**, if appropriate.

**First page of text** should carry the title and author at the top of the page; **second page** should have only the author's name and professional mailing address, to be used as an unnumbered footnote on the first page of printed text.

**Center heads** of whatever level should be typed with initial caps of major words, with extra space above and below the head, but no other preparation (such as all caps or underline, except for the underline necessary for generic and specific epithets). Run-in paragraph heads should use period/dashes or colons as necessary.

**Tabulations** within text (lists of data, often in parallel columns) can be typed on the text page where they occur, but they should not contain rules or numbered table captions.

**Formal tables** (numbered, with captions, boxheads, stubs, rules) should be submitted as carefully typed, double-spaced copy separate from the text; they will be typeset unless otherwise requested. If camera-copy use is anticipated, do not draw rules on manuscript copy.

**Taxonomic keys** in natural history papers should use the aligned-couplet form for zoology and may use the multi-level indent form for botany. If cross referencing is required between key and text, do not include page references within the key, but number the keyed-out taxa, using the same numbers with their corresponding heads in the text.

**Synonymy** in zoology must use the short form (taxon, author, year:page), with full reference at the end of the paper under "Literature Cited." For botany, the long form (taxon, author, abbreviated journal or book title, volume, page, year, with no reference in "Literature Cited") is optional.

**Text-reference system** (author, year:page used within the text, with full citation in "Literature Cited" at the end of the text) must be used in place of bibliographic footnotes in all Contributions Series and is strongly recommended in the Studies Series: "(Jones, 1910:122)" or "... Jones (1910:122)." If bibliographic

footnotes are required, use the short form (author, brief title, page) with the full citation in the bibliography.

**Footnotes**, when few in number, whether annotative or bibliographic, should be typed on separate sheets and inserted immediately after the text pages on which the references occur. Extensive notes must be gathered together and placed at the end of the text in a notes section.

**Bibliography**, depending upon use, is termed "Literature Cited," "References," or "Bibliography." Spell out titles of books, articles, journals, and monographic series. For book and article titles use sentence-style capitalization according to the rules of the language employed (exception: capitalize all major words in English). For journal and series titles, capitalize the initial word and all subsequent words except articles, conjunctions, and prepositions. Transliterate languages that use a non-Roman alphabet according to the Library of Congress system. Underline (for italics) titles of journals and series and titles of books that are not part of a series. Use the parentheses/colon system for volume (number): pagination: "10(2):5-9." For alignment and arrangement of elements, follow the format of recent publications in the series for which the manuscript is intended. Guidelines for preparing bibliography may be secured from Series Section, SI Press.

**Legends** for illustrations must be submitted at the end of the manuscript, with as many legends typed, double-spaced, to a page as convenient.

**Illustrations** must be submitted as original art (not copies) accompanying, but separate from, the manuscript. Guidelines for preparing art may be secured from Series Section, SI Press. All types of illustrations (photographs, line drawings, maps, etc.) may be intermixed throughout the printed text. They should be termed **Figures** and should be numbered consecutively as they will appear in the monograph. If several illustrations are treated as components of a single composite figure, they should be designated by lowercase italic letters on the illustration; also, in the legend and in text references the italic letters (underlined in copy) should be used: "Figure 9b." Illustrations that are intended to follow the printed text may be termed **Plates**, and any components should be similarly lettered and referenced: "Plate 9b." Keys to any symbols within an illustration should appear on the art rather than in the legend.

**Some points of style:** Do not use periods after such abbreviations as "mm, ft, USNM, NNE." Spell out numbers "one" through "nine" in expository text, but use digits in all other cases if possible. Use of the metric system of measurement is preferable; where use of the English system is unavoidable, supply metric equivalents in parentheses. Use the decimal system for precise measurements and relationships, common fractions for approximations. Use day/month/year sequence for dates: "9 April 1976." For months in tabular listings or data sections, use three-letter abbreviations with no periods: "Jan, Mar, Jun," etc. Omit space between initials of a personal name: "J.B. Jones."

**Arrange and paginate sequentially every sheet of manuscript** in the following order: (1) title page, (2) abstract, (3) contents, (4) foreword and/or preface, (5) text, (6) appendixes, (7) notes section, (8) glossary, (9) bibliography, (10) legends, (11) tables. Index copy may be submitted at page proof stage, but plans for an index should be indicated when manuscript is submitted.

