

The Origin of Marine Turtles: A Pluralistic View of Evolution

JOSEPH J. KINNEARY¹

¹City of New York, Department of Environmental Protection,
Marine Section, Wards Island, New York 10035 USA

Turtles, an ecologically diverse group, are found throughout the tropics and most of the world's temperate regions. Their distribution appears to be limited primarily by climatic conditions of higher latitudes and altitudes (Obst, 1986). Although turtles have apparently evolved from terrestrial stem groups (Carroll, 1988; Reisz and Laurin, 1991; Lee, 1993), most of the 257 living species can be found in aquatic (freshwater) habitats (Ernst and Barbour, 1989). Some groups, such as the land tortoises (Testudinidae) and several emydid genera including *Pixidea*, *Geoemyda*, and *Terrapene*, have secondarily adapted to a terrestrial existence (McDowell, 1964; Pritchard and Trebbau, 1984; Ernst and Barbour, 1989). Relatively few living turtles are marine. Seven species of sea turtles (Dermochelyidae, Cheloniidae) and one emydid (*Malaclemys*) are found primarily in marine or estuarine habitats in which the water salinity is more concentrated than the turtle's body fluids. Several species are occasionally found in brackish water (Dunson, 1984; Dunson and Mazzotti, 1989).

There are numerous fossil groups which are presumed to be marine. A conservative approach would suggest that 24 marine (including estuarine) taxa have evolved from at least four separate freshwater aquatic or semiaquatic lineages within the microorder Chelonioida and families Plesiochelyidae, Pelomedusidae, and Emydidae (after Gaffney and Meylan, 1988). Physiological evidence, showing a gradation in osmoregulatory adaptations to hyperosmotic water in extant species (Dunson, 1984, 1986; Dunson and Mazzotti, 1989), reinforces the inference that marine lineages have evolved from freshwater aquatic or semiaquatic ancestors.

Some marine taxa have morphological characteristics which appear to be functionally related to a pelagic existence. The Chelonioida, which includes all present-day groups and 16 extinct genera of sea turtles, can be united on the basis of features of the forelimb such as digit elongation, restricted joint surfaces and changes in the humerus, and carpal and tarsal elements (Gaffney and Meylan, 1988). The resulting flipper-like forelimb allows locomotion by means of dorsoventral strokes as contrasted by freshwater turtles, which propel their bodies by means of lateral strokes of the hind limbs (and in some cases all four limbs) (Zangerl, 1953; Walker, 1973). Other structural features which have been associated with adaptation to the marine environment include reduction in dermal bone (Zangerl, 1980), skeletal

growth patterns which may be unique to rapidly growing marine species (Rhodin, 1985), and a nearly or completely roofed skull which may be associated with the streamlining effect of a nonretractible neck (Pritchard and Trebbau, 1984).

The correlation of morphological change with adaptation to marine life is not always justified. *Carettochelys insculpta* is a relatively large turtle with marine-type flippers and mode of locomotion. Although it can apparently withstand brackish conditions, it is found primarily in freshwater habitats throughout its range in New Guinea and northern Australia (Ernst and Barbour, 1989; Georges and Rose, 1993). Wood (1976) has speculated that *Stupendemys geographicus*, a large fossil pelomedusid turtle, may have been a freshwater form in which one or both pairs of limbs were modified into flippers. Other fossil pelomedusid turtles (*Taphrosphys*) are generally presumed to be marine primarily because of their deposition in near-shore marine environments (Wood, 1972, 1975). Some extinct marine taxa included within the thalassemyid and toxochelyid groups (Zangerl, 1953; Zangerl and Sloan, 1960; Zangerl, 1980) show varying degrees of aquatic specialization with regard to the forelimb skeleton and, by inference, the mode of locomotion.

The initial shift to the marine environment undoubtedly involved extensive reliance on behavioral osmoregulation and acquisition of physiological specialization to reduce net water loss and net salt uptake. Feeding adaptations to reduce the incidental drinking of saline water may also be important (Table 1) (Dunson and Mazzotti, 1989). Evidence concerning the origin of changes in habitat is unlikely to be deciphered from the fossil record because changes in behavior, soft anatomy, and physiology are not preserved. In addition, while the shallow waters of continental margins and inland seas are ideal areas for the preservation and subsequent exposure of fossils, it may be difficult to determine whether the animals actually lived in this area, inhabited a more truly marine environment, or washed in from freshwater streams or lakes (Carroll, 1988). Although the salinity milieu of many fossil localities where marine forms have been found can be characterized on a general scale, a thorough understanding of adaptation to habitats along the saltwater-freshwater ecotone requires knowledge of microgeographical and temporal changes in water salinity. For example, the seas that spread over continents during mid and late Cretaceous periods of marine transgressions are associated with broad warm weather zones and widespread moist climates (Hallam, 1992). These epicontinental seas were probably characterized by sluggish circulation patterns (Vermeij, 1995). In these relatively stagnant, shallow seas it is likely that freshwater runoff from adjacent land and rainfall provided microhabitats of reduced salinity. The salinity relationships of the snapping turtle (*Chelydra serpentina*) show that nascent marine forms may spend only a limited amount of time in aquatic habitats hyperosmotic to body fluids, and water salinity can be a dominant factor limiting geographic

range (Kinneary, 1993) (Fig. 1; Table 2). Physiologically significant vertical salinity gradients and tidal fluctuations can also be important variables (Kinneary, 1992a, 1993).

The diamondback terrapin (*Malaclemys terrapin*), the only living turtle found exclusively in estuarine habitats, can serve as a model to illustrate how difficult it might be to gain an understanding of the incipient stages of marine adaptation from fossil evidence. This species, although possessing a unique suite of behavioral and physiological adaptations to the marine environment (Robinson and Dunson, 1976; Davenport and Macedo, 1990), is difficult to distinguish on osteological grounds from *Graptemys* and other closely related freshwater groups (McDowell, 1964; Wood, 1977). Fossil *Malaclemys* have been recovered from the same deposits as *Pseudemys nelsoni*, a species that physiological and distributional studies show is less tolerant of saline conditions (Dobie and Jackson, 1979; Dunson and Seidel, 1986). Likewise, in terms of traditional experimental science, the shift to a new adaptive zone is difficult to observe directly because it is a relatively slow process. A plausible causal scenario concerning the origin of marine turtles can be modeled through both experimentation and observation of natural populations, which show a gradation in use of marine habitats. The evidence suggests there are a multitude of pathways and causal factors involved.

Preadaptation. — An examination of groups that appear to be actively invading the marine environment suggests that preadaptations can be a factor in the evolution of marine forms. Preadaptation is used here in the same sense as exaptation (Gould and Vrba, 1982). The term describes a character that assumes a new use, occasionally facilitating a shift into a new habitat. Those typically freshwater species that are sometimes found in hyperosmotic habitats common to coastal areas, such as the North American snapping turtle (*Chelydra serpentina*) (Dunson, 1986; Kinneary, 1993), African and Asiatic softshell turtles (*Trionyx triunguis*, *Pelochelys bibroni*) (Pritchard, 1979; Rhodin et al., 1993), and Malaysian emydids (*Batagur baska*, *Callagur borneoensis*) (Dunson and Moll, 1980; Davenport and Wong,

1986) are relatively large turtles, suggesting that increased body size is a preadaptation (Moll, 1994). Although integumental permeability to water and ions and behavioral osmoregulation is of primary importance, particularly to nascent marine groups (Dunson, 1986; Mazzotti and Dunson, 1989), the skin is nevertheless a major site of water efflux even in the most advanced marine reptiles (Minnich, 1982). In the dehydrating conditions present in salt water, a relatively large body size, with the concomitant reduction in surface/volume ratio, is an advantage particularly to incipient marine forms without other adaptations. Experimental evidence confirms this hypothesis. Growth is reduced to zero in slider turtles, *Trachemys decussata*, at a significantly lower salinity for hatchlings than for juvenile turtles (Dunson and Seidel, 1986). Hatchling snapping turtles show a strong inverse correlation between body size and mass loss when in hyperosmotic brackish water (Kinneary, 1992a). In addition, although the data are inconclusive, it is of interest that of seven snapping turtles held in experimental enclosures in a brackish tidal creek, only the largest was able to maintain body weight (Table 2; Fig. 1). It is possible the size advantage is also due to ontogenetic change in some aspect of osmoregulatory physiology (Dunson, 1986). Large body size may also be an important advantage when the problems associated with thermoregulation in cold subpolar waters and the energetics of long distance travel are considered (Carr and Goodman, 1970; Hendrickson, 1980; Paladino et al., 1990).

Adaptive mechanisms for terrestrial survival can, at least in one case, be considered as a preadaptation for an estuarine existence. Mud turtles (*Kinosternon*) are generally considered to be aquatic turtles that spend a relatively large part of their life cycle in the terrestrial environment (Bennett et al., 1970; Gibbons, 1983; Frazer et al., 1991). Although they show little physiological specialization for life in saline water (Dunson, 1979, 1981), mud turtles do inhabit small islands in the Florida Keys (*K. baurii*) and along the Atlantic coast (*K. subrubrum*) in which the aquatic habitats are subject to wide fluctuations in salinity. They are apparently able to live in these high salinity areas by using terrestrial retreats when water salinities reach stressful levels (Gibbons and Coker, 1978; Dunson, 1981).

Direct Selection. — Ample evidence suggests that natural selection for marine adaptations is an important causal factor in the evolution of marine turtles. Direct selection operates on variations in a specific trait and, when such variation is genetically transmitted, it may result in differential representation of that trait which is more adaptive (Mitchell, 1992). Dunson (1986) studied coastal snapping turtles and found evidence for a salt marsh ecotype. Hatchlings from coastal Virginia grew faster in brackish than in freshwater, while inland New Jersey hatchlings grew faster in freshwater. I have reported on an estuarine population of the same species from coastal Long Island, New York (Kinneary, 1992b, 1993). Comparison with hatchlings from an inland New Jersey freshwater site showed that observed differences in the salinity of growth optima are due to a marked inability of the estuarine group to grow in freshwater

Table 1. The feeding habits, weight changes, and plasma osmotic concentrations of two snapping turtles captured on the south (sea) shore of Long Island, New York (Fig. 1B) and held for 25 days each in fresh (tap) and then brackish water (Instant Ocean) in a 160 liter outdoor aquarium. Salinity (‰) and temperature (°C) were recorded daily. The turtles were offered whole sea smelt at irregular intervals, but at least once per week. The number of fish consumed over a 2–3 hour period was recorded and any remaining food was removed from the tank (Kinneary, 1992a). Values are means ± SD, weights in kg.

	Initial Weight	Final Weight	% Change In Weight	Temp. (°C)	Plasma Osmotic Concentration (mOsmolal)		% Food Consumed
					Initial	Final	
Freshwater	5.6	5.6	0	26.9 ± 2.2	275.0	273.0	100
Brackish	5.6	5.1	-8.9	24.5 ± 2.9	273.0	374.5	*

* When switched to brackish water both turtles continued to feed, consuming 90% of the food offered at three feeding periods during the first 10 days (salinity = 13.2 ± 2.3 ‰); however the animals refused to eat for the remainder of the 25 day test period (salinity = 12.7 ± 3.4 ‰).



Figure 1. Snapping turtles, *Chelydra serpentina*, were kept individually in wire holding pens (A) at capture sites in a brackish tidal creek (B) on the south shore of Long Island, New York. Comparison with a freshwater control suggests water salinity is a dominant factor limiting snapping turtle distribution (Kinneary, 1993).

rather than to enhanced growth in saline water. Physiological evidence together with the glacial history of the study area suggests the coastal group represents a very early stage in the evolution of adaptation to the marine environment.

Dunson and Mazzotti (1989) have reconstructed a general evolutionary sequence for the gradual selection for marine adaptations in reptiles. Their scenario concerns the problems associated with hypo-osmoregulation in seawater and follows a temporal hierarchy, extending from a primary reliance on behavioral osmoregulation to selection for the most derived conditions (development of large salt glands and external morphological changes for a pelagic life). The turtle kidney is unable to excrete urine hyperosmotic to the plasma (Dantzler, 1976). In the dehydrating conditions present in the marine environment, a turtle must use extrarenal mechanisms to aid in ion and water balance. Experimental evidence shows intraspecific geographic variation in water and electrolyte budgets in softshell turtles (*Apalone spinifer*) and snapping turtles from freshwater and brackish habitats (Seidel, 1975; Dunson, 1986).

The salt gland is a major route of extrarenal salt excretion in the most advanced marine groups, such as the sea turtles (Cheloniidae, Dermochelyidae) and the estuarine *Malaclemys terrapin*. It has evolved independently at least twice in the three groups from its "nonfunctional" homo-

logue, the lacrimal gland (Dunson, 1976). Although an empirically justified and general explanation for the evolution of changes in form and function of tissues and organs does not exist (Muller and Wagner, 1991), the evidence strongly suggests that salt glands have evolved as a direct selective response to the rigors of osmoregulation in seawater (Dunson, 1984).

Hendrickson (1980) has looked at selective factors other than those involving osmoregulation and derived an evolutionary history of sea turtles based upon the ecological strategies of modern groups. His scenario points to the vast physical extent of the ocean environment, remoteness of nesting beaches, and devastating mortality rates of hatchlings and juveniles as driving the selection for relatively large, highly mobile, and fecund marine forms.

Indirect Selection. — When a trait evolves as a secondary consequence of selection for a different suite of traits it is termed indirect selection (Mitchell, 1992). The distinction between direct and indirect selection is important because there may not always be a direct causal relationship between natural selection and the evolution of marine adaptations in turtles (Endler, 1986). For example, Dunson and Travis (1991) have shown that biotic factors, such as competition for food, and abiotic factors, such as water salinity, may play an integrative role in determining habitat segregation along abiotic clines. Dunson (1986) has suggested that interspecific competition is an important factor in determining the spatial distribution of turtles along salinity gradients. In this case the competitive interactions between species would have an incidental or indirect effect on the amount of selection pressure for physiological adaptation to salinity.

Similarly, the correlation of environmental variables may indirectly influence the results of natural selection. There is circumstantial evidence that nesting ecology, in those species of turtles which live near the freshwater-saltwater ecotone, has played an indirect but important role in the evolution of marine groups. In these habitats there is frequently a correlation between otherwise suitable nesting sites and physiologically stressful, high-salinity water.

In general, the criteria for nest site selection among species is variable. Physical factors such as soil type, amount of vegetation cover, steepness and compass direction of ground slope, and exposure to sunlight, apparently influence site selection (Burger and Montevecchi, 1975; Ehrenfeld, 1979). Moll (1994) considers the thermal environment of potential nesting habitat to be a primary factor influencing the selection of sea beach nesting sites by the freshwater *Trachemys scripta venusta* from Caribbean Costa Rica. In addition, the extremely high rates of egg and hatchling predation suggest that over evolutionary time this biotic factor is a major determinant of nest site selection (Mortimer, 1982). Hendrickson (1980) has suggested that predation by large land animals on adult turtles is the overriding factor in the selection for behavioral patterns leading to choices of isolated beaches for nesting marine turtles. The salinity of the aquatic environment to which hatchling turtles will be exposed does not appear to play a primary role in the

Table 2. The effect on body weight when snapping turtles were held in enclosures at capture sites of relatively high salinity (Fig. 1). To insure that food was not limiting, an excess was placed in the pens twice a week. Five specimens kept as a control at a nearby freshwater site showed no change in body weight (adapted from Kinneary, 1993). Values are \pm SD, weights in kg.

Specimen	Days in Enclosure	Salinity (‰)	Initial Weight	% Change In Weight	Remarks
1	11	14.2 \pm 0.6	2.5	-	Died at 11 days
2	16	10.3 \pm 4.1	3.0	-6.7	
3	21	10.5 \pm 3.3	3.3	-9.1	
4	27	9.6 \pm 3.5	3.4	-20.6	Died at 33 days
5	15	20.9 \pm 5.5	3.8	-26.7	
6	12	17.2 \pm 8.0	8.7	-12.6	
7	14	14.6 \pm 2.1	12.0	0	
Means:	16.6 \pm 5.6	13.9 \pm 4.2	5.2 \pm 3.6	-12.6 \pm 9.7	

selection of nesting sites in some populations (Dunson and Moll, 1980; Pritchard and Trebbau, 1984). It is likely that the choice of a nesting site is a compromise between opposing environmental constraints and selection factors.

Evidence suggests that some turtles nest at sites which expose hatchlings to stressful salinities and by inference, strong selection for the evolution of behavioral and physiological adaptations to the marine environment. Dunson (1985) has found that hatchling diamondback terrapins are unable to grow in the high salinities found in the vicinity of many nesting sites without periodic access to freshwater for drinking. *Callagur borneoensis* nests on Malaysian ocean beaches along with sea turtles. Hatchlings and juveniles are not physiologically specialized for high salinities (Davenport and Wong, 1986), yet they may traverse as much as 3 km of high-salinity water in order to reach suitable habitat (Dunson and Moll, 1980). There are reports of other typically non-marine species, such as *Batagur baska*, *Pelochelys bibroni*, and *Carettochelys insculpta*, occasionally using sea beach nesting sites (Georges and Rose, 1993; Rhodin et al., 1993; Moll, 1994). I have observed that snapping turtles from coastal Long Island, New York, will occasionally use nesting sites at which the nearest water is not suitable for hatchlings because of high salinity. Additional considerations concerning site fidelity and communal nesting behavior characteristic of some groups (Moll, 1978; Obbard and Brooks, 1980) indicate that nesting ecology may play an important role in the indirect selection of marine adaptations.

Chance Factors. — As in many evolutionary scenarios, chance must be considered as a causal factor in the evolution of marine adaptations in turtles. Stochastic factors play an important and oft forgotten role in natural selection. It is often a chance event which individuals survive predation and natural catastrophes (Mayr, 1988). Random events become particularly important when one considers the highly variable physical nature of salt marshes and other coastal habitats (Teal and Teal, 1969; Brown and Gibson, 1983). Sea-level variations due to tectonic movements and related climatic changes may be plausibly linked to the diversity of fossil marine taxa through increased provincialization and promotion of allopatric speciation (Vermeij, 1995). Zangerl

(1980) shows the temporal relationships for twenty toxochelyid taxa found in marine formations from coastal and interior North America. These groups extend from the Coniacian stage of the late Cretaceous to the beginning of the Paleocene, a period of about 23 million years, during which there is evidence for at least five significant marine transgression-regression events in the US western interior, with a maximum sea-level about 250 m above the present (Hallam, 1992). Glacial and interglacial sea level fluctuations along the US Atlantic and Gulf coasts during the Pliocene and Pleistocene are speculated to have been a factor in the evolution of the estuarine *Malaclemys* (McKown, 1972) and related freshwater *Graptemys* (Lovich and McCoy, 1992).

Conclusion

When the evolution of marine turtles is viewed from a holistic perspective, it can reasonably be inferred that a serendipitous constellation of causal factors must fall into place for evolutionary change to occur. Living taxa can be used to model different stages in the evolution of marine groups. For example, preadaptations, such as relatively large adult body size (*Chelydra serpentina*, *Pelochelys bibroni*), allow increased use of marine habitats and possible selection for local ecotypes as exemplified by some coastal populations of snapping turtles (Dunson, 1986; Kinneary, 1992b).

The sea beach nesting patterns of slider turtles, *Trachemys scripta venusta*, illustrate how some of these causal factors may have been involved in the origin of marine forms. Relatively large body size of the adult female turtles, the coincidental correlation of suitable nesting habitat with physiologically stressful, high salinity aquatic habitat, and biotic factors concerning predation on adults, hatchlings, and eggs all appear to be factors resulting in marine excursions and selection of sea beach nesting sites (Pritchard and Trebbau, 1984; Moll, 1994). Moll (1994) has suggested that the relative gigantism characteristic of this slider turtle population has evolved in response to biotic and abiotic, direct and indirect selective pressures associated with the marine phase of its life history.

The vicariant events associated with past variations in sea level may also be considered as factors in the origin of marine taxa. Over evolutionary time a multitude of causal factors interact simultaneously and synergistically, making it difficult to assign them relative importance or temporal hierarchy. Preadaptations, together with various direct and indirect selection processes involving behavioral, physiological, and life history adaptations to marine life interact with stochastic factors both intrinsic and extrinsic to the organism. A pluralistic and dynamic viewpoint is necessary for a realistic understanding of much evolutionary change, particularly regarding the complex pathways associated with a shift to a new habitat.

Acknowledgments. — I thank William A. Dunson, Samuel B. McDowell, and anonymous reviewers for com-

ments on various drafts of the manuscript. Daniel C. Wilhoft offered much encouragement during the course of this study. Editorial comments by Anders G.J. Rhodin and Peter C.H. Pritchard are greatly appreciated. This work was drawn in part from a dissertation submitted to Rutgers University in partial fulfillment of the requirements for a Ph.D. degree. Partial funding was provided through grants from the Lerner-Gray Fund for Marine Research (AMNH) and the James D. Anderson Memorial Research Fund (Rutgers University).

Literature Cited

- BENNETT, D.H., GIBBONS, J.W., AND FRANSON, J.C. 1970. Terrestrial activity in aquatic turtles. *Ecology* 51:738-740.
- BROWN, J., AND GIBSON, A. 1983. *Biogeography*. St. Louis: C.V. Mosby, 643 pp.
- BURGER, J., AND MONTEVECCHI, W.A. 1975. Nest site selection in the terrapin *Malaclemys terrapin*. *Copeia* 1975:113-119.
- CARR, A., AND GOODMAN, D. 1970. Ecological implications of size and growth in Chelonia. *Copeia* 1970:783-786.
- CARROLL, R.L. 1988. *Vertebrate Paleontology and Evolution*. New York: W.H. Freeman and Company, pp. 192-216.
- DANTZLER, W.H. 1976. Renal function (with special emphasis on nitrogen excretion). In: Gans, C., and Dawson, W.R. (Eds.). *Biology of the Reptilia*. Vol. 5. New York: Academic Press, pp. 447-503.
- DAVENPORT, J., AND MACEDO, E.A. 1990. Behavioral osmotic control in the euryhaline diamondback terrapin *Malaclemys terrapin*: response to low salinity and rainfall. *J. Zool. (London)* 220:487-496.
- DAVENPORT, J., AND WONG, T.M. 1986. Observations on the water economy of the estuarine turtles *Batagur baska* (Gray) and *Callagur borneoensis* (Schlegel and Moller). *Comp. Biochem. Physiol.* 84A:703-707.
- DOBIE, J.L., AND JACKSON, D.R. 1979. First fossil record for the diamondback terrapin, *Malaclemys terrapin* (Emydidae), and comments on the fossil record of *Chrysemys nelsoni* (Emydidae). *Herpetologica* 35:139-145.
- DUNSON, W.A. 1976. Salt glands in reptiles. In: Gans, C. and Dawson, W.R. (Eds.). *Biology of the Reptilia*. Vol. 5. New York: Academic Press, pp. 413-441.
- DUNSON, W.A. 1979. Salinity tolerance and osmoregulation of the Key mud turtle, *Kinosternon b. bairii*. *Copeia* 1979:548-552.
- DUNSON, W.A. 1981. Behavioral osmoregulation in the Key mud turtle *Kinosternon b. bairii*. *J. Herpetol.* 15:163-173.
- DUNSON, W.A. 1984. The contrasting roles of the salt glands, the integument and behavior in osmoregulation of marine and estuarine reptiles. In: Pequeux, A., Giles, R., and Bolis, L. (Eds.). *Osmoregulation in Estuarine and Marine Animals*. Vol. 9. *Lecture Notes on Coastal and Estuarine Studies*. New York: Springer-Verlag, pp. 107-129.
- DUNSON, W.A. 1985. Effect of water salinity and food salt content on growth and sodium efflux of hatchling diamondback terrapins (*Malaclemys*). *Physiol. Zool.* 58:736-747.
- DUNSON, W.A. 1986. Estuarine populations of the snapping turtle (*Chelydra*) as a model for the evolution of marine adaptations in reptiles. *Copeia* 1986:741-756.
- DUNSON, W.A. AND MAZZOTTI, F. 1989. Salinity as a limiting factor in the distribution of reptiles in Florida Bay: a theory for the estuarine origin of marine snakes and turtles. *Bull. Mar. Sci.* 44:229-244.
- DUNSON, W.A. AND MOLL, E.O. 1980. Osmoregulation in sea water of hatchling emydid turtles, *Callagur borneoensis*, from a Malaysian sea beach. *J. Herpetol.* 14:31-36.
- DUNSON, W.A., AND SEIDEL, M. 1986. Salinity tolerance of estuarine and insular emydid turtles (*Pseudemys nelsoni* and *Trachemys decussata*). *J. Herpetol.* 20:235-243.
- DUNSON, W.A., AND TRAVIS, J. 1991. The role of abiotic factors in community organization. *Amer. Natur.* 138:1067-1091.
- EHRNFELD, D.W. 1979. Behavior associated with nesting. In: Harless, M., and Morlock, H. (Eds.). *Turtles, Perspectives and Research*. New York: John Wiley and Sons, pp. 417-434.
- ENDLER, J.A. 1986. *Natural Selection in the Wild*. New Jersey: Princeton University Press, 336 pp.
- ERNST, C.H., AND BARBOUR, R.W. 1989. *Turtles of the World*. Washington, D.C.: Smithsonian Institution Press, 313 pp.
- FRAZER, N.B., GIBBONS, J.W., AND GREENE, J.L. 1991. Life history and demography of the common mud turtle *Kinosternon subrubrum* in South Carolina, USA. *Ecology* 72:2218-2231.
- GAFFNEY, E.S., AND MEYLAN, P.A. 1988. A phylogeny of turtles. In: Benton, M.J. (Ed.). *The Phylogeny and Classification of the Tetrapods*. Vol. 1. Oxford: Clarendon Press, pp. 157-219.
- GEORGES, A., AND ROSE, M. 1993. Conservation biology of the pig-nosed turtle, *Carettochelys insculpta*. *Chelon. Conserv. Biol.* 1(1):3-12.
- GIBBONS, J.W. 1983. Reproductive characteristics and ecology of the mud turtle *Kinosternon subrubrum* (Lacepede). *Herpetologica* 39:254-271.
- GIBBONS, J.W., AND COKER, J.W. 1978. Herpetofaunal colonization patterns of Atlantic coast barrier islands. *Amer. Midl. Natur.* 99:219-233.
- GOULD, S., AND VRBA, E.S. 1982. Exaptation - a missing term in the science of form. *Paleobiol.* 8:4-15.
- HALLAM, A. 1992. *Phanerozoic Sea-Level Changes*. New York: Columbia University Press, 266 pp.
- HENDRICKSON, J.R. 1980. The ecological strategies of sea turtles. *Amer. Zool.* 20:597-608.
- KINNEARY, J.J. 1992a. Salinity relations of the common snapping turtle, *Chelydra serpentina*, in a Long Island estuary. Ph.D. Thesis, Rutgers University, Newark.
- KINNEARY, J.J. 1992b. The effect of water salinity on growth and oxygen consumption of snapping turtle (*Chelydra serpentina*) hatchlings from an estuarine habitat. *J. Herpetol.* 26:461-467.
- KINNEARY, J.J. 1993. Salinity relations of *Chelydra serpentina* in a Long Island estuary. *J. Herpetol.* 27:441-446.
- LEE, M.S.Y. 1993. The origin of the turtle body plan: bridging a famous morphological gap. *Science* 261:1716-1720.
- LOVICH, J.E., AND MCCOY, C.J. 1992. Review of the *Graptemys pulchra* group (Reptilia: Testudines: Emydidae), with descriptions of two new species. *Ann. Carnegie Mus.* 61:293-315.
- MAYR, E. 1988. *Toward a New Philosophy of Biology*. Cambridge: Belknap Press, 564 pp.
- MAZZOTTI, F.J., AND DUNSON, W.A. 1989. Osmoregulation in crocodilians. *Amer. Zool.* 29:903-920.
- MCDOWELL, S.B. 1964. Partition of the genus *Clemmys* and related problems in the taxonomy of aquatic Testudinidae. *Proc. Zool. Soc. Lond.* 143:239-279.
- MCKOWN, R.R. 1972. Phylogenetic relationships within the turtle genera *Graptemys* and *Malaclemys*. Ph.D. Thesis, University of Texas, Austin.
- MINNICH, J.E. 1982. The use of water. In: Gans, C., and Pough, F. (Eds.). *Biology of the Reptilia*. Vol. 12. New York: Academic Press, pp. 325-395.
- MITCHELL, S.D. 1992. On pluralism and competition in evolutionary explanations. *Amer. Zool.* 32:135-144.

- MOLL, D. 1994. The ecology of sea beach nesting in slider turtles (*Trachemys scripta venusta*) from Caribbean Costa Rica. *Chelon. Conserv. Biol.* 1(2):107-116.
- MOLL, E.O. 1978. Drumming along the Perak. *Nat. Hist.* 87:36-43.
- MORTIMER, J.A. 1982. Factors influencing beach selection by nesting sea turtles. In: Bjørndal, K. (Ed.). *Biology and Conservation of Sea Turtles*. Washington D.C.: Smithsonian Institution Press, pp. 45-51.
- MULLER, G.B., AND WAGNER, G.P. 1991. Novelty in evolution: restructuring the concept. *Ann. Rev. Ecol. Syst.* 22:229-256.
- ORBARD, M.E., AND BROOKS, R.J. 1980. Nesting migrations of the snapping turtle (*Chelydra serpentina*). *Herpetologica* 36:158-162.
- OBST, F.J. 1986. *Turtles, Tortises and Terrapins*. New York: Saint Martin's Press, 231 pp.
- PALADINO, F.V., O'CONNOR, M.P., AND SPOTILA, J.R. 1990. Metabolism of leatherback turtles, gigantothermy, and thermoregulation of dinosaurs. *Nature (London)* 344:858-860.
- PRITCHARD, P.C.H. 1979. *Encyclopedia of Turtles*. Neptune, N.J.: T.F.H. Publications, 895 pp.
- PRITCHARD, P.C.H., AND TREBBAU, P. 1984. The Turtles of Venezuela. *Soc. Stud. Amphib. Rept. Contr. Herpetol.* No. 2, 403 pp.
- REISZ, R.R., AND LAURIN, M. 1991. *Owenetta* and the origin of turtles. *Nature (London)* 349:324-326.
- RHODIN, A.G.J. 1985. Comparative chondro-osseous development and growth of marine turtles. *Copeia* 1985:752-771.
- RHODIN, A.G.J., MITTERMEIER, R.A., AND HALL, P.M. 1993. Distribution, osteology, and natural history of the Asian giant softshell turtle, *Pelochelys bibroni*, in Papua New Guinea. *Chelon. Conserv. Biol.* 1(1):19-30.
- ROBINSON, G.D., AND DUNSON, W.A. 1976. Water and sodium balance in the estuarine diamondback terrapin (*Malaclemys*). *J. Comp. Physiol.* 105:129-152.
- SEIDEL, M.E. 1975. Osmoregulation in the turtle *Trionyx spiniferus* from brackish and freshwater. *Copeia* 1975:124-128.
- TEAL, J., AND TEAL, M. 1969. *Life and Death of the Salt Marsh*. New York: Ballantine Books, 274 pp.
- VERMEIJ, G.J. 1995. Economics, volcanoes, and Phanerozoic revolutions. *Paleobiol.* 21:125-152.
- WALKER, W.F. 1973. The locomotor apparatus of Testudines. In: Gans, C., and Parsons, T.S. (Eds.). *Biology of the Reptilia*. Vol. 4. New York: Academic Press, pp. 1-100.
- WOOD, R.C. 1972. A fossil pelomedusid turtle from Puerto Rico. *Breviora* 392:1-13.
- WOOD, R.C. 1975. Redescription of *Bantuchelys congolensis*, a fossil pelomedusid turtle from the Paleocene of Africa. *Rev. Zool. Africa* 89:128-144.
- WOOD, R.C. 1976. *Stupendemys geographicus*, the world's largest turtle. *Breviora* 436:1-31.
- WOOD, R.C. 1977. Evolution of emydine turtles *Graptemys* and *Malaclemys* (Reptilia, Testudines, Emydidae). *J. Herpetol.* 11:415-421.
- ZANGERL, R. 1953. The vertebrate fauna of the Selma Formation of Alabama. Part 3. The turtles of the family Protostegidae. Part 4. The turtles of the family Toxochelyidae. *Fieldiana Geol. Mem.* 3:61-277.
- ZANGERL, R. 1980. Patterns of phylogenetic differentiation in the toxochelid and cheloniid sea turtles. *Amer. Zool.* 20:585-596.
- ZANGERL, R., AND SLOAN, R.E. 1960. A new specimen of *Desmatochelys lowi* Williston, a primitive cheloniid sea turtle from the Cretaceous of South Dakota. *Fieldiana Geol.* 14(3):7-40.

Received: 2 November 1994. Accepted: 2 May 1995.

Occurrence and Diet of Juvenile Loggerhead Sea Turtles, *Caretta caretta*, in the Northwestern Gulf of Mexico

PAMELA T. PLOTKIN¹

¹*Department of Bioscience and Biotechnology,
Drexel University, 32nd and Chestnut Streets, Philadelphia,
Pennsylvania 19104 USA [Fax: 215-895-1273]*

Subadult loggerheads (*Caretta caretta*) are the most common sea turtles in the northwestern Gulf of Mexico (Hildebrand, 1983), occurring nearshore where they feed primarily on benthic invertebrates (Plotkin et al., 1993). Adult loggerheads also occur in the northwestern Gulf but appear to be less abundant than subadults, do not regularly nest on any beach in this region (Dodd, 1988; Shaver, 1991), and presumably migrate to rookeries in the eastern Gulf of Mexico or the western Atlantic Ocean, including the Caribbean Sea (Meylan, 1982; Dodd, 1988). A few documented reports of post-hatchling and juvenile loggerheads exist from the northwestern Gulf of Mexico, most of which come from individuals stranded on the Texas coast within the size range (< 40 cm curved carapace length) once referred to as the "lost year," but more recently termed "pelagic stage" (Carr, 1986, 1987). Pelagic stage loggerheads are known inhabitants of driftlines and convergence zones where they find refuge and food in *Sargassum* and other items that accumulate in these surface circulation features (Fletemeyer, 1978; Carr and Meylan, 1980; Van Nierop and Den Hartog, 1984; Carr, 1986; Richardson and McGillivray, 1991; Witherington, 1993). Pelagic stage loggerheads are rare in US waters (Carr, 1986), but recent strandings in Texas suggest they may be more common than previously believed (Plotkin, 1989).

Between 1987 and 1993 I examined 10 juvenile loggerheads that were stranded on the south Texas coast (Mustang Island, North and South Padre Islands). I measured curved carapace length (CCL) and noted the general condition of each turtle. I performed necropsies on seven dead specimens, collected and preserved digestive tract contents in 10% buffered formalin, and identified food items to the lowest taxon possible. Three live turtles were generally in poor physical condition and were held in captivity, rehabilitated, and then released. The results of these studies are presented in Table 1.

The size of the loggerheads I examined ranged from 10.8 to 32.5 cm CCL ($x = 20.7$ cm, $SD = 8.7$). These juvenile loggerheads are within the pelagic stage size range which Carr (1986) reported missing from US waters and which are abundant in the eastern North Atlantic Ocean near Madeira and the Azores (Bolten et al., 1993). Carr's (1986) dispersal scenario for neonate