

TURTLES

Perspectives and Research



edited by Marion Harless & Henry Morlock

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Perspectives and Research

MARION HARLESS

HENRY MORLOCK

A Wiley-Interscience Publication

JOHN WILEY & SONS, New York • Chichester • Brisbane • Toronto

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Library of Congress Cataloging in Publication Data:

Main entry under title:

Turtles: perspectives and research.

“A Wiley-Interscience publication.”

Bibliography: p.

Includes index.

1. Turtles. I. Harless, Marion. II. Morlock, Henry.

QL666.C5T87 598.1'3 78-16177

ISBN 0-471-35204-7

Printed in the United States of America

10 9 8 7 6 5 4 3 2 1

***To those who further our knowledge of Turtles
without endangering any of the earth's populations
of Turtles***

Contributors

Walter Auffenberg
Department of Natural Science
The Florida State Museum
University of Florida
Gainesville, Florida

R. Bruce Bury
National Fish and
Wildlife Laboratory
U.S. Fish and Wildlife Service
Fort Collins, Colorado

Stephen D. Busack
Museum of Vertebrate Zoology
University of California
Berkeley, California

H. Robert Bustard
United Nations Development
Programme
New Delhi, India

Howard W. Campbell
Gainesville Station
National Fish and Wildlife Service
U.S. Fish and Wildlife Service
Gainesville, Florida

Charles C. Carpenter
Department of Zoology
University of Oklahoma
Norman, Oklahoma

David W. Ehrenfeld
Department of Horticulture and
Forestry
Cook College
Rutgers University
New Brunswick, New Jersey

Michael A. Ewert
Department of Zoology
University of Indiana
Bloomington, Indiana

Eugene V. Gourley
Department of Biology
Radford College
Radford, Virginia

Terry E. Graham
Department of Biology
Worcester State College
Worcester, Massachusetts

A. M. Granda
Institute for Neuroscience and
Behavior
University of Delaware
Newark, Delaware

Marion Harless
P. O. Box 253
Elkins, West Virginia

Victor H. Hutchison
Department of Zoology
University of Oklahoma
Norman, Oklahoma

John B. Iverson
Department of Biology
Earlham College
Richmond, Indiana

Crawford G. Jackson, Jr.
San Diego Natural History
Museum
San Diego, California

Donald C. Jackson
Division of Biological and Medical
Sciences
Brown University
Providence, Rhode Island

John Klicka
Department of Biology
Wisconsin State University
Oshkosh, Wisconsin

Warren K. Legler
Department of Physiology
University of Kansas Medical
Center
Kansas City, Kansas

I. Y. Mahmoud
Department of Biology
Wisconsin State University
Oshkosh, Wisconsin

Marion L. Manton
Department of Biological Sciences
Macquarie University
Sydney, Australia

James H. Maxwell
Institute for Neuroscience and
Behavior
University of Delaware
Newark, Delaware

Edward O. Moll
Department of Zoology
Eastern Illinois University
Charleston, Illinois

Henry Morlock
Department of Psychology
SUNY College of Arts
and Sciences
Plattsburgh, New York

Michael V. Plummer
Department of Biology
Hardy College
Searcy, Arkansas

Alice S. Powers
Department of Psychology
Bryn Mawr College
Bryn Mawr, Pennsylvania

Peter C. H. Pritchard
Florida Audubon Society
Maitland, Florida

CONTRIBUTORS

ix

Anton J. Reiner
Department of Psychiatry and
Behavioral Science
Health Sciences Center
SUNY at Stony Brook
Stony Brook, New York

Thomas R. Scott, Jr.
Department of Psychology and
Institute for Neuroscience and
Behavior
University of Delaware
Newark, Delaware

Irwin M. Spigel
Department of Psychology
Erindale College
University of Toronto
Mississauga, Ontario, Canada

Warren F. Walker, Jr.
Department of Biology
Oberlin College
Oberlin, Ohio

Preface

Turtles have adapted to oceans, forests, swamps, and deserts with a success that is as close to permanency as we find in the vertebrate world. The variation in adaptations suggests that there exists no representative or composite turtle to be used as a model for all turtles. The stereotyped notion of "the turtle" should become conceptually extinct with the publication of this book. Some chapters focus on a single species, not as a representative of all chelonians, but as the species with which the investigator is most familiar. Frequently similar kinds of information are lacking for other species, for in reality we have very little knowledge of most turtles. We may succeed in eliminating the habitats of some species before we learn of their present environmental relationships or of their possible behavioral and physiological adaptations to changing environments. Recent actions by interest groups and governments may save some of the species that seemed certain candidates for extinction in this century; some may not survive.

Upon merging independently prepared bibliographies of turtle research several years ago, it appeared to us that many investigators were unaware of the techniques and findings of their colleagues. The purposes of this book are to bring together the diverse approaches to studying turtles, to describe useful techniques, to present and interpret data, and to indicate directions for future research and thought.

A single scientific name for each genus and species is used throughout the book, even though some authors preferred a different taxonomic designation.

Biochemistry, parasitology, gross anatomy, morphology, and paleontology are included peripherally, not because of lack of interest in these areas or denial of their importance, but because of desire to restrict topics to those most clearly related to behavior, physiology, and ecology.

The research methods are not meant as final solutions to the problems associated with data collection, nor are the research results of subsequent chapters meant to be the permanent pronouncements they may appear to be. Future research may benefit from the suggestions in these chapters. More important, future research will benefit from the ideas not in these chapters, but generated by readers who synthesize these many thoughts in terms of their own experiences.

We thank Mindy Rogers Bean and Jill Mason Pritchard for their help in assembling and preparing the original bibliographies. We are also thankful to Mindy for her typing of the voluminous correspondence associated with the beginning of this project. And we are very grateful to Mary M. Conway, Life Science Editor of Wiley-Interscience, for her patience and many helpful suggestions.

MARION HARLESS
HENRY MORLOCK

Elkins, West Virginia
Plattsburgh, New York
August 1978

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CHAPTER 1

Taxonomy, Evolution, and Zoogeography

PETER C. H. PRITCHARD

TAXONOMY

Turtles, being poikilothermous, laying cleidoic eggs, and having a typically scaled integument, are unquestionably reptiles. Within the class Reptilia, turtles are usually classified with the earliest or "stem" reptiles of the order Cotylosauria in the subclass Anapsida. This designation alludes to the absence of true temporal fossae in the turtle skull, in contrast to the other reptilian subclasses in which one or two temporal fossae are present on each side of the skull. Only a few living turtles have fully roofed-over skulls; these include the Cheloniidae, Dermochelyidae, Platysternidae, and to some extent *Pseudemydura umbrina* and *Peltocephalus tracaxa*, essentially the forms in which the head is incompletely retractile or nonretractile. More typically, the skull roof is strongly emarginated from behind, leaving a relatively narrow quadratojugal arch. In a few genera (e.g., *Heosemys*) this arch may disappear completely. In one family, the Chelidae, the skull roof is emarginate from below, leaving a narrow parietosquamosal arch, which also disappears completely in one genus (*Chelodina*). Such emarginations are not considered true temporal fossae, even though they serve the same function of allowing the bunched jaw muscles to expand outward when the mouth is forcibly closed.

The earliest attempts to classify the different kinds of turtles, apart from the initial monogeneric arrangement of Linnaeus, relied on habitat

differences; Brongniart in 1805 classified the land turtles as *Testudo*, the freshwater forms as *Emys*, and the marine forms as *Chelonia*. Other early classifications separated the turtles on the basis of whether the digits were fused together or separate, the presence or absence of a plastral hinge, or the retractibility of the extremities. Modern classifications usually focus on the plane of retraction of the neck, since this difference not only is reflected in the cervical vertebrae, but also shows a strong correlation with pelvic structure. This classification establishes the Cryptodira, a group of 10 living families in which the neck is vertically retractile, and the Pleurodira, which include the two families of side-necked turtles. Some authorities make the initial taxonomic division of the testudines into the Athecae and the Thecophora, the former containing only the highly divergent *Dermochelys*. Many extinct turtles do not fit into either the Cryptodira or the Pleurodira and are placed in a separate suborder, the Amphichelydia, in which the neck is nonretractile and the neck vertebrae primitive, lacking ginglymes.

Zangerl (1969) proposed a new arrangement of the higher divisions of the testudines, characterized by four "levels of organization," or suborders, the Amphichelydia, Mesochelydia, Metachelydia, and Neochelydia.

The Amphichelydia of Zangerl is used in a restrictive sense, to include only the very early turtles of the families Proganochelyidae, Proterochersidae, and Kallokibotiidae. This suborder is characterized by very broad vertebral scutes, unstable and variable numbers of shell bones and scutes, extensive series of supramarginals and inframarginals, two pairs of mesoplastra, and intergular, caudal, and intercaudal scutes.

The Mesochelydia include most of the families traditionally placed in the Amphichelydia, as well as the living Chelidae and Pelomedusidae. In these turtles the scute patterns have become more stabilized, though supramarginals and inframarginals are still usually present. The living side-necks, especially the Chelidae, have undergone considerable modification of the scute mosaic, but still retain an "archaic complexion" and, in the Pelomedusidae, such primitive features as mesoplastra.

The diverse and successful suborder Metachelydia includes all the living and extinct marine turtle families, the soft-shells, snapping turtles, mud turtles, Carettochelyidae and Dermatemydidae, and the extinct Aperotemporalidae, Sinemydidae, and Plesiochelyidae. At this level, the costal scutes are stabilized at four pairs (except in *Caretta* and *Lepidochelys*), supramarginals are present only in *Macrochelys*, and the vertebral scutes are relatively narrow. Scutes disappear completely in the Trionychidae, and nearly in the Carettochelyidae. *Kinosternon* and *Sternotherus* lack the entoplastron, while the Trionychidae lack peripheral bones but have neomorphic "preplastra," no entoplastron, and fused

epiplastra. The Dermochelyidae lack scutes and neural and peripheral bones, and have ribs that remain free throughout life.

The Neochelydia, which lack supramarginals, inframarginals, intergu-lars, and similar features, and have relatively narrow vertebral scutes and a repeated tendency toward shell kinesis, are very successful at present in terms of number of species, though only two families, the Testudinidae and the Emydidae, are recognized, and these are often combined into one.

Zangerl's intelligent and sophisticated though also controversial classification can be criticized because of the extreme diversity of turtles included in the Mesochelydia and Metachelydia. Other arrangements of turtle families are given by Romer (1956), Mlynarski (1969), Ckhikvadze (1970), and Williams (1950). All are worthy of consideration, and no attempt is made here to extol the merits of one at the expense of the others.

Turtle taxonomy has traditionally been based almost entirely on osteological and external morphological criteria. This is inevitable in a group in which the fossil forms assume such great importance. However in recent years several efforts have been made to supplement the traditional osteological approach with biochemical or anatomical comparisons in an attempt to provide a wider spectrum of criteria for the classification of the living forms. Notable among these efforts have been the chromatographic and electrophoretic studies of serum proteins of Frair (1964, 1972), the comparisons of fatty acid compositions and ratios of Ackman, Hooper, and Frair (1971), and the studies of comparative penis morphology of Zug (1966).

Frair's studies have generally confirmed traditional views of turtle classification but have provided some interesting insights; for example, not only are the Trionychidae peculiar anatomically, they also have a highly distinctive serum electrophoresis pattern. On serological grounds, *Dermatemys* appears to be closely related to *Staurotypus*, and there is indeed a fossil form (*Xenochelys*) that is a morphological intermediate. The snapping turtles (Chelydridae), on the other hand, appear to be more closely related to the Emydidae than to the Kinosternidae, and this apparent relationship agrees with the anatomical studies of McDowell (1964). The marine turtles, even the divergent *Dermochelys*, have similar serum patterns. McDowell's separation of the Emydidae into Batagurinae and Emydinae is confirmed by a difference in serum patterns between the two groups. *Platysternon* appears to be relatively close to the emydids and quite distinct from the kinosternids and chelydrids. Within the genus *Kinosternon* the small North American species give a different pattern from the larger tropical forms.

The fatty acid studies of Ackman, Hooper, and Frair (1971) indicate that the living marine species are distinct from all others in having *trans*-6-hexadecanoic acid in their depot fat, that *Dermochelys* is exceptional in having 9.5% lauric acid, and the *Dermatemys* can be differentiated from the other freshwater species by details of fatty acids indicative of an herbivorous diet.

Zug's studies of the penis show a close relationship between the cheloniid and dermochelyid sea turtles; a distinction between the Emydidae and the Batagurinae; a close relationship between *Chrysemys* and *Pseudemys*, and between *Deirochelys*, *Emydoidea*, and *Malaclemys*; a close relationship between *Dermatemys* and the kinosternids, and between the carettochelyids and the trionychids. The tortoises (Testudinidae) are distinct from, though related to, the Emydidae in penial morphology, while the Platysternidae appear to be closely related to the Emydidae. The penis of the chelydrids conforms Frair's findings of a relationship between the snapping turtles and the Testudinidae and Emydidae. Within the genus *Sternotherus*, a study of penial morphology would place *S. carinatus* apart from *S. minor* and *S. odoratus*.

EVOLUTION

It was held for many years that a small fossil reptile from the middle Permian of Welt Vreeden (Beaufort West), South Africa, known as *Eunotosaurus africanus*, represented the "missing link" between the cotylosaurs and the turtles. *Eunotosaurus* had a broadened body with eight pairs of expanded ribs, and this, together with the appropriate geological horizon, was considered by Watson (1914) to suggest strongly that *Eunotosaurus* was the ancestral chelonian. Recent authors, notably Parsons and Williams (1961), have argued otherwise; the ribs of *Eunotosaurus*, though expanded, are leaf shaped, thus differ from the pleural bones of true turtles, which initially develop mesially near the vertebral column and have lateral flanges. These flanges progress outward as the turtle matures, so that they eventually form jagged sutures throughout their lengths with their neighbors. Moreover, the fossils of *Eunotosaurus* showed no signs of either plastron or abdominal ribs, and recent studies by Cox of the University of London have shown that *Eunotosaurus* has no dermal armor and no other features suggesting relationship with the turtles. Some critical parts of *Eunotosaurus*, including the skull roof, the neck, and the feet, remain unknown. Since no fossil turtles are found outside Europe earlier than the Jurassic, it would seem reasonable to postulate an origin for the group in what is now Europe.

The oldest unmistakable chelonians, the Proganochelyidae, are from the Triassic of Germany. The closely related *Triassocheilus dux* and *Proganochelys quenstedti* had such primitive features as teeth in both jaws and palate, and numerous marginals and supramarginals. However the peculiarly universal arrangement of four pairs of costal scutes and five vertebrae was already present.

One can only speculate how the Proganochelyidae evolved from the primitive reptile stem. Deraniyagala (1930, 1939) postulated an evolutionary "armadillo" stage and illustrated the "saurotestudinate," the "missing link" in turtle evolution. As Mlynarski (1956) pointed out, there is no fossil evidence to support this hypothesis.

Carroll (1969) remarked that there are only two certainties regarding the origin of turtles: (1) that they did not evolve from any group that had already developed a lateral or dorsal temporal opening, and (2) that they did not evolve from any form in which the palate was fused to the braincase. This means that the turtle lineage was already separate in the early Permian. Gregory (1946) and Olson (1947) both assumed that turtles evolved from the diadectomorph cotylosaurs, a group that flourished from the Carboniferous to the Triassic. These primitive reptiles had a complete, imperforate temporal region and a well-defined otic notch, both features shared with the turtles. On the other hand, the later diadectomorphs had the palate solidly attached to the braincase, and it is therefore assumed that the turtles had already become separate by the time this modification occurred.

It is most probable that the earliest known turtles of the family Proganochelyidae were marsh dwelling; the fully aquatic preference of most modern turtles is presumably a secondary modification, since the scaled integument and shelled, terrestrial eggs of turtles and other reptiles are essentially adaptations that permitted these animals to escape from dependence on an aquatic medium. Nevertheless, the broad, shell-encased body inevitably makes turtles slow on land, with little chance of escape from strong-jawed predators, and the move back to the fresh-water medium was a rather early development for the group; the vast majority of both modern and extinct turtle genera have or had a fresh-water habitat.

One of the first truly terrestrial turtles was the Upper Cretaceous dermatemyid *Zangerlia testudinimorpha*, a relatively large species from the Lower Nemegt Beds of Mongolia (Mlynarski, 1972). The assumed terrestrial habitat is postulated on several grounds: the deep shell, the very strong dorsal sulci (which suggest thick, sculptured scutes such as are typical of many terrestrial tortoises today), the shortened phalanges, and the extensive fusion of the carpal elements. On the other hand, several other features, such as the straight humerus, the somewhat reduced

plastron, and the extensive superficial sculpturing of the shell (similar to that of *Carettochelys* or *Tretosternon*) show the influence of recent aquatic ancestors.

The Upper Cretaceous meiolaniid *Niolamia argentina* may have been another Mesozoic terrestrial form. However the true tortoises of the family Testudinidae did not appear in the fossil record until the mid-Eocene; presumably there were primitive tortoises in existence in the Paleocene. They perhaps reached their greatest abundance and diversity in the Pliocene. Tortoises evolved from primitive emydid turtles, and the emydids have subsequently given rise to several other terrestrial lines (e.g., *Terrapene*, *Pyxidea*, *Rhinoclemys*).

Turtles entered the marine environment at an early stage, and indeed some isolated cervical vertebrae from the early Triassic of Germany, which have been described under the generic name *Chelyzöon*, may conceivably have belonged to a marine turtle, according to Staesch (in Goode, 1967b). The Lower Cretaceous *Desmemys* type of the subfamily Desmemydinae of the family Pleurosternidae, was a marine form, whereas the extinct Toxochelyidae and Protostegidae and the living Cheloniidae and Dermochelyidae are comprised of entirely marine species. The amphichelid family Thalassemyidae, from the Upper Jurassic to the Upper Cretaceous of Europe and Asia, was also marine. Since neither the Desmemydinae nor the Thalassemyidae were ancestral to the Chelonioidea, it appears that turtles have independently evolved marine lineages at least three times. In addition, some of the early side-necks of the Pelomedusidae were marine, and a few of the modern emydids show a preference for estuarine or brackish situations.

Related to the Proganochelyidae, and distinguished by the absence of fusion between the pelvis and the plastron, is *Proterochersis robusta*, the sole species of the family Proterochersidae, and also from the Triassic of Europe. This species had a carapace length of about 30 cm, two pairs of mesoplastra, caudal and intercaudal scutes, very broad vertebral scutes, and a somewhat cruciform plastron. Its vaulted shell suggests a largely terrestrial life.

ZOOGEOGRAPHY

Chelydridae

The family Chelydridae, although represented only by two living species, constitutes an important element in the modern New World turtle fauna. The more widespread species is the common snapping