BIOLOGY OF THE REPTILIA

VOLUME 4

CARL GANS
and
THOMAS S. PARSONS

BIOLOGY OF THE REPTILIA

Edited by

CARL GANS

The University of Michigan
Ann Arbor, Michigan, U.S.A.

VOLUME 4

MORPHOLOGY D

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University of Toronto
Toronto, Ontario
Canada

1973

ACADEMIC PRESS
LONDON AND NEW YORK
A Subsidiary of Harcourt Brace Jovanovich, Publishers

ACADEMIC PRESS INC. (LONDON) LTD
24–28 Oval Road
London, NW1

U.S. Edition published by
ACADEMIC PRESS INC.
111 Fifth Avenue
New York, New York 10003

Second Printing 1976

Library of Congress Catalog Card Number: 68-9113
ISBN: 0-12-274604-X

REPRODUCED PHOTOLITHO IN GREAT BRITAIN BY
J. W. ARROWSMITH LTD., BRISTOL

BIOLOGY OF THE REPTILIA

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Preface

The bones, muscles, and connective tissues of an animal's body determine its shape. Studies and descriptions of this system date back to pre-Linnaean times and, at least for the turtle (*Emys orbicularis*), the best pure description was prepared by Bojanus a century and a half ago. Yet the early investigators asked different questions and many of those who followed them seemed to have lacked an appreciation of the extent of individual, of populational and of interspecific variation. As modern functional anatomy came into vogue one realized that the purely descriptive phase of characterization had left an inadequate legacy.

Far from providing us with detailed anatomy of various "types", coupled perhaps with variations upon the theme, we have been left with a most diverse spectrum of morphological facts. Certain bones and muscles have been sampled in many species although the identification of the species used in older studies may pose a bit of a puzzle. Other, often adjacent, structures appear to have been missed or only examined in a very few reptiles indeed. Certain, particularly osteological, characteristics have become favored by taxonomists and are illustrated in a series of volumes not ordinarily consulted by nor available to many morphologists. This absence of a clear record must be seen against the absolute conviction of certain authorities that all useful things have been done and that further study of the bone-muscle system is useless, even for "classical" anatomists.

For these reasons, the editors consider themselves fortunate in having obtained for Volume 4 the collaboration of the present slate of authors. Not only do our participants have first-hand information of the various systems, but we have also obtained an evaluation and interpretation of the extensive peripheral literature (although the enormous number of such studies makes this a relative rather than an absolute statement).

One key item in presenting a broadly based discussion of muscular anatomy is the requirement for synonymies reconciling the views of the different authors that have dealt with diverse animals. We have encouraged their inclusion. The nomenclature actually chosen is, of course, that preferred by the author of the individual chapter. The structures may in the text be referred to by the Latin or by an anglicized version of the Latin name, as we have not insisted on a unified usage. The Latin name obviously characterizes the formal and sequential description of structures. However, in discussion and in other sections, English usage is often employed for convenience. In the latter case, the ending has generally been changed; thus the M. testocoracoideus is referred to as the testocoracoid muscle.

While the present volume and its companion which will deal with the skulls, osteology and myology of other groups will contain a remarkable assemblage of data, they can hardly be considered an adequate summary. Indeed their preparation emphasized the limitations of our knowledge even in the most purely descriptive areas. Additional limitations remain in aspects of development, innervation and vascularization; even homologies within groups often suggest a remarkable degree of uncertainty. The authors have provided some brief statements regarding general functional patterns, but these only represent the beginnings of reptilian functional anatomy. As yet we lack electromyographic studies of locomotor or feeding patterns in any reptile. Only incidental functional topics have thus far been touched and these will be dealt with in the volumes on reptilian behavior.

Drs R. G. Albright, A. d'A. Bellairs, E. H. Colbert, P. Dullemeijer, E. S. Gaffney, J. C. George, G. Haas, N. N. Iordansky, E. T. Kochva, D. Langebartel, F. Medem, I. Poglayen, A. S. Romer, G. H. Schumacher, D. M. Secoy, K. C. Sondhi, R. C. Snyder, W. W. Tanner, and G. Zug reviewed individual manuscripts and Mrs Gloria Griffin, Miss Janet Britcher, and Mrs Mary Jane Stewart provided editorial assistance. My coeditor, Dr Thomas S. Parsons, carried an unusually heavy share of the load, particularly in the revisions required in the manuscript on squamate head muscles. Drs James A. Peters, G. Zug and Heinz Wermuth critically read the manuscripts for usage and accuracy of the Latin names employed. National Science Foundation grant GN-815 provided for some financial assistance, and the Department of Biology of the State University of New York at Buffalo and the Department of Zoology of The University of Michigan paid the considerable bills for postage and copying.

May, 1973 Carl Gans

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CHAPTER I

The Locomotor Apparatus of Testudines

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I. Introduction

Some turtles are terrestrial, most are semiaquatic, and some are highly adapted to the aquatic environment, yet all have the ability to move about both on land and in the water. Terrestrial species occasionally are caught in a flood or for other reasons enter the water, the aquatic ones come onto the land at least to deposit their eggs, and the semiaquatic species move with ease in both media. There are, of course, differences in the locomotor apparatus of these diverse forms, but the differences are modifications of a limb architecture that is surprisingly alike in all species. I felt, therefore, that a review of the locomotor apparatus of chelonians would be particularly useful if one common, semiaquatic species was selected as a type and described in some detail. After each unit of material, major variations known to occur in other groups are then discussed. The purpose of this review is to make available a complete description of the basic anatomy of the chelonian locomotor apparatus, to define the major parameters of variation, and to begin to correlate these with phylogenetic groups and patterns of locomotion. I hope that further work will be stimulated for as many questions are raised as answers given.

The parts of the locomotor apparatus considered are the skeleton of the girdles and appendages, and the true appendicular muscles, i.e., those muscles believed to develop from mesenchyme within the limb bud. Certain trunk and visceral muscles that secondarily attach onto the girdles are mentioned since they must be cut through when the appendages are dissected, but they are not considered in detail. Nerve plexuses and exact descriptions of nerve supply have been omitted, but the main pattern of innervation of groups of muscles is given.

Pseudemys scripta elegans (Wied), commonly called the red-eared turtle, has been selected as a type because it is quite representative of the largest subfamily of chelonians, the Emydinae, as well as being fairly typical of turtles in general. It is common and wide-ranging throughout the central parts of the United States. Dissections of this species have been compared with reports in the literature, and with new dissections of specimens representing widely divergent patterns of locomotion and taxonomic groups. The following cryptodires have been dissected for this study. Testudinidae: *Pseudemys scripta elegans*, *Testudo graeca*, *Geochelone elephantopus*; Trionychidae: *Trionyx spiniferus*; Cheloniidae: *Caretta caretta* (pelvic limb), *Lepidochelys kempii* (pectoral limb). The following pleurodires have been dissected. Pelomedusidae: *Pelomedusa subrufa*; Chelidae: *Chelodina longicollis*. In addition, I have studied the osteological features of the limbs of representatives of most of the chelonian families and subfamilies in the collections of the Museum of Comparative Zoology at Harvard College.

There is, unfortunately, only a little precise information on turtle locomotion. Zangerl (1953) has made a functional analysis of the appendicular skeleton of freshwater and sea turtles; I have studied sea turtle swimming (Walker, 1971a) the relations between walking, body form, and the structure of the appendicular skeleton in *Chrysemys picta* (Walker, 1962, 1971b, 1972), and have made some preliminary observations of the forces developed at the feet during locomotion in *Emys* (Walker, 1963). Zug (1971) has studied the gait of many cryptodires and also the movements of their hind legs.

There is, however, a large literature on the anatomy of turtle limbs. Bojanus (1819–1821) in his classic paper, "Anatome Testudinis Europaeae" (= *Emys orbicularis*) was the first to undertake a careful study of chelonian anatomy, including that of the appendages. Many other studies of certain aspects of the locomotor apparatus appeared during the nineteenth century; the works of Rüdinger (1868), Fürbringer (1874), and Gadow (1882) are the most important of these. Rüdinger studied the pectoral muscles of *Emys orbicularis**, *Testudo graeca*, *Caretta caretta*, and *Chelonia mydas*; Fürbringer reviewed earlier work and dissected the shoulder region of *Emys orbicularis*, *Pseudemys s. scripta*, *Geochelone denticulata*, *Trionyx sinensis*, and *Dermochelys coriacea*; and Gadow studied the pelvic muscles of *Emys orbicularis*, *Pseudemys s. scripta*, *Geochelone denticulata* and *G. e. elephantopus*. Boulenger (1889) reviewed the earlier work on osteological variation; he used osteological features in defining the major chelonian groups. Hoffmann, writing at about the same time (1890), did not make any new dissections of the appendages, but prepared an extensive review of limb skeleton and muscles as part of his book on turtle anatomy. He does not always make clear just which species he is referring to, but his descriptions of the pectoral muscles appear to be based on the following: *Emys orbicularis*, *Geoemyda punctularia*, *Pseudemys s. scripta*, *Clemmys* sp., *Trionyx sinensis*, *Eretmochelys imbricata*, and *Dermochelys coriacea*, but reference is made to certain muscles of

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* See "Addendum" for names used in the older literature.

Terrapene sp., *Pelomedusa subrufa*, and *Chelus fimbriatus*. Descriptions of pelvic muscles are based on the same group of species except that *Trionyx* is referred to only briefly and the pelvic muscles of *Dermochelys* were not known at that time. The works of Boulenger and Hoffmann are taken as the primary starting points in the present review; however, I have checked the major earlier works and included the terms used by these investigators in the synonomies.

Since Hoffmann's time, Burne (1905) has reported briefly on the limb muscles of *Dermochelys coriacea*. Ribbing (1907) includes *Emys orbicularis* and "*Sternothaerus*" sp.* in his study of the forearm muscles of tetrapods. Sieglbauer (1909) has written a very extensive and valuable review of the muscles and nerves based on new dissections of *Chelydra serpentina*, *Emys orbicularis*, *Testudo graeca*, *Geochelone radiata*, *G. denticulata*, *Cyclanorbis senegalensis*, *Trionyx ferox*, *Caretta caretta*, *Emydoidea blandingii*, *Eretmochelys imbricata*, and *Hydromedusa tectifera*. Ogushi (1911, 1913) followed this with a thorough account of the limb anatomy of *Trionyx sinensis*. Axt (1917) described the lumbosacral plexus and the flexor muscles of the pelvic girdle and limb of *Emydoidea blandingii*. Walther (1921) compared the skeleton of both limbs, as well as the forelimb muscles, of *Carettochelys insculpta* with corresponding parts of *Trionyx*. Ruckes (1929a, b) has analysed the biomechanics of the chelonian pelvis and the ontogeny of the relationship between the girdles and carapace. Thomson (1932) described the anatomy of *Testudo gracea*, but includes only the skeleton of the limbs. Szalai (1932–1933) briefly compared the pectoral girdle and certain arm muscles of sea turtles with those of non-marine turtles. Haines (1935, 1939) includes brief remarks on certain thigh muscles of *Geochelone pardalis*, he describes the extensor muscles of the forearm of *Emys orbicularis*, in his reports on reptilian muscles. Turtles are included, although treated somewhat superficially, in the reviews of the tetrapod limb skeleton (Nauck, 1938) and vertebrate limb muscles (Ribbing, 1938) in the "Handbuch der vergleichenden Anatomie der Wirbeltiere." Schwarz (1939) also studied the carpus. Walker (1947) described the embryonic development of the shoulder and upper arm muscles of *Chrysemys picta marginata*. Romer (1956) included a great deal of information on turtles in his important "Osteology of Reptiles". George and Shah (1957, 1958) have described the limb muscles of *Lissemys punctata*, and Shah and Patel (1964) have followed this with a description of the pectoral muscles of *Geochelone elegans*, *Eretmochelys imbricata*, and *Lissemys punctata*. Unfortunately the works of George, Shah and Patel are difficult to interpret because these authors neither included synonyms nor referred to most of the

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* Ribbing refers to his specimen as "*Sternothaerus?*" Since he gives no locality it is impossible to tell whether it really is *Sternotherus* or the pleurodire *Pelusios* (formerly *Sternothaerus*).

important preceding work on turtles. Kriegler (1961) wrote a very useful review of the pelvic muscles of reptiles, including new investigations on the pelvic muscles of *Testudo graeca ibera*, *Trionyx sinensis*, and *Eretmochelys imbricata*. The most thorough study of the pelvic apparatus of turtles is that of Zug (1971). He dissected the muscles of the following 24 species*: *Chelydra serpentina*, *Rhinoclemys* (*Geoemyda* auct.) *punctularia*, *Chrysemys* (*Pseudemys* auct.) *floridana*, *C. picta*, *C.* (*Pseudemys* auct.) *scripta*, *Clemmys guttata*, *C. insculpta*, *Emydoidea blandingii*, *Malaclemys* (*Graptemys* auct.) *geographica*, *M. terrapin*, *Terrapene carolina*, *T. ornata*, *Platysternon megacephalum*, *Geochelone carbonaria*, *Gopherus berlandieri*, *G. polyphemus*, *Dermatemys mawii*, *Kinosternon integrum*, *Sternotherus carinatus*, *Claudius angustatus*, *Staurotypus triporcatus*, *Lissemys punctata*, *Trionyx ferox* and *T. spiniferus*. He has also studied the pelvic skeletons of all but one of these genera (*Geochelone*) and of most of the species. The skeletons of 15 more species have also been examined, including representatives of the following additional genera: *Macroclemys*, *Mauremys* (*Clemmys* auct.), *Deirochelys*, *Kinixys*, *Carettochelys*, and *Pelochelys*.

Two laboratory manuals include brief descriptions of both the turtle limb skeleton and muscles. Noble and Noble (1940) base their account on *Clemmys marmorata*, and Ashley (1955) his on "the painted turtle," probably *Chrysemys*. Neither manual is complete, especially with regard to the muscles of the forearm and shank, and both make extensive use of Bojanus's (1819–1821) terminology. Since these descriptions may be more available than most technical papers, their terms have been included in the synonymies.

To save space, it has been necessary to generalize somewhat in reviewing the variations reported by these investigators. Groups in which there are significant departures from the condition described for *Pseudemys* are mentioned. If a species reported in the literature is not mentioned, it can be assumed that to the best of my interpretation it is substantially like *Pseudemys*. Readers interested in further details should consult the original reports.

A word of explanation is appropriate concerning descriptions of muscle action. Most accounts of the limb muscles discuss the action of the muscles, for this is important in understanding muscle morphology. But, to the best of my knowledge, these descriptions, including those given in this report, are inferred from morphological relationships. This is perfectly legitimate provided it is recognized that such conclusions are preliminary. In life, muscles interact in complex ways; some complementing, restricting, or altering the direction of the pull of others. Two electromyographic studies, those of Gans and Hughes (1967) and Gaunt and Gans (1969) deal with turtle respiratory muscles, some of which are also appendicular muscles, but no study

* The terminology here is that of McDowell (1964).

of this type has been made for muscles as they are used in locomotion. This must be done before a complete knowledge of muscle action can be attained.

In describing muscle actions, I have followed Barclay's modification (1946) of Gray's definitions (1944). Flexion and extension are limited to movements of the distal parts of the limb and to the hand and foot. Forward and backward movements of the humerus and femur in the horizontal plane are referred to as protraction and retraction respectively. An action which causes the distal end of the humerus or femur to move away from the body's midventral line is abduction; the opposite movement is adduction.

Terminology of reptilian muscles has been a problem. Early workers, including Bojanus (1819–1821), applied human terms to those muscles having general relationships comparable to muscles in man. Not wanting to use terms which implied a homology not really established, Fürbringer in the 1870's devised a terminology based on the attachment of muscles. This was followed by Gadow (1882) and most later workers, despite the limitation, as Davis (1936) points out, that obviously homologous muscles with slightly different attachments carry different names. In more recent years many homologies have become established between muscles in different reptilian groups, and between reptilian and mammalian muscles, so that certain terms in one group are legitimately available for another group. With respect to reptiles, terms for lizard muscles are relatively stabilized; hence I have followed certain previous workers in using these terms for turtle muscles where appropriate. However, this means that the descriptive name of the muscle cannot always be taken literally; thus, for example, the puboischiofemoralis internus may also arise from the ilium. Tables of synonymy should make clear the sense in which a term is being used, and facilitate the interested reader in tracing a particular muscle back through the literature.

My work on the turtle locomotor apparatus has been undertaken over a period of years, and I am indebted to many individuals and institutions for courtesies granted me. In connection with this review, I am particularly indebted to the Marine Studios, Marineland, Florida and to Mr F. G. Wood, for an opportunity to study sea turtle locomotion and anatomy; to Dr Pieter Dullemeijer of the University of Leiden who helped with an x-ray analysis of locomotion; to Dr Ernest E. Williams of the Museum of Comparative Zoology for permission to dissect a number of specimens; to Dr Milton Hildebrand, University of California at Davis, for the loan of a dried muscle-skeletal preparation of *Geochelone elephantopus*; to Dr George R. Zug, Smithsonian Institution, for the use of Figs 1, 2 and 3; and to Dr Dietrich Starck, Director of the Anatomical Institute of the University of Frankfurt a.M., for the hospitality of his institution during the final writing of this report.

II. Locomotion

Although our knowledge of turtle locomotion is far from complete, a summary of major aspects can form the basis for some correlations between limb movement and structure. Zug (1971) has analysed the terrestrial gait of 16 cryptodire species representing 11 genera and ranging from terrestrial to aquatic forms: *Chelydra*, *Cuora*, *Chrysemys*, *Clemmys*, *Emydoidea*, *Malaclemys*, *Terrapene*, *Gopherus*, *Kinosternon*, *Sternotherus*, *Trionyx*. Although there is some variation in gait patterns, there is no consistent correlation between gait and taxon. In Hildebrand's (1965, 1966) graphic system of gait analysis, which Zug uses (Fig. 1), movement of the hind feet and speed is expressed by the percentage of the stride that the left hind foot is on the ground. Other feet are on the ground for nearly the same length of time in symmetrical gaits. As would be expected, turtles walk slowly, and each foot has contact with the ground for about 70% to 90% of the stride. The motions of the forelegs as a pair are related to the motions of the hind legs as a pair by expressing the percent of the stride that the foot-fall of the left forefoot follows that of the left hind foot. Lateral sequence gaits, which are frequently employed by turtles, are ones in which the left forefoot is next placed on the ground and it follows the left hind foot by no more than 45% of the stride interval. In a diagonal couplet gait, which is the most common of the lateral sequence gaits found in turtles, there is a lag in the placement of the left foot of from 30% to 45% of the stride. As a consequence the right hind foot, which is the next one to be placed, is placed shortly after the left front one. Therefore, a contralateral front and hind foot (i.e., a diagonal couplet) are placed on and removed from the ground rather close together in time. This gait (Zug, 1971; Walker, 1971b) maximizes periods of tripedal or quadrupedal support as shown in the insert of Fig. 1. This is particularly important for a turtle which carries its short, broad trunk close to the ground. In a walking trot, which Zug finds is also common in turtles, a contralateral front and hind leg swing more closely together in time; however, these legs seldom swing precisely together so there are periods of tripedal support.

I have shown that the stability provided by the gait and limb support sequence is enhanced in turtles by a foot placement that lies rather far lateral to the median longitudinal axis. Turtles have a wider stance and track in relation to stride length than have other living tetrapods. However, semiaquatic species such as *Chrysemys* often drag the posterior corners of the plastron on the ground when they walk (Walker, 1971b).

Zug has studied the sequence of limb movements in two types of aquatic locomotion: the paddling type of swimming utilizing all legs, and bottom-walking. Although the limbs propel in both, they play no role in support during swimming and only a little in bottom-walking. Since support is not a