NUMBER 647 MAY 13, 1966

OCCASIONAL PAPERS OF THE MUSEUM OF ZOOLOGY
UNIVERSITY OF MICHIGAN
ANN ARBOR, MICHIGAN

THE PENIAL MORPHOLOGY AND THE RELATIONSHIPS OF CRYPTODIRAN TURTLES

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E. D. COPE (1894, 1895, 1896) was the first to demonstrate the systematic usefulness of penial morphology. His studies on the hemipenes of lizards and snakes set the stage for similar investigations in other vertebrate groups. It has been only recently, however, that his lead has been followed in vertebrates other than snakes. Studies of penial morphology in rodents (Hooper, 1958; Hooper and Musser, 1964) and snakes (Dowling and Savage, 1960) illustrate the information that can be derived from such studies.

Although Stannius (1856) recognized the presence of many differences in the copulatory organs of turtles, there have been no published attempts to determine what, if any, systematic information can be obtained from the study of the chelonian penis. With this question in mind, the present study was initiated.

HISTORICAL RESUME

Previous investigations of the chelonian intromittent organ are strictly anatomical and usually deal with a single species. An exception to this is Schmidtgen's (1907) study of the cloaca and its associated organs. He examined 24 species of turtles representing 7 families. Although his study was mainly descriptive, he provided some comparative information and also suggested the possibility of using the cloaca and penis as systematic characters. Unfortunately, he did not make detailed observations on the condition of the glans penis which might have resulted in an earlier recognition of the chelonian penis as a useful character. In addition to his anatomical descriptions, Schmidtgen reviewed the literature concerning the chelonian urogenital system up to 1907; therefore, I shall cite only the publications on the morphology of chelonian penes that have appeared subsequently.

In 1914, Petterer and Neuville described the penis of *Testudo ele-*

phantina (Geochelone gigantea); their description is short and incomplete. Jones (1915) considered the chelonian penis from a phylogenetic viewpoint. He believed that the different degrees of development of the chelonian copulatory organ could be used to demonstrate the evolutionary development of the mammalian penis. He proposed that the chelonian penis evolved from a primitive protuberance on the cloacal floor to an advanced condition reminiscent of the embryonic mammalian penis.

An excellent histological study of the penis of *Testudo graeca* was published by Gerecke in 1932. In addition to a detailed histological description, he attempted to demonstrate homologies with the intromittent organ of crocodiles, monotremes, and possibly the higher mammals. Nicholson and Risley (1942) examined the urogenital system of *Emys blandingii (Emydoidea blandingi).* They illustrated and described the penis; however, their main interests were the gonads and urogenital ducts. An anatomical and histological description of the penis of *Lissemys punctata* was published by Seshadri (1956); Majupuria (1959) also described the penis of this species.

GENERAL PENIAL ANATOMY

The penes of cryptodiran turtles are highly diverse in structure. For this reason, it is difficult to describe a generalized penis which would include all the structural differences observed in the various chelonian families. I have, therefore, selected for this general description the penis of *Chelydra serpentina* because it does not appear to be highly specialized; it thereby provides a basis for the interpretation of the penial morphology of other cryptodiran genera.

In the relaxed state, the penis lies ventromedially in the cloaca (Fig. 1A). It is not, however, a separate structure lying free on the cloacal floor, but only a modified portion of the floor; it is divided into a proximal shaft and a distal glans penis lying near the vent. The shaft consists of a pair of lateral seminal ridges bordering a medial seminal groove. The seminal groove extends from the urethral opening on the anterior wall of the urogenital sinus posteriorly into the highly folded glans. Anteriorly, the seminal ridges are low, but posteriorly, as they approach the glans, they gradually increase in size and are most prominent anterior to the glans.

The glans penis is a highly folded or ridged structure. Three distinct folds are present. The largest fold, plica externa, forms the lateral and distal boundaries of the glans; it is U-shaped with enlarged proximal ends. A second U-shaped fold, the plica media, lies within the plica

externa. It is very similar to the plica externa in possessing enlarged proximal ends, but it is not as large as the former fold. The seminal groove terminates medially on the internal surface of the plica media. A pair of flaccid folds or flaps, the plicae internae, lie in the center of

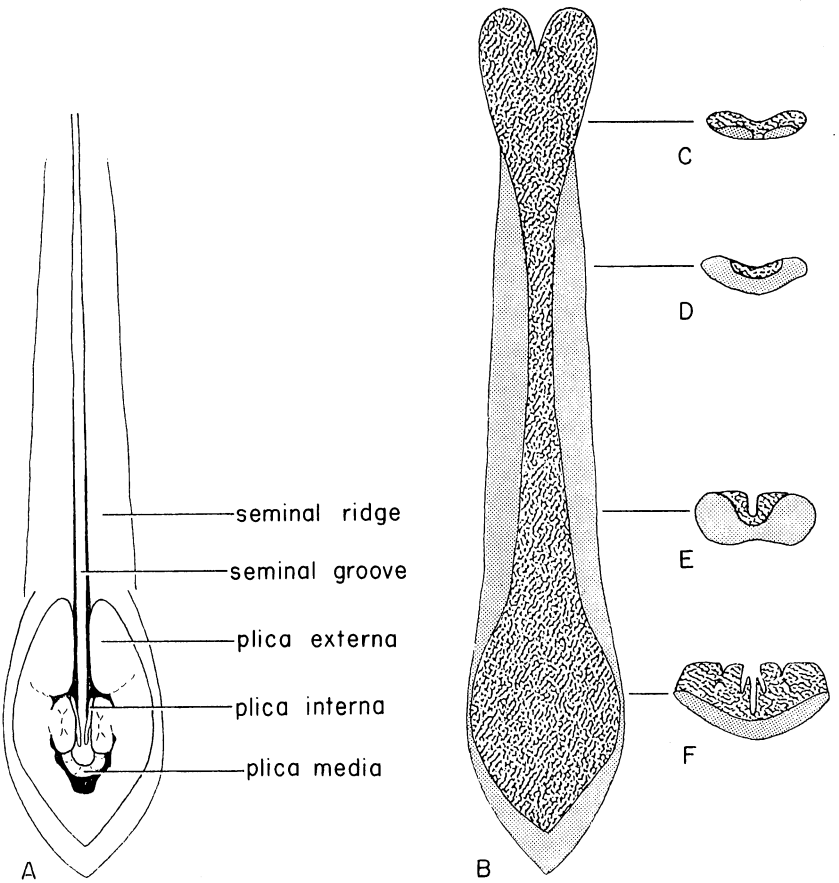

FIG. 1. Schematic representation of a relaxed penis of *Chelydra serpentina*. A. dorsal view of the penis; B. dorsal view of the erectile tissue (mottled, corpus spongiosum; stippled, corpus fibrosum); C–F. cross sections through B at levels indicated.

the glans, one on each side of the seminal groove. Only one previous author, Gerecke (1932), has assigned names to the folds of the glans; his terminology for the plica externa, plica media, and plicae internae is "Seitenwulst der Glans 1," "Seitenwulst der Glans 2," and "Papillien auf der Glans," respectively.

There are three pairs of sinuses (surface depressions) on the distal half of the penis. They may represent vestiges of the openings of peritoneal canals, for the canals of extant turtles end blindly in the penis. On each side of the seminal ridge, just proximal to the plica externa, there is a sinus on the dorsomedial surface. Another sinus is found distally on the inner surface of each enlarged end of the plica externa. A third sinus is present on each side on the outer base of the enlarged end of the plica media. In the descriptive section these sinuses will be referred to as sinus of the seminal groove, anterior sinus of the glans, and posterior sinus of the glans, respectively.

Two distinct types of erectile tissue are present in the penis (Fig. 1B-F). The corpus spongiosum, a heavily vascularized connective tissue containing many sinusoids, forms the glans penis and the medial margins of the seminal ridges. The corpus fibrosum, a thick, elastic plate of connective tissue, provides the main support for the penis. Proximally, beneath the urethral opening, the corpus spongiosum arises as a pair of bulba corpora spongiosa. These two lobes of the corpus spongiosum fuse beneath the urogenital sinus and decrease in size. At this point, the corpus fibrosum appears as a pair of thin lobes which fuse distally to form an elongated lanceolate plate with upturned edges. The upturned edges of the corpus fibrosum form the main support for the seminal ridges. The corpus spongiosum is greatly reduced in the area of fusion of the corpus fibrosum and lies only on its dorsomedial surface. Distally, the corpus spongiosum gradually increases in size, thereby increasing the size of the seminal ridges. The glans penis is formed entirely of corpus spongiosum resting on the corpus fibrosum; the latter tissue extends distally beyond the glans and ends in a point. I have purposely refrained from using the terms corpus cavernosum penis and corpus cavernosum urethrae in order to avoid the implication of homology between mammalian and chelonian erectile tissue, although the homology probably does exist.

The chelonian penis is extruded, not everted as in snakes and lizards. If extrusion of the penis is followed as a sequence of separate events, the manner of erection can be easily visualized. At first, the penis extends posteriorly through the vent; as the size and tension increases the penis bends ventrally and then slightly anteriorly. Thus, at complete extrusion the glans penis and the seminal ridges and groove occupy a ventral or posteroventral position. The penis is withdrawn into the cloaca by the retractor penis muscle, which originates on the sacral ribs and inserts on the ventral surface of the corpus fibrosum beneath the glans.

PENIAL DESCRIPTION

The general penial morphology of each family is presented first, in order to indicate the morphological characters which are found in all the representatives of the family. This is followed by a detailed description of the glans of each genus and of inter- and intraspecific variation when it was observed. The descriptions are of the glans penis and its associated structures as examined from dorsal view, i.e., the normal relaxed state of the penis as it lies on the floor of the cloaca. Unless otherwise stated, the description is based on adult male specimens. In some instances, it was possible to examine only the genitalia of immature or hatchling individuals; the difficulties involved with such specimens will be considered in the discussion section. The classification of Williams (1950) as modified by McDowell (1961, 1964) is followed.

CHELYDRIDAE.—Morphologically, the glans is nearly identical in *Chelydra* (Fig. 1A) and *Macroclemys* (Fig. 2), except for an additional fold in the latter. The three plicae are present and relatively large. The plica externa is a heavy U-shaped fold with enlarged proximal ends. The plica media is also U-shaped with enlarged proximal ends which are fused laterally to the medial wall of the plica externa. A pair of folds, plicae internae, are separated medially by the seminal groove; each fold is fused proximally to the adjacent enlarged end of of the plica media. The seminal groove is morphologically single and terminates medially at the base of the plica media. Functionally, the seminal groove may be bifurcate, since the seminal fluid may pass upward in the grooves formed by the fusion of the plica media and the plicae internae. It seems more likely, however, that the seminal fluid passes upward over the entire medial face of the plica media, since there is no distinct bifurcation in the preserved material.

All three pairs of sinuses are present. Proximal to the glans, the sinuses of the seminal groove lie on the medial surface of the seminal ridges. The anterior sinuses of the glans are on the distomedial walls of the enlargements of the plica externa, and the posterior sinuses of the glans are on the distal bases of the enlargements of the plica media.

An accessory fold of the plica externa is characteristic of the glans of *Macroclemys* but is absent in *Chelydra*. The accessory fold lies between the plicae externa and media, distal to the enlargements of the plica media. Distally, the accessory fold has a circular swelling.

TESTUDINIDAE.—This family is composed of four subfamilies, Batagurinae, Emydinae, Platysterninae, and Testudininae. As would be

expected in such a large and diverse family, the penial morphology is quite varied. The plica externa is present in the four subfamilies, but only poorly developed in the Testudininae. A well-developed plica media is always present and is frequently double. The plicae internae are absent only in the Platysterninae. The seminal groove is morphologically single in the Emydinae, Batagurinae, and Platysterninae. In the Testudininae, it is bifurcate distally. Only the pair of sinuses of the seminal groove are present. These sinuses remain as distinct depressions in the other subfamilies and appear to be absent in the Testudininae.

Batagurinae: In *Rhinoclemys* (Fig. 2), the plica externa is a low fold which is divided distomedially. Proximally, the ends of the plica externa are elevated but decrease rapidly as they extend distally. The plica media is a double, U-shaped fold. The lateral fold of the plica media is large and heavy with an elongate protuberance in the middle of each side. The medial fold of the plica media is smaller and lower; its proximal ends are fused laterally to the wall of the lateral fold at the base of the protuberances. Each plica interna is fused to the proximal end of the medial fold of the plica media. The seminal groove is single and ends on the medial fold of the plica media. Medial to the proximal ends of the plica externa on the seminal ridges is a pair of sinuses. The sinuses are pigmentless areas usually containing a small cleft with a small papilla. The glans penis of *Mauremys* is so similar to that of *Rhinoclemys* that the above description is also accurate for *Mauremys,* except that the sinuses of the seminal groove were not observed.

Emydinae: The plica externa of *Chrysemys* (*sensu* McDowell, 1964) is a low but distinct fold (Fig. 2). It is bisected distomedially; each half is enlarged proximally, decreases in size as it extends distally, and then becomes slightly enlarged distolaterally. The plica media, a distinct, double, spade-shaped fold, rises from the middle of the glans. The lateral fold of the plica media is a heavy fold that is separated from the flaccid medial fold by a shallow sulcus. The plicae internae are a pair of large folds; each fold is fused medially to the adjacent wall of the medial fold of the plica media. The seminal groove is unbranched. The sinuses of the seminal groove are pigmentless, slightly papillated areas on the dorsal surface of the seminal ridges proximal to the proximal ends of the plica externa. Very little variation has been observed in this genus. *Chrysemys picta* differs only slightly from *C. scripta, C. nelsoni, C. floridana,* and *C. concinna,*

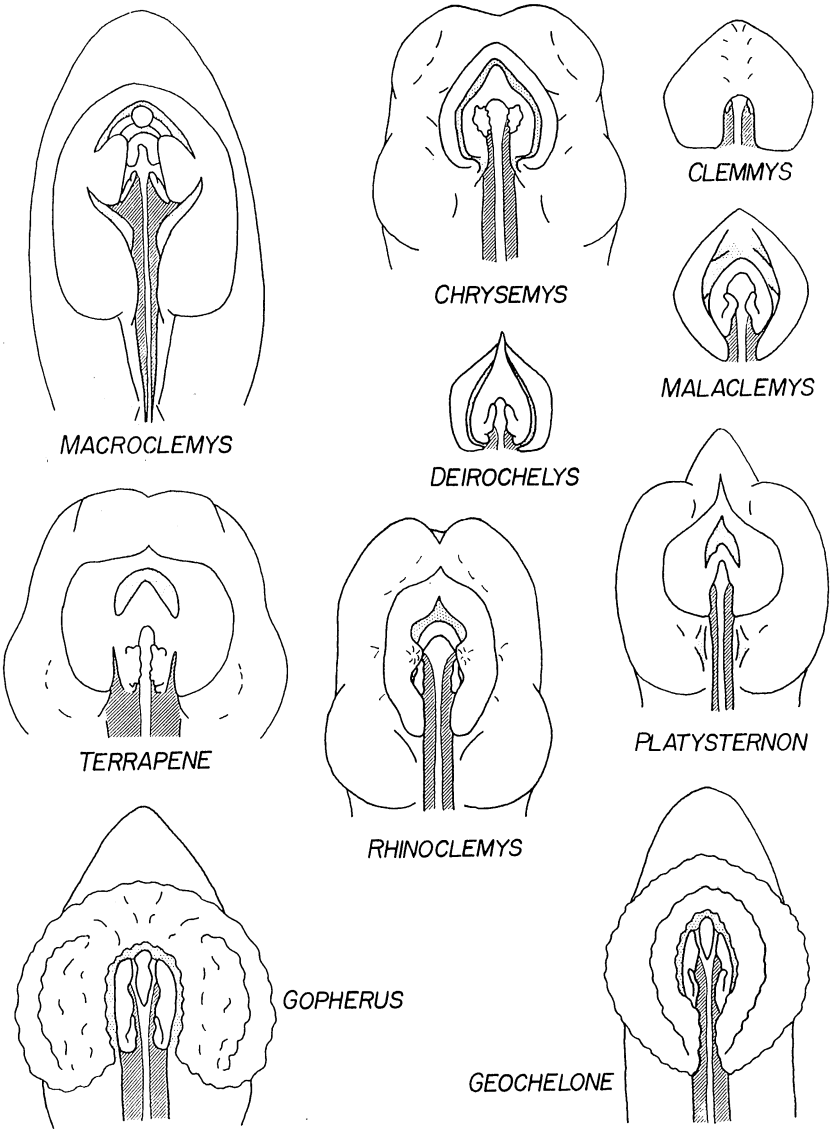

FIG. 2. Schematic representation of the penes of *Macroclemys temmincki, Chrysemys concinna, Clemmys marmorata, Deirochelys reticularia, Malaclemys barbouri, Terrapene carolina, Rhinoclemys areolata, Platysternon megacephalum, Gopherus polyphemus,* and *Geochelone carbonaria.* Only the plicae media and internae of *Clemmys, Deirochelys,* and *Malaclemys* are shown.

which form a homogeneous group. In *C. picta,* the lateral fold of the plica media appears to be proportionately thicker, and the sulcus separating the plica media folds is less well defined than in the other species.

In the genus *Clemmys* (Fig. 2), the plica externa is a low heavy fold. It is bisected distally into two lateral halves; each half has a proximal and distolateral enlargement. The plica media is a broad, spade- or diamond-shaped fold which is not distinctly divided by a sulcus into two folds. The lateral border of plica media is, however, much more solid than the median portion. Proximally, the ends of the plica media are slightly enlarged, and in *Clemmys guttata* and *C. muhlenbergi* a circular elevation is present distally on the enlargement of each side. These elevations are proprotionately larger in *C. muhlenbergi.* Each of the thin plicae internae is fused to its adjacent wall of the plica media. The seminal groove is single; it ends medially on the plica media. The pigmentless, paired sinuses of the seminal groove are found on the dorsomedial walls of the seminal ridges medial to the proximal enlargements of the plica externa.

The glans of *Deirochelys* (Fig. 2) is similar to that of *Chrysemys.* The plica externa is a low, distally bisected fold. This plica has the characteristic proximal and distolateral enlargements of which the former is the larger. The plica media is a spade- or diamond-shaped fold; it is divided into a lateral and a median fold by only a shallow sulcus. The lateral portion of the plica media is heavy and wide, particularly the proximal half. The median portion is flaccid and only slightly enlarged proximally. A pair of large plicae internae are fused laterally to the medial wall of the plica media. The sinuses of the seminal groove lie on the seminal ridges proximomedial to the proximal enlargements of the plica media.

The glans of *Emydoidea* is similar to that of *Deirochelys.* The only difference is in the structure of the plica media. The plica media is an elevated spade-shaped fold with only a very faint indication of a sulcus which barely divides it into lateral and median folds. Although the sulcus is very shallow, the lateral edge is solid, and the median portion is flaccid, thus indicating a division.

In the specimens of *Malaclemys* (*sensu* McDowell, 1964) examined, the structure of the glans is similar to that of *Chrysemys.* The plica externa is a low fold which is divided distally into two lateral halves. Each half possesses two enlargements, a proximal and a distolateral one, of approximately equal size. An elevated, double plica media is round to diamond-shaped (Fig. 2). The lateral fold is heavy and dis-

tinctly separated from the median fold by a sulcus. The median fold is more flaccid than the lateral one. It is joined to the lateral fold by a low ridge on each side; however, this ridge does not effectively interrupt the sulcus. The plicae internae are a pair of large, thin flaps fused medially to the wall of the median fold of the plica media. The seminal groove is single and ends medially on the median fold of the plica media. On the seminal ridges medial to the proximal enlargements of the plica externa are the sinuses of the seminal groove. They are pigmentless regions lying in a shallow fold.

The plica externa of *Terrapene* (Fig. 2) is greatly reduced and consists mainly of a pair of proximal round swellings which diminish rapidly as they extend distally; they have only a very small distolateral enlargement. The plica media is a double fold with an oblong or circular outline. The lateral fold of the plica media is broad and well developed. The median fold is also fairly large and is U-shaped. The median fold is connected on each side to the lateral fold by a ridge; this ridge effectively interrupts the deep sulcus which separates the two folds proximally and distally. Fused to the proximal ends of the median fold of the plica media are the paired plicae internae. These folds or flaps are relatively large in most *Terrapene* (*carolina* and *ornata*), but in *coahuila* they are reduced. A single seminal groove terminates medially on the median fold of plica media. The sinuses of the seminal groove were not seen in all specimens. They appear as pigmentless areas, usually in shallow folds, on the seminal ridges.

Platysterninae: The plica externa of *Platysternon* (Fig. 2) is a low fold; it is bisected distally. Each lateral half has a slight proximal enlargement and an indistinct distolateral one. The plica media is a double fold and rises above the surface of the penis. The lateral fold is the largest and widest, slightly broader proximally than distally. The median fold is fused proximally to the inner wall of the lateral fold. Distally, the median fold is separated by a deep sulcus from the lateral fold. The plicae internae are absent. The seminal groove is single and terminates medially on the median fold of the plica media. The sinuses of the seminal groove are well-developed clefts on the seminal ridges proximomedial to the proximal ends of the plica externa.

Testudininae: Characteristically, the glans in this subfamily has a low, indistinct plica externa and a bifurcate seminal groove.

In *Gopherus* (Fig. 2), the plica externa is an extremely low and poorly delineated fold; in contrast, the plica media is a large circular fold. The plica media is strongly raised above the surface and is double.

The lateral fold is broad and also double. The external edge of the lateral fold has a distinct heavy border. On the proximal half of the lateral fold, the inner portion is crescent-shaped and then tapers distally to a thinner fold. The small U-shaped median fold is separated from the lateral fold by a distinct but shallow sulcus. Distomedially on the median fold is a tear-shaped elevation. Proximally, the plicae internae form large elevations on each side. The seminal groove enters the glans singly, bifurcates medially, and each branch extends upward along its respective lateral margin of the tear-shaped elevation of the plica media. There is no evidence of any sinuses.

The glans of *Geochelone* (Fig. 2) also has an indistinct plica externa. The plica media is a large fold with a circular outline. It is distinctly double with a wide lateral portion separated from a small sunken U-shaped median fold by a distinct sulcus. The lateral fold also appears to be double with an outer ridge much wider than the inner ridge. The ridges are separated only by a very shallow sulcus. As in *Gopherus,* the median fold of the plica media has a distomedial elevation which separates the two branches of the bifurcate seminal groove. The plicae internae are a pair of raised elevations on the proximal ends of the median fold of the plica media. No sinuses were observed.

KINOSTERNIDAE.—Representatives of the four kinosternid genera, *Claudius, Kinosternon, Sternothaerus,* and *Staurotypus,* have glans penes which are only slightly different. There is a heavy U-shaped plica externa. The plica media does not exhibit the folding characteristic of the previously described families. It is composed of three parts—a pair of proximal papillae and a single, large, distomedial triangular or cordiform fold. The distomedial fold is usually connected laterally and distally by low ridges to the inner wall of the plica externa. The seminal groove is divided into four branches. At the proximal base of the plica media, the seminal groove trifurcates; each lateral branch extends laterally up the medial surface of its respective papilla of the plica media. The medial branch extends distally onto the distomedial fold of the plica media, thus medially bisecting this fold. Distally, on the large fold, the median branch bifurcates around a protuberance and then terminates. In the Kinosterninae, the papillae of the plica media are proportionately larger than in the Staurotypinae. The plicae internae are not present, although they may have been incorporated into the papillae of the plica media.

All three pairs of sinuses are present. The sinuses of the seminal groove lie on the seminal ridges proximal to the plica externa. The

anterior sinuses of the glans lie at the bases of the proximal enlargements of the plica externa, lateral to the papillae of the plica media. The posterior sinuses of the glans are distolateral to the distomedial fold of the plica media on the sulcus between the plica media and plica externa.

Staurotypinae: Because of the similarity of the glans penis in *Claudius* and *Staurotypus* (Fig. 3), a single description will suffice for both. The glans penis is composed of a U-shaped plica externa which is wider proximally than distally. Distally, within the cavity formed by the plica externa is the large, cordiform fold of the plica media; this fold is joined laterally to the plica externa by a low ridge on each side. Proximally, the plica media forms a papilla-like fold on each side. The seminal groove sends a branch up each of the papillae and a third branch medially onto the distomedial fold which it bisects. Distally, the median branch of the seminal groove bifurcates around a small protuberance that is usually hidden in the lateral folds of the groove. The three pairs of sinuses are present and in the positions previously mentioned.

Kinosterninae: Plica externa is a heavy U-shaped fold with slightly enlarged proximal ends in *Kinosternon* (Fig. 3). A large, triangular fold of the plica media lies distally in the cavity formed by the plica externa. Laterally, the triangular fold is connected on each side to the plica externa by a low ridge. Proximally, the plica media forms a pair of papillae-like folds, one on each side of the seminal groove. The seminal groove enters the glans singly, but as it passes the proximal base of the plica media, it trifurcates. Each lateral branch extends upward along the medial surface of its corresponding papilla, and the medial branch passes onto the triangular fold. Near the distal end of the triangular fold, the seminal groove bifurcates around a small protuberance on the floor of the groove.

No differences have been observed in the structure of the glans in the six species of *Kinosternon* examined. In a *K. flavescens* (UMMZ 74654), however, the right papilla of the plica media is anomalous. The dorsal portion is not completely developed, and the corresponding lateral branch of the seminal groove extends only partially onto the papilla.

In the genus *Sternothaerus,* the structure of the glans can be divided into two general groups, a *depressus-minor-odoratus* type and a *carinatus* type. In both types, the plica externa is a heavy U-shaped fold with enlarged proximal ends, and it is divided distolaterally into two lateral halves. The plica interna is absent. It is the morphology of the plica

media that is different in the two groups. The plica media of *S. depressus, S. minor,* and *S. odoratus* (Fig. 3) shows the typical kinosternid condition with a large distal block-like fold bisected medially by a branch of the seminal groove and a pair of proximal papilla-like folds. The distomedial fold differs from the kinosternid condition, as the fold in these three species appears to have been tilted so that the median branch of the seminal groove is on the anterior face of the fold rather than on the dorsal surface. The seminal groove trifurcates at the base of the papillae, and a branch extends up each of the papillae. The median branch extends onto the block-like fold; after a short distance this branch bifurcates and ends alongside a circular protuberance. This is the condition found in specimens of *S. m. minor, S. m. peltifer,* and *S. depressus;* however, in *S. odoratus,* the distomedial fold is greatly elongated as is also the protuberance around which the median branch of the seminal groove bifurcates.

The plica media of *S. carinatus* (Fig. 3) is also composed of three folds; however, the distomedial fold is reduced in size, whereas the pair of proximolateral folds or papillae are much enlarged. The seminal groove enters the glans singly, and at the base of the large proximolateral folds it bifurcates. A branch of the seminal groove extends upward along the distal margin of each of the enlarged folds. The distomedial fold is triangular and has remnants of the median branch of the seminal groove on its proximal face, but this branch is not continuous with the seminal groove.

The sinuses of the seminal groove and anterior sinuses of the glans occupy the same positions in all species of *Sternothaerus* as in the other kinosternid species. The posterior sinuses of the glans in *S. depressus, S. minor,* and *S. odoratus* lie distal to the distomedial fold of the plica media and are separated by a small ridge. Only a single sinus lies distal to the plica media in *S. carinatus.*

DERMATEMYDIDAE.—A heavy U-shaped plica externa with enlarged proximal ends is present in *Dermatemys* (Fig. 3). The plica media is divided into a pair of elaborate papilla-like folds and a large, distomedial, diamond-shaped fold.

The seminal groove enters the glans singly and bifurcates at the base of the distal fold. The branches diverge as they extend upward and proximally onto the papilla-like folds and terminate dorsally on the papillae. The plica interna is absent, either through reduction or incorporation in the papilla-like folds of the plica media.

All three pairs of sinuses are present. The sinuses of the seminal groove are on the seminal ridges proximal to the plica externa. The

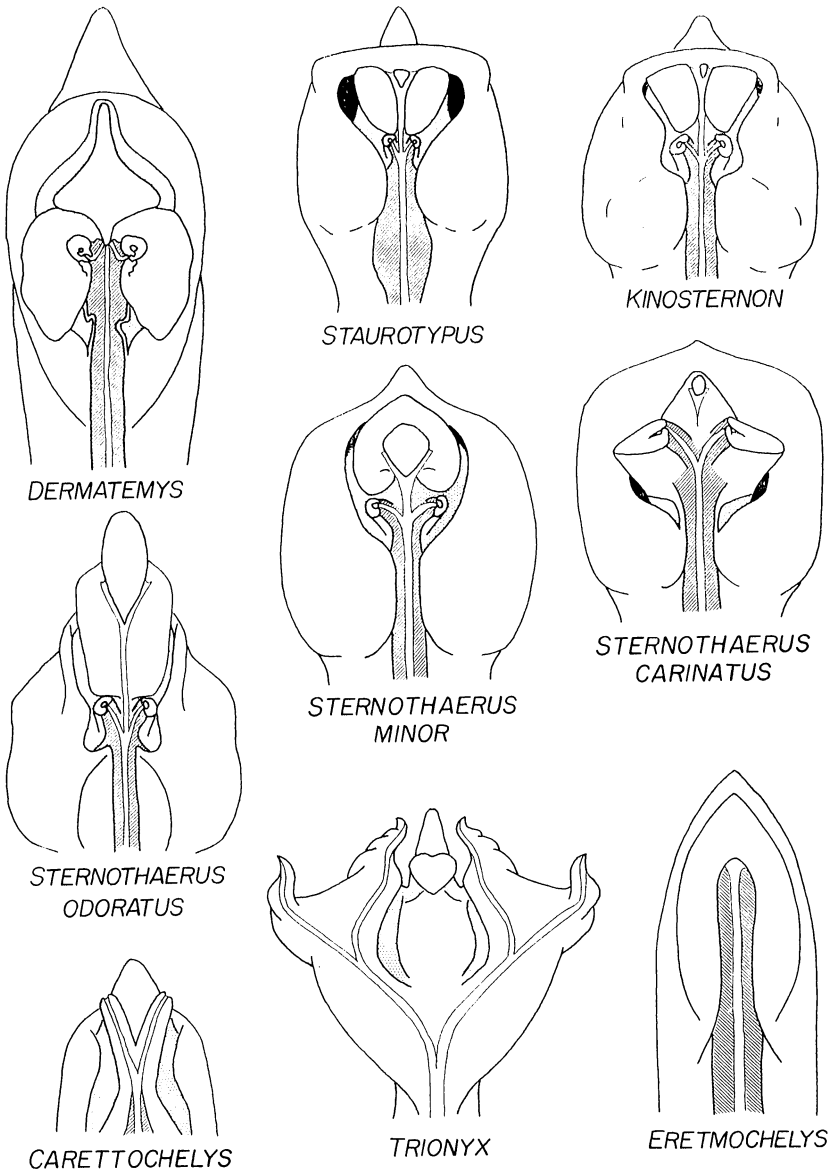

FIG. 3. Schematic representation of the penes of *Dermatemys mawi, Staurotypus triporcatus, Kinosternon subrubrum, Sternothaerus odoratus, Sternothaerus minor, Sternothaerus carinatus, Carettochelys insculpta, Trionyx ferox,* and *Eretmochelys imbricata.* The genitalia of *Carettochelys* and *Eretmochelys* are from unsexed hatchling specimens.

anterior sinuses of the glans are on the distomedial wall of the enlarged ends of the plica externa. The posterior sinuses of the glans are distolateral to the distal fold of the plica media.

CARETTOCHELYIDAE.—Only juvenile specimens of *Carettochelys* have been examined. The phallus is a three-lobed structure (Fig. 3). The distomedial lobe is the tip of the plate of the corpus fibrosum. The two lateral lobes are composed of corpus spongiosum and form the main body of the glans. Since the lateral lobes bear the seminal grooves, they probably represent a highly modified plica media. The seminal groove enters the glans singly and bifurcates at the base of the lateral lobes. A branch extends upward on the dorsal surface of each lobe and ends at its distal tip. No sinuses were observed.

TRIONYCHIDAE.—The penis of *Trionyx* (Fig. 3) is a five-lobed structure, a single distomedial lobe, a pair of distolateral lobes, and a pair of proximolateral lobes. The tip of the corpus fibrosum forms the distomedial lobe; proximally on this lobe, there is a small dorsal fold which may be a remnant of the plica externa as also may be the ventrolateral ridges on the lateral lobes. The distolateral and proximolateral lobes are the plica media and are composed entirely of corpus spongiosum. These lobes support the branches of the seminal groove. As the single seminal groove enters the glans, it bifurcates. Each branch extends laterally onto the base of the plica media. The seminal groove bifurcates again at the base of the proximolateral and distolateral lobes of the plica media. Each branch of the second bifurcation extends onto a lobe and ends at its tip; thus, each lateral lobe bears a branch of the seminal groove. The sinuses of the seminal groove are pigmentless spots located distally on the seminal ridges.

CHELONIIDAE AND DERMOCHELYIDAE.—Four genera of sea turtles, *Caretta, Chelonia, Dermochelys,* and *Eretmochelys,* were examined for this study, and all were juveniles. The phalli of the four genera are similar in structure (Fig. 3). A single U-shaped fold forms the glans; this fold appears to be an enlarged continuation of the seminal ridges. The seminal groove is single and terminates medially on the inner surface of the fold. No sinuses have been observed.

DISCUSSION

As is typical of most studies of this nature, the first and foremost problem to arise is the question of the homology of the compared structures. Those folds and sinuses which bear the same name are considered homologous. Homologies are inferred from structural similari-

ties, i.e., position in relation to other plicae, sinuses, and seminal groove, also gross histological character, and morphology of the plicae. Since homology is based on derivation from the same structure in a common ancestor, an attempt to determine either the primitive or least specialized condition of the glans is of interest. Of the extant crypodiran turtles, four taxa, Dermatemydidae, Emydinae, Trionychidae, and Cheloniidae, have a fossil history extending from the Cretaceous. In these taxa, the glans varies from simple to complex, as does also the habitus of these turtles. The cheloniids have the simplest glans of all cryptodires, yet they are some of the more specialized turtles. The dermatemydids have, however, an elaborate glans, but an unspecialized habitus. The trionychids are specialized in both body form and penial morphology. One method of determining primitiveness is to use those characteristics which are found most frequently (Table 1). If this criterion is used the following characteristics are suggested as being primitive: single seminal groove, plicae externa and media present and not double, plica interna absent, sinuses of seminal groove present and other sinuses absent. No taxa exhibit all these characters, although *Platysternon* comes the closest.

Of no less importance is the actual function of the glans. It may have a stimulatory effect, anchoring action, or it may release sperm in close proximity to the female's genital ducts. All three suggestions may be acceptable; however, in some turtles it is difficult to visualize the glans serving any of these functions. Can the single plica of the sea turtle's glans effectively anchor the penis in the cloaca or does it stimulate the female? In the female as in the male, each genital duct opens anteriolaterally in the cloaca; thus, it would seem more efficient to have a single bifurcation of the seminal groove, but only *Dermatemys, Carettochelys,* and the Testudininae have a bifurcation of the groove. Owen (1866) proposed that "the development of the penis bears relation to the physical impediments to coitus, caused by shape, extent, and completeness of the shell, and by the medium in which the act takes place, thus the penis is least developed in the marine species, with a flattened carapace and incomplete plastron." The accuracy of the last clause of Owen's statement is beyond question; however, the aquatic softshelled turtles, Trionychidae, have an equally reduced plastron and flattened carapace, and the penis is elaborate. Even the aquatic snapping turtles, Chelydridae, show a similar trend in shell modification, and they have a well-developed penis. Thus, it seems more reasonable to conclude that the morphology of the penis illustrates its own distinct evolutionary trend unrelated to the modifications of the shell.

TABLE 1

SUMMARY OF THE CONDITION OF THE SEMINAL GROOVE, PLICAE, AND SINUSES OF THE PENIS IN THE CRYPTODIRAN FAMILIES
A plus denotes the presence and a minus the absence of a structure

Group	Seminal Groove	Plicae			Sinuses of		
		Externa	Media	Internae	Seminal groove	Anterior glans	Posterior glans
Cheloniidae	undivided	−	+	−	?	?	?
Dermochelyidae	undivided	−	+	−	?	?	?
Carettochelyidae	bifurcate	−	+	−	?	?	?
Trionychidae	doubly bifurcate	+ (?)	+	−	+	−	−
Dermatemydidae	bifurcate	+	+	−	+	+	+
Kinosternidae							
Staurotypinae	trifurcate with median branch bifurcate	+	+	−	+	+	+
Kinosterninae	trifurcate with median branch bifurcate	+	+	−	+	+	+
Chelydridae	undivided	+	+	+	+	+	+
Testudinidae							
Batagurinae	undivided	+	+	+	+	−	−
Emydinae	undivided	+	+	+	+	−	−
Platysterninae	undivided	+	+	−	+	−	−
Testudininae	bifurcate	+	+	+	−	−	−

My examination of juvenile specimens of Carettochelyidae, Dermochelyidae, and Cheloniidae has resulted in two specific problems. Is there ontogenetic change in the development of the phallus? Since the sex of juveniles cannot be determined by gross dissection, is the female phallus structurally different from that of the male? At the present, I am able to offer only a partial solution to these questions. In a small series of *Trionyx,* there is no evidence of ontogenetic change; a hatchling *Trionyx* (33 mm plastron length) with an umbilical scar has a five-lobed phallus with a doubly bifurcate seminal groove. This suggests that there is no ontogenetic change in penial morphology. Schmidtgen (1907) stated that in males and females of the same species, the clitoris and the penis have exactly the same appearance. In the three mature female *Trionyx* examined, the glans clitoris does, indeed, appear as a miniature glans penis with five lobes and a doubly bifurcate groove.

Penial morphology indicates that there are four major groups of cryptodiran turtles (Fig. 4); unfortunately, it provides little information of the relationships between these groups. The sea turtles, Cheloniidae and Dermochelyidae, are a very homogeneous group; they have an undivided seminal groove and a glans with a single fold. The Carettochelyidae and Trionychidae comprise a single unit that is characterized by a lobed glans and a basal bifurcation of the seminal groove. The Dermatemydidae and Kinosternidae share a plica media of three parts, a pair of proximolateral papilla-like folds and a distomedial block-like fold. The glans of Chelydridae and Testudinidae have U-shaped plicae externa and media, usually a pair of plicae internae, and almost always an undivided seminal groove.

The simple appearance of the sea turtle penis is an enigma. It allows two opposite interpretations which are of equal validity, i.e., illustrates the primitive condition or a highly modified condition. Although I favor the latter interpretation, there is no strong evidence to support this contention other than that all the other cryptodiran turtles have a more elaborate glans penis. The fossil history of the sea turtles extends back to the late Triassic, and presumably the extant sea turtles represent a continuum of this line of evolution. If this is true, Dermochelyidae and Cheloniidae cannot be expected to show any close relationships with the other cryptodiran families, and their penial morphology might well represent a primitive condition. The similarity of the phalli of Dermochelyidae and Cheloniidae seems to indicate a close relationship betwen these two families. Perhaps *Dermochelys* is only an extremely specialized cheloniid.

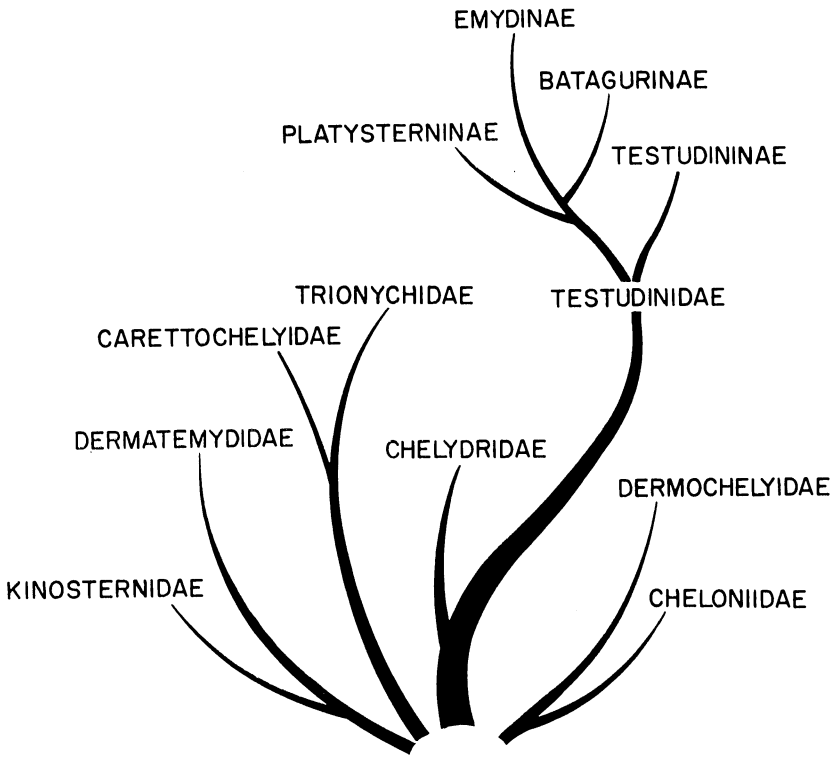

FIG. 4. Diagram of the proposed familial relationships of cryptodiran turtles as determined by penial morphology. Neither primitiveness nor the degree of divergence is directly implied in the diagram except for divergences within each of the four basal lines.

The general body form and penial morphology seem to indicate that Trionychidae and Carettochelyidae form a natural group. *Carettochelys* seems to have the less specialized penis of the two families with a plica media of two main lobes and a single, basal bifurcation of the seminal groove. In Trionychidae, each of the two main lobes may have been subdivided, thus, forming two lobes on each side; the seminal groove has a basal bifurcation and each branch bifurcates at the base of the lateral lobes. The number of branches of the seminal groove is in agreement with the number of lobes of the plica media, two branches in *Carettochelys* and four branches in *Trionyx*.

In Kinosternidae and Dermatemydidae, the seminal groove has either two or four branches, the plica media is divided into a pair of proximolateral folds and a single distomedial fold, and the plica interna is

absent. The unique modifications of the penis in these two families argue against Williams' (1950) inclusion of the kinosternid genera with the Chelydridae and support McDowell's (1961) contention of a relationship between *Dermatemys* and the kinosternids. The unique structure of the plica media suggests that the kinosternids and the dermatemydids arose from a common ancestor. The original condition of the seminal groove may have been trifurcate, and in the Kinosternidae, the median branch then became secondarily bifurcate. The median branch of the seminal groove may have been lost in *Dermatemys;* the reduction of the median branch in *Sternothaerus carinatus* supports this conclusion.

All four kinosternid genera have a heavy U-shaped plica externa, a tripartite plica media, no plica interna, and a seminal groove ending in four branches. *Claudius* and *Staurotypus* have proportionately smaller papilla-like folds of the plica media than either *Kinosternon* or *Sternothaerus.* Only in *Sternothaerus* does the structure of the glans show interspecific differences. In fact the penial morphology of the species of *Claudius, Kinosternon,* and *Staurotypus* are more similar to one another than is the structure of the penis among the species of *Sternothaerus.* The penial morphology of the four species of *Sternothaerus* can be divided into two types—the *carinatus* and *odoratus;* the latter type includes *S. depressus, S. minor,* and *S. odoratus.* In the *odoratus* type, the papilla-like folds of the plica media are similar to the other kinosternids, but in *S. carinatus,* these folds are greatly enlarged. In both types, the distomedial fold of the plica media appears to be tilted anteriorly in contrast to the condition seen in the other kinosternids, and also the protuberance on this fold is enlarged in *Sternothaerus.* In *S. minor* and *S. depressus* the distomedial fold is proportionately equal in size to that of *Kinosternon;* however, this fold is greatly elongated in *S. odoratus* as is also the protuberance. The distomedial fold and its associated protuberance is greatly reduced in *S. carinatus.* There is also a difference in the condition of the seminal groove in the two types. The *odoratus* type possesses the usual kinosternid condition of the seminal groove, i.e., it is trifurcate at the base of the papilla-like folds; each lateral branch extends upward on its adjacent papilla-like fold; the median branch extends onto the distomedial fold and bifurcates. In *S. carinatus,* the median branch is present and bifurcates distally; however, it is not continuous proximally with the seminal groove. The penial morphology of *Sternothaerus* supports Tinkle's (1958) conclusions that *S. minor* and *S. odoratus* are closely related. Also, the close similarity of the penes of *S. minor* and *S. depressus* is in agreement with

Tinkle's findings. I would, however, suggest that *S. carinatus* diverged earlier from the *odoratus* line than Tinkle supposed (See Fig. 5).

The Chelydridae and the Testudinidae share a similar penial morphology which seems to indicate that they are more closely related to one another than to any of the other cryptodiran families. All three plicae are usually present in both families; the plicae externa and media tend to be U-shaped, and the seminal groove is undivided, except for

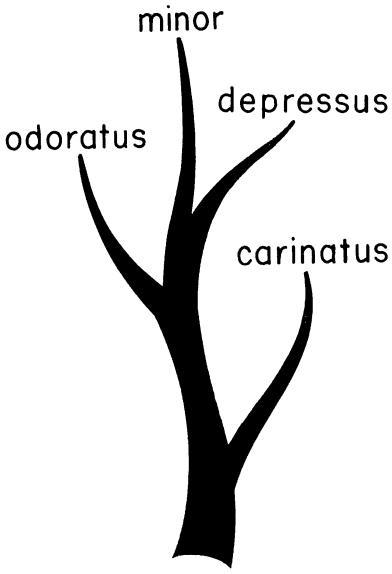

FIG. 5. Diagram of the relationships of species of *Sternothaerus* based on penial morphology. The diagram illustrates the approximate degree of divergence but not primitiveness.

the Testudininae in which it is bifurcate. The penial morphology of *Chelydra* and *Macroclemys* is so similar that there is little doubt that the two are closely related. The only difference is that the plica externa has an accessory fold in *Macroclemys,* but not in *Chelydra.*

The Testudinidae can be divided into two evolutionary lines on the basis of penial morphology. In the Emydinae, Batagurinae, and Platysterninae line, the plica externa is reduced but still distinct; the plica media is frequently a double fold with varying degrees of separation; the seminal groove is undivided; the sinuses of the seminal groove are present. The structure of the plica media, absence of the plicae internae, and the large anterior sinuses of the seminal groove in *Platysternon* indicate that this genus was probably derived from the emydine-batagurine line. The second evolutionary line, the Testudininae, typ-

ically has a greatly reduced plica externa, a bifurcate seminal groove, and probably no sinuses of the seminal groove. The striking differences in penial morphology of the two subfamilial lines suggest that they have had long independent histories.

In 1964, McDowell published a reclassification of the aquatic testudinids. An important aspect of McDowell's work was the establishment of a new subfamily, Batagurinae, which includes most of the previous palearctic emydine genera. Unfortunately, I have seen representatives of only two batagurine genera, *Mauremys* and *Rhinoclemys*. The very similar penial morphology of these two genera and their differences from the emydines hints that the Batagurinae may be a natural taxon. The similarity of the glans in *Pseudemys, Trachemys,* and *Chrysemys* supports McDowell's (*op. cit.*) contention that they should all be considered members of a single genus, *Chrysemys*. Also in agreement with McDowell's views, penial morphology suggests that *Deirochelys, Emydoidea,* and *Malaclemys* are closely related to the *Chrysemys* complex. I have been unable to interpret the relationships of *Clemmys* and of *Terrapene* from penial morphology, since both genera are distinctly different from each other and from the other emydine genera.

ACKNOWLEDGMENTS

The original idea for the usefulness of penial morphology in turtle systematics can be traced to the late Dr. Norman Hartweg; however, I received the idea indirectly from one of his students, Dr. Albert Schwartz. Dr. Hartweg had amassed a collection of turtles penes which I have found most useful. I am particularly grateful to two individuals for their constant encouragement and suggestions through different phases in the research of this problem. Dr. William J. Riemer guided my earlier work and was exceedingly helpful in editing a thesis on this subject which was submitted to and accepted by the University of Florida Graduate School. Dr. Charles F. Walker has provided many suggestions and ideas during the final stages of this work; he has also critically read the manuscript. I wish also to thank Dr. Arnold G. Kluge and Mr. Kraig Adler for their valuable comments in the preparation of the manuscript. Mr. John L. Tottenham has offered suggestions and aid in the preparation of the illustrations, and I am grateful for his help. I thank my wife, Patricia, for her patience and efforts in typing the many versions of the manuscript.

Many individuals have loaned and donated specimens from their collections: Mr. Charles M. Bogert, American Museum of Natural History (AMNH); Dr. Harold A. Dundee, Tulane University Collections

(TU); Dr. Claude W. Hibbard, University of Michigan Museum of Paleontology (UMMP); Dr. William J. Riemer, Dr. Walter Auffenberg, and Mr. Lewis D. Ober, University of Florida Collections (UF); Dr. Charles F. Walker, University of Michigan Museum of Zoology (UMMZ); and Dr. Ernest E. Williams, Museum of Comparative Zoology (MCZ). Specimens in my own collection are preceded by Z. To all of these individuals, I am indebted. I am grateful to a large number of friends for their assistance in collecting turtles for me. This study was supported in part by a National Science Foundation grant (GB-3366) to the University of Michigan Museum of Zoology.

SPECIMENS EXAMINED

CHELYDRIDAE.—*Chelydra osceola,* UMMZ 56618, Z 53; *Chelydra serpentina,* UMMZ 37827, 113211, Z 81; *Macroclemys temmincki,* Z 54.

TESTUDINIDAE.—**Batagurinae:** *Mauremys caspica,* UF 13902.2; *Rhinoclemys areolata,* UMMZ 118297–98, 118301; *Rhinoclemys pulcherrima,* UMMZ 117437. **Emydinae:** *Chrysemys concinna,* UMMZ 86664, Z 66–67; *Chrysemys floridana,* Z 68; *Chrysemys nelsoni,* Z 69; *Chrysemys picta,* UMMZ 64781, Z 59; *Chrysemys scripta,* UMMZ 72530, 76449, 117087, Z 70; *Clemmys guttata,* UMMZ 105104, Z 60; *Clemmys insculpta,* UMMZ 75958, Z 61; *Clemmys marmorata,* UMMZ 112258; *Clemmys muhlenbergi,* UMMZ 76612, 76619; *Deirochelys reticularia,* UMMZ 106309, Z 62; *Emydoidea blandingi,* UMMZ 92635, 115743; *Malaclemys barbouri,* UF 6531.1, 6537.1; *Malaclemys geographica,* UMMZ 44603, Z 84; *Malaclemys terrapin,* UF 7970.5; *Terrapene carolina,* Z 72, 99; *Terrapene coahuila,* UMMZ 126149; *Terrapene ornata,* UMMZ 62476, 85099. **Platysterninae:** *Platysternon megacephalum,* AMNH 30122. **Testudininae:** *Geochelone carbonaria* UMMZ 112407, UMMP (no number); *Gopherus berlandieri,* UMMZ 72524, 90029, 92748; *Gopherus polyphemus,* UMMZ 36071, Z 73.

KINOSTERNIDAE.—**Staurotypinae:** *Claudius angustatus,* UMMZ 41689; *Staurotypus salvini,* UMMZ 87737; *Staurotypus triporcatus,* UMMZ 79121, Z 58. ***Kinosterninae:*** *Kinosternon bauri,* UMMZ 108253, 108481, 109236, Z 56; *Kinosternon cruentatum,* UMMZ 75203; *Kinosternon flavescens,* UMMZ 69124, 72527, 74654, 101292; *Kinosternon hirtipes,* UMMZ 97129; *Kinosternon leucostomum,* UMMZ 75225; *Kinosternon subrubrum* UMMZ 93877, 93880, 119680; *Sternothaerus carinatus,* TU 74816.4, Z 79; *Sternothaerus depressus,* TU 17136.3; *Sternothaerus minor,* TU 16876.5, Z 57, *Sternothaerus odoratus,* UMMZ 64385, 74197, 10368, 117201.

DERMATEMYDIDAE.—*Dermatemys mawi,* Z 55.

CARETTOCHELYIDAE.—*Carettochelys insculpta,* MCZ 53772, UMMZ 123941.

TRIONYCHIDAE.—*Trionyx ferox,* UMMZ 64178, Z 74; *Trionyx muticus,* UMMZ 59092, 90002, 92657; *Trionyx spinifer,* UMMZ 64063, 70748, 89926, 92652, 92667, 113038.

CHELONIDAE.—*Caretta caretta,* UF 19612, 19615, 19618, 19620–21; *Chelonia mydas,* UF 5927.3, 10758.9, 10759.4, 19570, 19579; *Eretmochelys imbricata,* UF 10553.1, 10555.3, 10555.6, 10557.3, 10557.4.

DERMOCHELYIDAE.—*Dermochelys coriacea,* UF 10366.2, 10367–68, 10371, 10373.

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Accepted for publication February 11, 1966