

THE TAXONOMIC RELATIONSHIP BETWEEN *MALACLEMYS* GRAY, 1844 AND *GRAPTEMYS* AGASSIZ, 1857 (TESTUDINES: EMYDIDAE)

JAMES L. DOBIE

*Department of Zoology-Entomology
Auburn University, Alabama 36849*

Abstract

The turtle genus *Graptemys* is a distinctive group clearly separable from *Malaclemys* on the basis of external and osteological features. The difference between the groups indicate that the degree of genetic relationship is no closer than that resulting from their both having presumably arisen from a *Pseudemys*-like stock or *Malaclemys* from a *Graptemys* stock.

INTRODUCTION

Investigators of *Malaclemys* and *Graptemys* have based their taxonomic allocations on penial, skull, shell, hind limb and pelvic girdle morphology and on head patterns. Osteological comparisons, when indicated, were usually limited to the skull, and in most cases, head patterns were used to distinguish taxa. The degree of evolutionary conservatism and parallelism exhibited by turtles argues against the use of external characters (e.g., head striping), alone in determining taxonomic and phylogenetic relationships. Thus, both osteological and surficial features have been examined in this study.

HISTORICAL REVIEW

The controversy about the relationship between *Malaclemys* and *Graptemys* began as a result of the lumping of *Graptemys* with *Malaclemys* by Boulenger (1889) and the re-establishment of the genus *Graptemys* by Baur in 1890. Since

that time, W.P. Hay (1904) and O.P. Hay (1908) followed Baur in recognizing the two genera, as did Carr in 1949. Later, however, Carr (1952) questioned the validity of separating the two genera and McDowell (1964), without presenting supporting data, lumped *Graptemys* with *Malaclemys*. Zug (1966, 1971), on the basis of similiar penial, pelvic girdle, and hind limb morphology for the two genera considered them congeneric, and Parsons (1960, 1968) found the choanal structures of both genera to be so variable that the evidence did not particularly support or refute the congeneric idea. Several other authors (Ernst and Barbour, 1972; McKown, 1972; Dundee, 1974; Killebrew, 1979; Dobie and Jackson, 1979; Pritchard, 1979; Vogt, 1978, 1980) have not supported the synonymy of *Graptemys* with *Malaclemys*; they evidently must believe that sufficient evidence has not been presented to lump the two genera together.

The purpose of this study is to clarify the generic status of *Malaclemys* and *Graptemys*.

MATERIALS AND METHODS

Representatives of each of the ten extant *Graptemys* species (Vögt, 1980) and their subspecies and individuals of several subspecies of the monotypic *Malaclemys* were examined. External features, includ-

EDITORIAL COMMITTEE FOR THIS PAPER:

DR. EUGENE S. GAFFNEY, Associate Curator, Department of Vertebrate Paleontology, American Museum of Natural History, New York, New York 10024

DR. JOHN J. IVERSON, Assistant Professor of Biology, Earlham College, Richmond, Indiana 47374

ng scute contracts, plastral patterns, and striping on the head and leg were analyzed in juvenile and adult turtles of both sexes. Skull and shell characters were analyzed on large sub-adult and adult females. Skull terminology is that of Gaffney (1972 a); scute and bone terminology is that used by Zangerl (1969).

The method used to elucidate the relationship between *Malaclemys* and *Graptemys* and to other North American emydid turtles is the search for taxa that have shared derived characters. This method was described by Hennig (1966), and has been used by others (Gaffney, 1972 b, 1975; W.E. Clark, 1978) and is called phylogenetic systematics or cladism.

DIAGNOSTIC CHARACTERISTICS

The diagnostic characteristics of *Graptemys*, *Malaclemys* and an outgroup comparison of those genera with the other North American emydid genera are listed in Table 1. Each feature is also designated as either ancestral (primitive) or advanced (derived).

SIGNIFICANCE OF DIAGNOSTIC CHARACTERISTICS

The number (s) in a bracket refers to the number of the diagnostic features in Table 1.

SKULL FEATURES

(1) Quadratojugal - maxilla contact. If the absence of contact between these two bones represents the primitive state, then the possession of the derived condition in three *Graptemys* species (in one *pseudogeographica* and in all *pulchra* and *barbouri*), in *M. terrapin*, and in some *Pseudemys* species suggests that *M. terrapin* could have been derived from one of these *Graptemys* or *Pseudemys* species. *Graptemys* could have come from any group lacking contact between the two bones.

(2) Spoon-shaped symphysis of lower jaw

(Fig. 1). The flattened spoon-shaped nature of the symphyseal part of the lower jaw apparently is a derived feature in *Graptemys*. The absence of such a structure in *Malaclemys* suggests that *Graptemys* was not ancestral to *Malaclemys* and that *Malaclemys* may have arisen from some *Pseudemys* species.

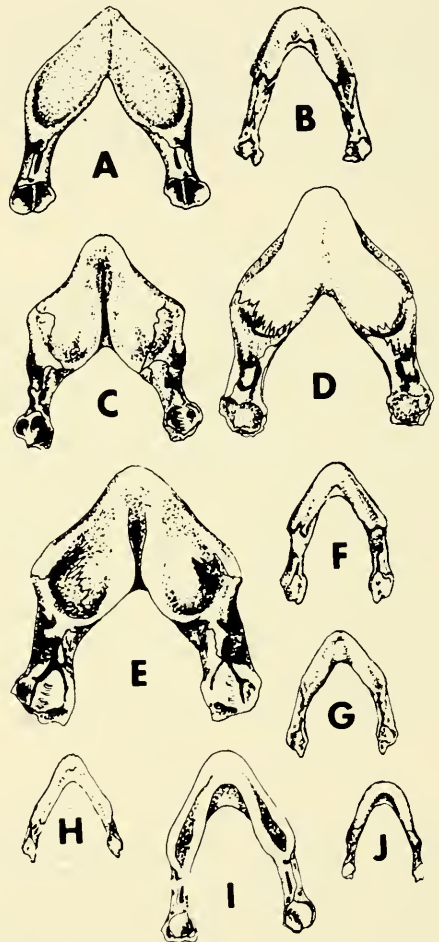


Figure 1. Shape of the symphyseal area of the lower jaw in mature females of (A) *Malaclemys terrapin*, (B) *Graptemys pseudogeographica*, (C) *G. geographica*, (D) *G. pulchra*, (E) *G. barbouri*, (F) *G. caglei*, (G) *G. versa*, (H) *G. ouachitensis sabinensis*, (I) *G. o. ouachitensis*, and (J) *G. flavimaculata* (the shape of the symphysis is the same for *flavimaculata*, *oculifera*, and *nigrinoda*).

(3) Bones surrounding the foramen palatinum posterius (Fig. 2). The bones surrounding that foramen in *Terrapene* and in the species of the *Pseudemys rubriventris* complex are the same as *Graptemys*; the other species of *Pseudemys* and the other N.A. emydid genera are like *Malaclemys*. Therefore, *Graptemys* and *Malaclemys* were possibly derived from different species of *Pseudemys*.

(4) The absence of contact between the ophisthotic and pterygoid due to the involvement of the exoccipital. If the condition in *Malaclemys* and *Deirochelys* represents a derived feature, this would strongly suggest that *Malaclemys* was not the ancestral stock from which *Graptemys* evolved. It could also indicate that a *Graptemys*, *Deirochelys*, or any other species of North American emydid turtle could have been ancestral to *Malaclemys*.

(5) The lack of a notch in the premaxillary bones. The lack of a notch in those bones in *Graptemys* and the presence of a notch in *Malaclemys* and the rest of the N.A. emyids, precludes determination of the possible ancestor for *Graptemys* and *Malaclemys* based on this feature.

SHELL FEATURES

(6) Flaring of carapace. The presence of such in *Graptemys* and to varying degrees in all other N.A. emyids except *Malaclemys* and some *Terrapene*, may indicate that flaring is an ancestral feature. If so, the upturning of the carapace in the last two genera would be a derived feature. This implies that *Graptemys* did not come from a *Malaclemys* stock.

(7) Double notching of some peripherals. The double notching of some of the peripherals is found only in *Graptemys* and in some individuals of *Pseudemys scripta* and *P. concinna*. This could indicate that *Graptemys* was not ancestral to *Malaclemys* and that a *Pseudemys* species was ancestral to *Graptemys*.

(8 and 9) The keel and its associated bosses (Fig. 3). A number of reports have dealt with the extent and development of the keel in *Malaclemys*. The last vertebral

scute is variable with respect to keel development. Say (1825) reported that the last vertebral in *M. terrapin centrata* was unkeeled; Wied (1865) noted that all of the vertebrals of *M. t. pileata* have a well developed keel. The keel in *Malaclemys t. centrata* was stated by W.P. Hay (1904) "to be rather low and rounded," whereas it was "always well developed," in *M. t. macrospilota*. A keel is thus not always present on the last vertebral, and I have not observed the end of the keel (the fifth boss area) to extend more than four-fifths the length of the last vertebral scute. W.P. Hay's (1904) statement about the keel and bosses of *M. t. littoralis* was: "the first vertebral plate is raised on the middle line to form a broad, low carina; on the second plate the elevation is greater, and stands out as a smooth boss . . . ; the elevation on the third plate has the form of a hemispherical button with a well-marked constriction around the posterior half of the base . . . ; on the fourth plate the elevation is raised into a knob-like protuberance from a base which is constricted all around . . . ; the fifth vertebral plate is flat or with only a trace of an elevation." Thus Hay's statement suggests that four or five bosses are present on the keel in *Malaclemys*. This is not always the case. Auburn University Museum of Paleontology (AUMP) specimen 2179 has only three bosses, and its shell structures are normal.

Concerning the total number of bosses on the keel in *Graptemys pulchra*, Carr and Goin (1955) said, "the dorsal keel . . . comprises a boss on each of the first four centrals, . . . weak to nearly lacking on the first and completely lacking on the fifth." A boss on the fifth central (vertebral) is not lacking in *pulchra*. Although it is not prominent in *G. pulchra* or in any other species of *Graptemys*, a terminal boss can be detected in all species. Cagle (1954, p. 182, Fig. 11) illustrated a juvenile *G. flavimaculata* that had five bosses on the carapace. I have never examined any specimen of *Graptemys*, including *G. flavimaculata*, in which the

TABLE 1

Diagnostic Characteristics of *Graptemyx* and *Malaclemys* and An Outgroup Comparison of Those Genera with the Other North American Emydid Genera. Each Feature is Designated As Either Ancestral (Primitive = P) or Advanced (Derived = D)¹.

<i>Graptemyx</i>	<i>Malaclemys</i>	Other N. A. Emydines and <i>Rhinoclemmys</i> , a Batagurine
1. Sutural contact of maxilla with quad-ratojugal lacking. (P?)	In contact. (D?)	Lacking in <i>Terrapene</i> , <i>Emydoidea</i> , <i>Clemmys</i> , <i>Deirochelys</i> , <i>Pseudemys scripta</i> , <i>Chrysemys</i> , <i>Rhinoclemmys</i> and in some <i>P. floridana</i> . (P?) In contact in <i>P. concinna</i> and in the members of the <i>P. rubriventris</i> complex. (D?)
2. Rounded-shaped symphyseal part of lower jaw. (D)	Symphysis pointed. (P)	Like <i>Malaclemys</i> . (P)
3. Foramen palatinum posterius bounded on mediolateral and outer lateral sides by palatine. (D)	Bounded on outer later side by maxilla. (P)	The members of the <i>P. rubriventris</i> complex, <i>Terrapene</i> , and <i>Clemmys</i> -like <i>Graptemyx</i> . (D). (<i>Chrysemys</i> , <i>Pseudemys scripta</i> , <i>P. concinna</i> , <i>P. floridana</i> , <i>Emydoidea</i> , and <i>Rhinoclemmys</i> -like <i>Malaclemys</i> . (P)
4. Exoccipital not responsible for the separation of the opisthotic and pterygoid when the latter two are not in contact. (P)	Exoccipital responsible for the separation of the two bones. (D)	<i>Chrysemys</i> , <i>Pseudemys</i> , <i>Emydoidea</i> , <i>Terrapene</i> , <i>Clemmys</i> , and <i>Rhinoclemmys</i> -like <i>Graptemyx</i> . (P) <i>Deirochelys</i> -like <i>Malaclemys</i> . (D)
5. Premaxillae without medial notch. (D)	With medial notch. (P)	Like <i>Malaclemys</i> . (P)
6. Hind edges of carapace flared but not curved upward. (P)	Fore, lateral and hind margins of carapace normally curled upward. (D)	Like <i>Graptemyx</i> except for some <i>Terrapene</i> . (P)
7. Posterior ends of some peripherals emarginate with double notching on at least some of those peripherals in juveniles and some adults. (D)	Same as in <i>Graptemyx</i> except none with double notching. (P)	Like <i>Malaclemys</i> except double notching in some <i>Pseudemys scripta</i> and some <i>P. concinna</i> . (P)
8. Carapace with a medial keel. (P) It normally reaches from anterior end of first vertebral scute to posterior of fifth vertebral scute.	Carapace usually with medial keel. (P) It normally reaches from posterior end of first vertebral scute to approximately four-fifths of the length of the fifth vertebral scute.	A medial keel present in most <i>Terrapene</i> , in <i>Emydoidea</i> , most <i>Pseudemys</i> , in <i>Deirochelys</i> , in two species of <i>Clemmys</i> , and in some <i>Rhinoclemmys</i> . (P) A very slight keel is present in some <i>Chrysemys</i> .
9. Keel with 5 bosses. (D)	Keel with from 3-5 bosses. (D)	No bosses. (P)

1. I am at present following the separation of *Chrysemys* into *Chrysemys* and *Pseudemys* based on the recent paper by Vogt and McCoy (1980). I am not following their division of *Pseudemys* into the genera *Pseudemys* and *Trachemys*.

10. Ventrolateral sides of nuchal bone (costiform process normally absent) extend laterally to contact the midline side of the first peripheral bone. (P)	Ventrolateral sides of nuchal bone (costiform process present) extend laterally to beyond the medial side of first peripheral bone (contact with second peripheral not unusual). (D)	Not in contact with second peripheral in <i>Pseudemys</i> , <i>Clemmys</i> , <i>Rhinoclemmys</i> , <i>Terrapene</i> , and <i>Emydoidea</i> . In fact, contact is on medial side of first peripheral in the latter two genera. (P) Just makes contact with second peripheral in <i>Deirochelys</i> . (D) No costiform process in <i>Emydoidea</i> . Costiform process in some <i>Clemmys</i> and in some <i>Rhinoclemmys</i> . Costiform process in <i>Deirochelys</i> , <i>Pseudemys</i> , and <i>Terrapene</i> .
11. Posterolateral borders of the nuchal bone at the area of the pleural scute sulci are notched. (P)	Not notched (except in one specimen). (D)	Notched in all <i>Terrapene</i> and in most <i>Chrysemys</i> , <i>Pseudemys</i> , and <i>Clemmys</i> . (P). Not notched in most <i>Deirochelys</i> and in all <i>Emydoidea</i> . (D) Notched in some <i>Rhinoclemmys</i> .
12. That part of the anterior border of the first costal bone is extended outward and notched. (P)	Border is straight and unnotched except in one specimen. (D)	Same as in 11.
13. Lateral edges of nuchal bone overlapped broadly by first pleural scute. (D)	Not overlapped or slightly overlapped by first pleural scute. (P)	Broad overlap in <i>Pseudemys</i> . (D) Slight to broad overlap in <i>Terrapene</i> . Not overlapped or only slightly overlapped in <i>Deirochelys</i> , <i>Chrysemys</i> , <i>Clemmys</i> , and <i>Rhinoclemmys</i> . (P) No overlap in <i>Emydoidea</i> .
14. Anterolateral border of the first vertebral scute confined to nuchal bone. (D)	Not always confined to nuchal bone. (P)	Not confined to nuchal bone in <i>Emydoidea</i> , <i>Clemmys</i> , <i>Rhinoclemmys</i> ; only rarely in <i>Deirochelys</i> and <i>Chrysemys</i> . (P) Confined to nuchal bone in <i>Pseudemys</i> . (D) May or may not be confined to nuchal bone in <i>Terrapene</i> .
15. Amount of nuchal scute underlap is small and distal width of nuchal scute underlap broader than length of nuchal scute underlap. (D)	Same as in <i>Graptemys</i> . (D)	Large amount of nuchal scute underlap in all N.A. emydid turtles, except in some <i>Rhinoclemmys</i> . Distal width smaller than length in all except some <i>Pseudemys</i> and <i>Terrapene</i> . (P)
16. Amount of nuchal scute overlap is small except in <i>G. geographica</i> . (D)	Small amount of overlap (D)	Large amount in <i>Pseudemys</i> , <i>Clemmys</i> , <i>Chrysemys</i> , <i>Emydoidea</i> , <i>Deirochelys</i> , and in some <i>Rhinoclemmys</i> . (P) Small amount of overlap in <i>Terrapene</i> . (D)
17. Eighth costal contacts the eighth neural but not the seventh neural (all of the <i>G. pulchra</i> examined from the Conecuh River in Alabama have lost the eighth neural; the contact between the eighth costal and the seventh neural is therefore an abnormal condition in that population of <i>G. pulchra</i>). (P)	Contact of eighth costal with seventh and eighth neural bones. (D)	With eighth neural in all except for some <i>Terrapene</i> (some of the latter have lost the eighth neural and thus contact is with seventh neural). (P) Derived for some <i>Terrapene</i> .

Table 1 continued on next page

18. Well developed lateral ridges on the undersides of the first and fifth costal bones. (D) Not well developed. (P) Like *Malaclemys*. (P)
19. Distal widths of the three widest costal bones $1 > 5 > 3$ or $1 > 3 > 5$. (P? or D?) Distal widths of three widest costal bones extremely variable but with costal 1 widest. Closest pattern to that for *Graptemys* was $1 > 3 > 5 > 6$ and that condition found in a single specimen. (P? or D?) Variable within all.
20. Scutes of carapace sculptured but not concentrically so. (P) Scutes of carapace concentrically sculptured. (D) Same as for *Graptemys* except for some Antillean *Pseudemys*, *Clemmys insculpta*, and some *Terrapene*. (P) No sculpturing in *Chrysemys*.
21. Carapace with pattern. (P) Carapace with pattern dissimilar to that of any *Graptemys*. (D) Same as in *Graptemys* except for *Clemmys guttata*. (P)
22. Bridge relatively wide. (P) Bridge relatively narrow. (D) Same as for *Graptemys*. (P)
23. Seventh marginal scute normally separated from abdominal scute by inguinal scute (except in some individual *G. pseudogeographica*). (P) Seventh marginal contacts abdominal scute. (D) Like *Graptemys*. (P)
24. Axillary and inguinal scutes not reduced in size or absent. (P) Axillary and inguinal scutes reduced in size or absent. (D) Like *Graptemys*. (P)
25. Typical plastral formula is gular< humeral< pectoral< abdominal> femoral< anal (89%). (P? or D?) Typical plastral formula is gular humeral< pectoral< abdominal> femoral< anal (76%). (P? or D?) Variable.
26. Among plastral scutes the abdominal longest in longitudinal dimensions 82% of cases; anal longest 18% of cases. (P? or D?) Among plastral scutes the abdominal longest in longitudinal dimensions 53% of the time; anal longest 47% of the time. (P? or D?) Variable.
27. Plastron of juveniles with generally an ornate plastral pattern (except in most *G. geographica* and in all *G. barbouri*) (P) Some individuals have dark spots as in *Malaclemys*. Plastron of juveniles with generally an ornate plastral pattern. The pattern is not similar to that of any *Graptemys* except for one *G. nigrinoda*. (D) Ornate plastral pattern in juveniles of *Chrysemys*, most *Pseudemys*, most *Terrapene*, *Clemmys*, *Emydoidea*, and *Rhinoclemmys*. (P) No pattern in *Deirochelys*. (D) Patterns of none are like those of *Malaclemys* except some mature *Pseudemys* males have dark spots.
28. Head, neck and limbs striped. (P) Not striped but blotched or spotted. (D) Like *Graptemys* except some *Rhinoclemmys* have stripes and spots on the head. (P)
29. Diploid chromosome number of 50. (D) Primitive number is 50 for emydines. Same as in *Graptemys*. (D) Same as in *Graptemys* except for *Rhinoclemmys* (52). Primitive number in batagurines may be 52.

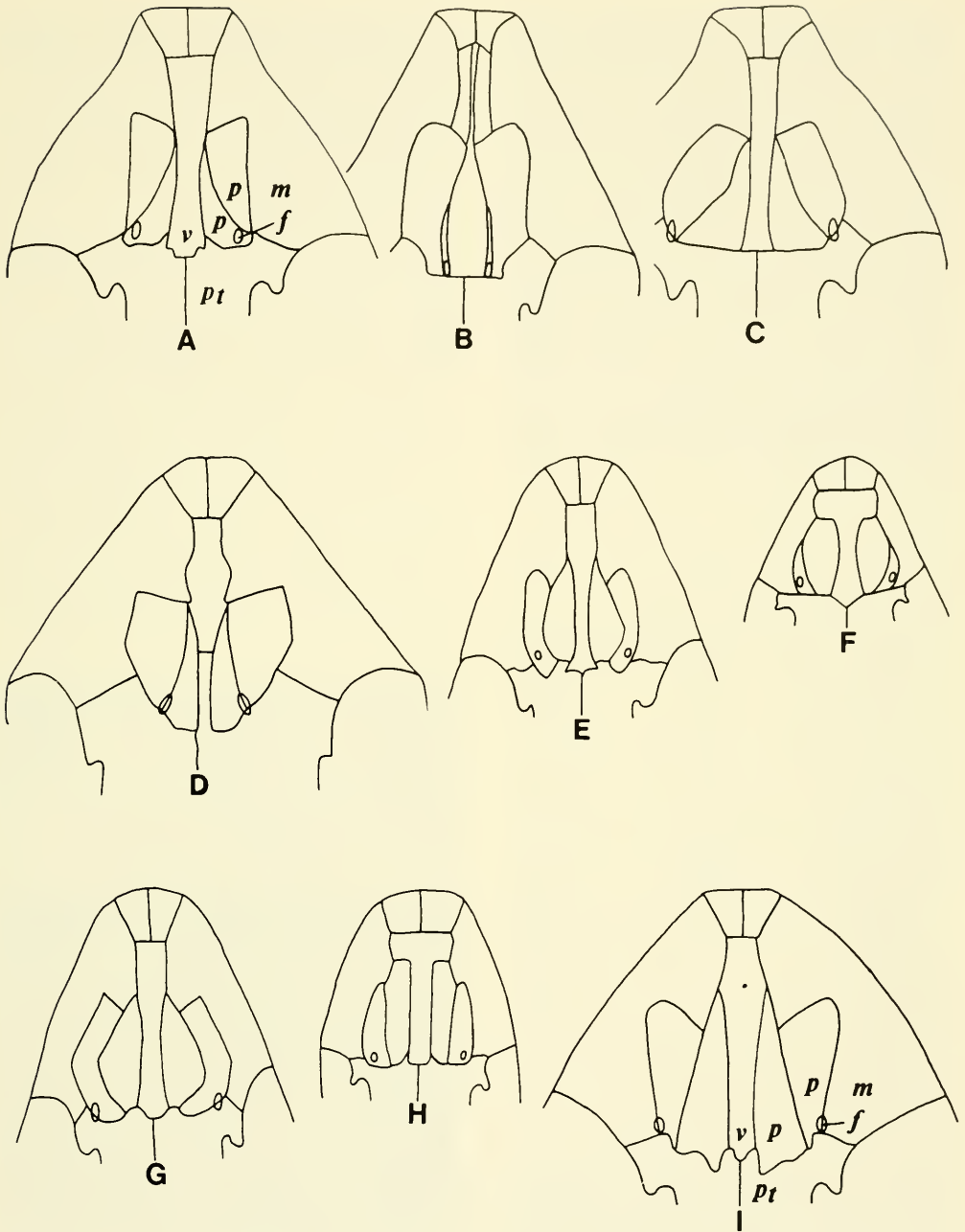


Figure 2. The location of the foramen palatinum posterius. The foramen is bounded on its mediolateral and outer lateral sides by the palatine in *Graptemys* (A) *pseudogeographica*, (B) *geographica*, (C) *pulchra*, (D) *barbouri*, (E) *caglei* and *versa*, (F) *o. sabinensis*, (G) *o. ouachitensis* and (H) *nigrinoda*, *oculifera*, and *flavimaculata*. It is bounded on its mediolateral and outer sides by the palatine and maxilla, respectively, in *Malaclemys terrapin* (I). Palatine (p). Maxilla (m). Foramen (f). Vomer (v). Pterygoid (pt).

fifth boss was located in the position illustrated by Cagle; the fifth boss is always at the posterior end of the last vertebral scute. The similar location of each boss in *Graptemys* and *Malaclemys* indicates their close relationship.

(10) Amount of ventrolateral extension of the nuchal bone and the costiform process of the nuchal bone. *Graptemys* normally lacks a costiform process; *Malaclemys* has one. Even though the nuchal of *Graptemys* is as wide as the same bone in *Malaclemys*, the distance the nuchal extends ventrolaterally is less in *Graptemys* than in *Malaclemys*. Therefore, the degree of such extension must not be solely a function of the width of the nuchal bone. This

seems to be the case since the distal width of the first peripheral is proportionately greater in *Graptemys* than in *Malaclemys*. Therefore, the presence of a narrower first peripheral and a costiform process in *Malaclemys* results in a greater ventrolateral extension of the nuchal in that genus than in *Graptemys*.

The other North American emydids that have a costiform process are *Pseudemys*, *Terrapene*, some *Clemmys* and *Deirochelys*, and the latter genus is the only group that has a ventrolateral extension similar to that of *Malaclemys*. I think it unlikely that *Deirochelys* was ancestral to *Malaclemys*; therefore, perhaps some *Pseudemys* turtle was the stock from which *Malaclemys* arose. The ancestral stock for *Graptemys* can not be determined with respect to this feature.

(11 and 12) The notching of the posterolateral borders of the nuchal bone and the anterior border of the costal bone (Figs. 4 and 5). The presence of such notching in *Graptemys*, *Terrapene* and in most *Clemmys* (14 of 16), *Pseudemys* (29 of 31), and *Chrysemys* (15 of 20), and not in *Malaclemys* (except in one specimen), *Emydoidea*, and most *Deirochelys* suggests that *Malaclemys* was not ancestral to

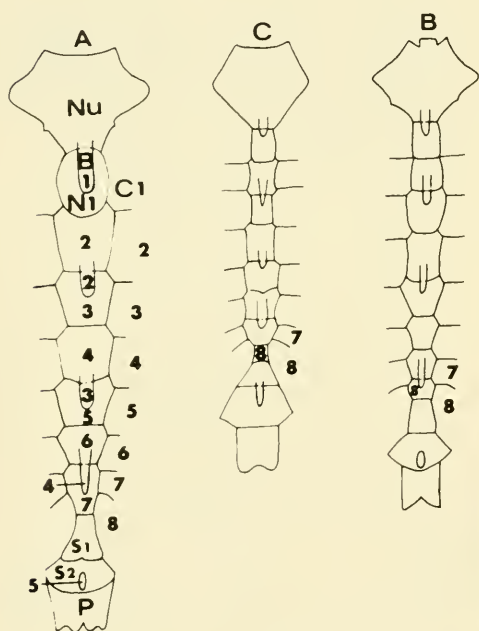


Figure 3. The location of the bosses in *Graptemys* (A) *pulchra*, (B) *nigrinoda*, and (C) *Malaclemys terrapin* and the contact of the eighth costal with the seventh neural in some *G. pulchra* due to the loss of the eighth neural bone. The normal contact is between eighth costal and eighth neural in *Graptemys* and eighth costal and seventh and eighth neurals in *Malaclemys*. Nuchal bone (Nu). Bosses (B 1-5). Neural bones (N 1-8). Suprapygals (S 1-2). Pygal bone (P). Costal bones (C 1-8).

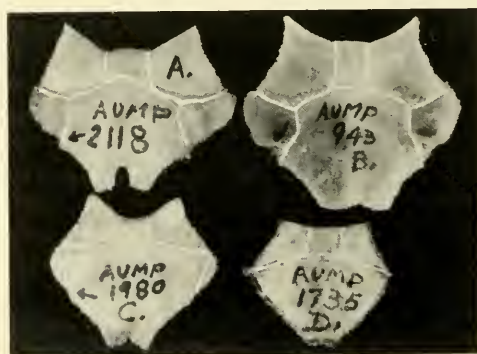


Figure 4. Dorsal view of the nuchal bone in *Graptemys* (A) *pseudogeographica*, (B) *pulchra* and (C and D) *Malaclemys terrapin*. Arrows indicate notches. The position of the anteromedial edge of the first pleural scute and the anterolateral borders of the first vertebral scute are not on the nuchal bone in some *Malaclemys* (D).

Graptemys if the absence of notching is a derived feature. However, *Graptemys* could have given rise to *Malaclemys*, as could have *Clemmys*, *Chrysemys*, *Pseudemys*, *Terrapene*, *Emydoidea*, and *Deirochelys*. *Emydoidea* and *Deirochelys* presumably would be the best candidates from which to derive *Malaclemys* if relationships are based on the presence of shared derived features. In spite of the presence of a shared derived feature between those genera and *Malaclemys*, I do not believe that either one is a good candidate for being the progenitor of *Malaclemys*. Therefore, *Graptemys*, *Pseudemys*, and *Chrysemys* are considered to be more likely candidates. (13 and 14) The amount of pleural scute overlap on the nuchal bone and first vertebral scute - nuchal bone relationships. A great deal of pleural scute overlap exists in *Graptemys*, *Pseudemys*, and

in some *Terrapene* and the pleural scute always contacts the margin of the first vertebral scute on the nuchal bone in the first two of the the three above (Dobie and Jackson, 1979). *Malaclemys* resembles most *Chrysemys* and some *Terrapene*, *Clemmys*, and *Deirochelys* in that there is little overlap of the pleural scute on the nuchal and the pleural scute does not always contact the first vertebral scute on the nuchal bone (Dobie and Jackson, 1979).

Malaclemys terrapin could have evolved from *Chrysemys* in which the extent of pleural scute overlap was minimal and the margin of the first vertebral scute did not always meet the pleural scute on the nuchal bone. If *M. terrapin* evolved from any species of *Graptemys* or *Pseudemys* that had a large amount of pleural scute overlap and contact between the two scutes on the nuchal bone, then presumably a reduction in the amount of pleural scute overlap must have occurred. *Graptemys* could have arisen from a *Pseudemys* stock.

(15 and 16) Amount of nuchal scute overlap and underlap and the width-length relationships of the underlap part of the nuchal scute (Figs. 6 and 7). The amount of nuchal scute overlap is small in *Malaclemys*, in some *Terrapene*, and in all extant species of *Graptemys*, except *G. geographica* (Dobie and Jackson, 1979). Both *Malaclemys* and *Graptemys* have smaller amounts of nuchal scute underlap than any other North American emydid turtle, and the distal width of the underlap part of the nuchal scute is broader than its length in both of those genera and in some *Pseudemys* and *Terrapene* (Dobie and Jackson, 1979). Based on these features, *Malaclemys* would seem to be more closely related to *Graptemys* than to any other extant North American emydid genus.

(17) Contact of the eighth costal bone with the seventh and eighth neurals (Fig. 3). The presence of such contacts in *Malaclemys* and the contact of the eighth costal with only the eighth neural in *Graptemys*



Figure 5. Dorsal view of the first left costal bone in *Graptemys* (A) *pseudogeographica*, (B) *pulchra* and (C and D) *Malaclemys terrapin*. That part of the anterior border of the costal bone that would adjoin the nuchal generally is straight and unnotched in *Malaclemys* as in (D). Arrows indicate notches.

(except for a single population of *G. pulchra*) and in all other North American emydid genera except *Terrapene* (the eighth neural is absent in some *Terrapene*) indicates that contact with the seventh neural is a derived character. The stock from which *Malaclemys* was derived presumably could have been any genus of North American emydid turtles; *Graptemys* could have come from *Pseudemys* or from any other North American emydid genus except *Malaclemys*.

(18) Lateral ridges on undersides of first and fifth costals (Fig. 8). The lateral ridges extending toward the midline of the carapace from the anterior and posterior ends of the bridge are well developed in *Graptemys* in contrast to those of *Malaclemys* and the rest of the North American emydid genera. The functional sig-

nificance of those ridges is not known but they may serve as supportive units for the carapace. *Malaclemys* and *Graptemys* presumably could have been derived from any one of those genera.

(19) Distal widths of the three widest costal bones. An attempt to indicate the degree of relationships of *Malaclemys* to any other emydid genus on the basis of this character would be impractical because of the extremely variable nature of the widths of the costal bones. The fairly consistent widths in the species of *Graptemys* does indicate that they are closely related.

(20) Sculpturing on the carapace. The sculpturing on the carapacial bones in *Graptemys* is similar to that of some species of *Pseudemys* (*P. floridana* and *P. concinna*) although the degree of sculp-

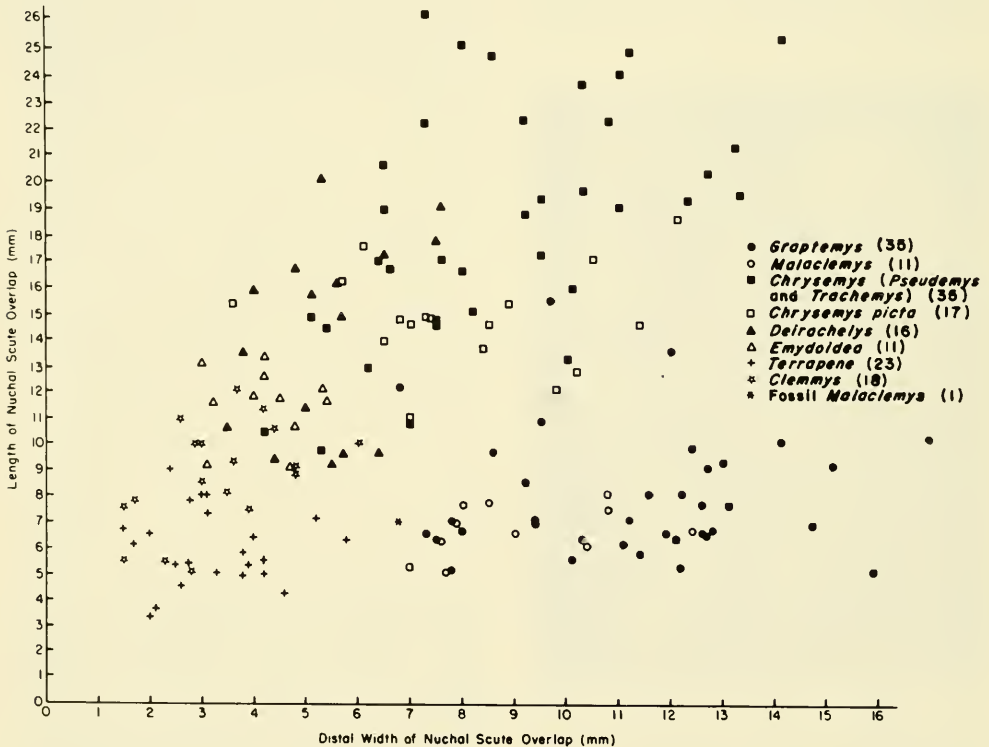


Figure 6. Length of nuchal scute overlaps versus distal width of nuchal scute overlap in various emydines including *Graptemys* (35) and *Malaclemys* (11).

turing in *Graptemys* is generally less than in any species of *Pseudemys* and more than that of *Chrysemys*. The type of concentric sculpturing in *Malaclemys* is unique and represents a derived feature (the species of *Terrapene*, some Antillean *Pseudemys*, and *Clemmys insculpta* also have concentric sculpturing (Zangerl, 1969; Dobie and Jackson, 1979) but the sculpturing patterns in the species of *Terrapene*, Antillean *Pseudemys*, and in *C. insculpta* are not the same as that demonstrated by *Malaclemys*. *Graptemys* may have arisen from *Pseudemys*; *Malaclemys* from any one of these genera including *Graptemys*.

(21) Carapacial pattern. The patterns on the carapace of the various *Graptemys* justify the name, "map turtle". Those patterns, although more similar to those patterns found in other North American emydids, except *Clemmys guttata*, are distinctive and were probably modified from a less elaborate carapacial pattern. The lack of similarity of the carapacial patterns of *Graptemys* and *Malaclemys* could mean that the patterns of both were independently derived from different an-

cestors or that they came from the same ancestor that had a less elaborate pattern.

(22) Bridge width (Fig. 9). The width of the bridge in *Graptemys* resembles that of most aquatic emydids. The relatively narrow bridge in *M. terrapin* is distinctive, presumably derived, and perhaps is an adaptation for increasing the animal's ability for bottom walking in that a narrow bridge could allow the limbs to be advanced to a greater degree anteriorly than in a turtle having a wide bridge. *Malaclemys* could have come from any one of several different genera on the basis of this feature.

(23 and 24) The separation of the seventh marginal scute from the abdominal scute by the inguinal scute and the sizes of the inguinal and axillary scutes. The separation of the two scutes by the inguinal scute in *Graptemys* indicates that the size of the inguinal scute is about the same size as that found in most other North American emydids. The contact between the abdominal and seventh marginal scutes in *Malaclemys* is due to the small size of the inguinal scute or the absence of that scute. The condition in *Malaclemys* is probably derived.

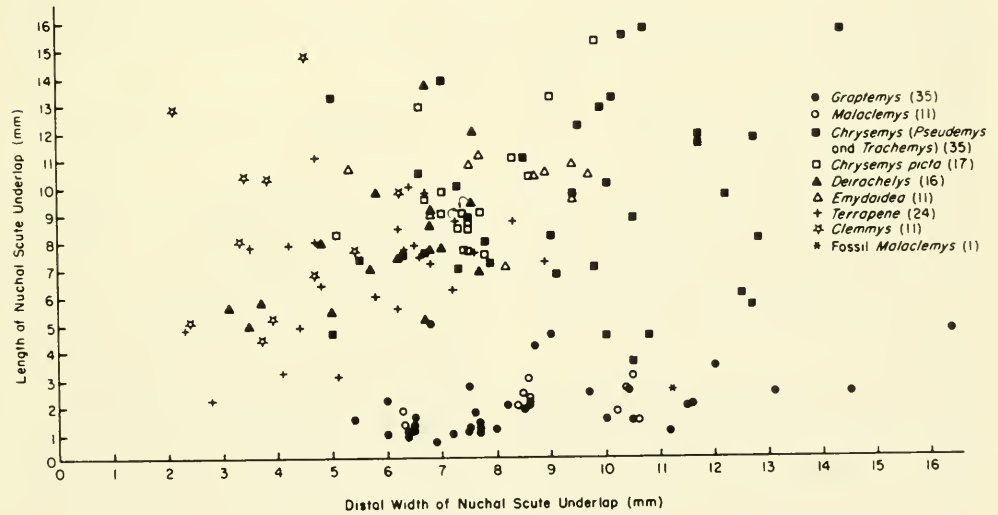


Figure 7. Length of nuchal scute underlap versus distal width of nuchal scute underlap in various emydines including *Graptemys* (35) and *Malaclemys* (11).

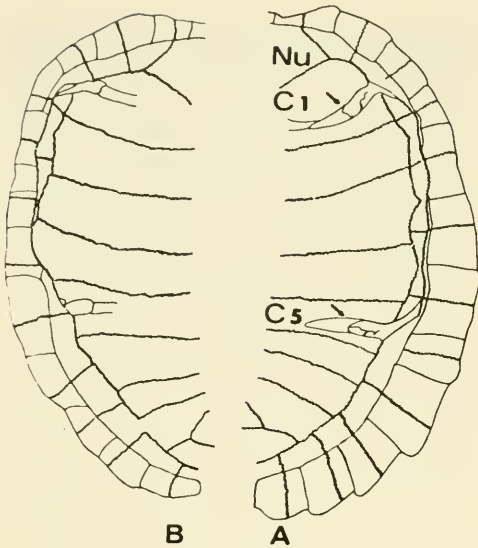


Figure 8. Lateral extensions of ridges on the ventral sides of the first and fifth costal bones in (A) *Graptemys nigrinoda* and (B) *Malaclemys terrapin*. The arrows indicate the ridges. Nuchal bone (Nu). Costal bone (C 1). Costal bone (C 5).

The size of the axillary scute in *Graptemys* is like that of most other emydids. It is either absent or very small in *Malaclemys*. The reduction in the size or loss of both the axillary and inguinal scutes is perhaps a result of the decrease in bridge width. Based on these features, *Graptemys* and *Pseudemys* are more similar than either is to *Malaclemys*.

(25 and 26) Plastral formulae and the length of the abdominal plastral scute. The two genera are more similar to each other in these two features than either is to any other North America emydid genus; they would thus appear to be closely related.

(27) Plastral patterns. The ancestral plastral pattern of *Graptemys* was probably ornate because to varying degrees ornate plastral patterns appear in all species of *Graptemys* except *G. barbouri*. The plastral patterns in *Malaclemys*, although ornate, do not resemble the pattern of any *Graptemys* species except for a single

specimen of *G. nigrinoda*. The ornate plastral patterns of both were probably derived from different ancestral stocks.

HEAD, NECK AND LIMB STRIPING

(28) Head, neck and limbs striped. The striping of such units is a typical emydid condition and *Graptemys* is no exception. According to Wood (1977), *Malaclemys* is striped although I and evidently Pritchard (1979) have never seen a striped individual and Ernst and Barbour (1972) use the absence of striping in *Malaclemys* as a feature in their key to U.S. turtles. If striping does occur in *Malaclemys*, it must be a rare condition. The absence of striping in *Malaclemys* is a derived feature. *Malaclemys* could have been derived from *Graptemys* or from any other North American emydid genus.

DIPLOID CHROMOSOME NUMBER

(29) Chromosome count. Because all emydines presumably have 50 chromosomes (Killebrew, 1977), *Graptemys* and *Malaclemys* could have been derived from each other, from any one of several different groups, or perhaps from a batagurine if in fact the 50 chromosome number of emydines is a derivation of the 52 chromosome number of the batagurines.

DISCUSSION AND CONCLUSION

All indications are that *Graptemys* represents a distinct group of closely related turtles. *Malaclemys* is undoubtedly more closely related to *Graptemys* than it is to any other extant genus, as would be evidenced by (1) the pterygoid forming a suture with the exoccipital except in some species of *Graptemys* (*G. nigrinoda* for example) and in some individuals of *M. terrapin*, (2) similarities in penial, pelvic girdle and hind limb morphology, (3) similarity in carapacial seam contacts (Tinkle, 1962), (4) similarity in the amount of nuchal scute underlap, and (5) similarity in the width-length relation-

ships of the underlap of the nuchal scute. In addition, the plastral scute formulae are the same for the two genera as are, generally, the locations of the bosses on the carapace.

The Oligocene species of *Graptemys*, *G. inornata* (Loomis, 1904) and *G. cordifera* (J. Clark, 1937) do not have shell characteristics that indicate a close relationship with *Malaclemys*. No other remains of *G. inornata* and *G. cordifera* are known. No fossils intermediate between *Graptemys* and *Malaclemys* are known, and only recently were fossil remains for *M. terrapin* discovered (Pleistocene age: South Carolina, [Dobie and Jackson, 1979]). Examination of an

Eocene specimen (South Dakota School of Mines and Technology, SDSM&T, 59187) identified as *Graptemys* by Bjork (1967), reveals that it is not *Graptemys* or *Malaclemys* because it lacks, among other things, a keel and bosses. The absence of the uniform fine granular tubercles on the external surface of the carapace of the Eocene fossil prevents its inclusion within *Compsemys* (a baenid turtle, Gaffney, 1972b) and the absence of a keel and rugosities rules out its inclusion within any genus of North American emydids except *Chrysemys* (some *Chrysemys* do have a slight keel). On the basis of the absence of the latter two features it is like *Chrysemys picta*. However, it cannot be

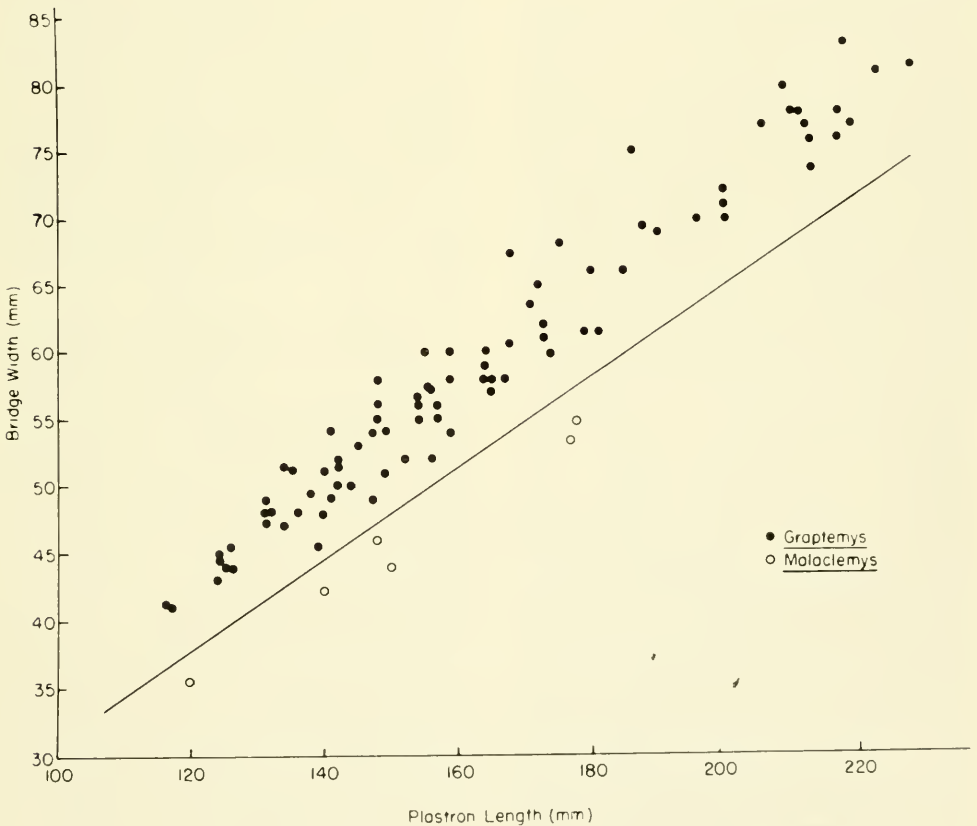


Figure 9. Relative bridge width in *Graptemys* and *Malaclemys*. The solid line depicts the separation of the two genera.

included within *Chrysemys picta* as the length of the sixth neural in *C. picta* is about twice as long as that of the fossil and the posterior width of the first suprapygial of the fossil is about twice the width of the same bone in *C. picta*. The neural bones of the fossil are narrow as compared to those of *Deirochelys carri*, *D. reticularia*, *Emydoidea blandingi*, *Malaclemys terrapin*, *Clemmys guttata*, and *C. insculpta* and this rules out the inclusion of the fossil into any of those genera.

The features possessed by the Eocene fossil do not fit those of *Graptemys*, *Malaclemys* or any extant North American emydid genus, thus, it may be a new taxon.

Although *Graptemys* and *Malaclemys* have several characteristics in common with some of the species of the Eocene emydid fossil turtles assigned to the genus *Echmatemys* (Table 2), I do not believe that either one of the two taxa nor any other new world emydid genus came from *Echmatemys*. O.P. Hay (1908) and Weaver and Rose (1967) proposed that *Chrysemys* came from *Echmatemys* and Hay (1908) also believed that *Echmatemys* was the ancestral stock for most other North American emydid genera. I reject the ancestral status of *Echmatemys* because to me many if not most of the species of *Echmatemys* appear to be members of *Rhinoclemmys* (e.g., McDowell, 1964, believed that *E. pusilla* belonged in the Neotropical batagurine genus *Rhinoclemmys*) and because most of the characters used to indicate relationships between *Echmatemys* and *Chrysemys* (in the sense of Weaver and Rose, 1967) were primitive characters and such can never be used to determine relationships. The *Graptemys* line may have arisen from some Eocene pre-*Pseudemys* of *Pseudemys* stock; *Malaclemys* may be an additional derivation of a *Pseudemys* stock or of a *Graptemys* stock, but its origin was probably somewhat later in the Tertiary (post-Miocene or later).

Loveridge and Williams (1957) believed

that *Graptemys* may have arisen from a *Pseudemys* stock, as did McDowell (1964), Ernst (1974), and Pritchard (1979), and that the ancestral *Malaclemys* was close to a *Graptemys* stock. The former is in disagreement with O.P. Hay's (1908) conclusion that *Graptemys* was from *Malaclemys*. Wood (1977) also considered *Graptemys* a *Malaclemys* derivative, and according to him, "most or all of these species evolved independently and perhaps also at different times during the latter part of the Pleistocene from *Malaclemys* rather than giving rise to one another." Assuming that each species of *Graptemys* was independently derived from *M. terrapin* as Wood believes, then each feature common to two or more *Graptemys* but absent in *M. terrapin* must exemplify convergence. A total of 24 features, at least 10 of which appear to be derived, are shared by all *Graptemys*, only six of these feature, at least three of which appear to be derived, are possessed by *Malaclemys*. It is highly unlikely that the remaining 18 features (seven derived and 11 ancestral) would have arisen independently in all *Graptemys* species.

Because of the number of features held in common by the species of *Graptemys* and because it is obvious to me and to other individuals (Cagle, 1952, 1953a, 1953b, 1954; McKown, 1972; Dundee, 1974; Killebrew, 1977; Vogt, 1978, 1980) that there are closely related complexes of *Graptemys* turtles, e.g., *G. nigrinoda*, *G. flavimaculata*, and *G. oculifera*; *G. pulchra* and *G. barbouri*; *G. pseudogeographica*, *G. ouachitensis*, *G. versa*, and *G. caglei*, (*G. geographica* belongs in a group by itself), I conclude that the various species of the *Graptemys* turtles were derived from other species of *Graptemys*. (The species of *Graptemys* are thus more closely related to each other than any one species is to *M. terrapin*.)

Wood (1977) apparently was unaware that there are two Oligocene fossil species of *Graptemys*. If the fossils are correctly assigned, the various species of *Grapt-*

TABLE 2

Characteristics of Various Genera of Emydine Turtles and of *Echmatemys*, a Genus that Presumably Has Members of the Batagurine Genus *Rhinoclemmys* Included Within It¹.

	<i>Graptemys</i>	<i>Malaclemys</i>	<i>Chrysemys</i>	<i>Pseudemys</i>	<i>Echmatemys</i>
1. Extensive overlaps of pleural scute on nuchal bone	+	-	-	+	-
2. Contact between first vertebral scute and pleural scutes always on nuchal bone	+	-	-	+	-
3. Extensive nuchal scute overlap on nuchal bone	±	-	+	+	+
4. Nuchal scute underlap short and length not exceeding its distal width	+	+	-	±	+
5. Inguinal scute normally separates the seventh marginal scute from the abdominal scute	+	-	+	+	+
6. Axillary and inguinal scutes always present and always relatively large	+	-	+	+	-
7. Premaxillae with medial notch	-	+	+	+	?
8. Exoccipital not responsible for the separation of opisthotic and pterygoid when the latter two bones are not in contact	+	-	+	+	?
9. Double notching on some peripherals	+	-	-	±	-
10. Eighth costal bone normally contacts only the eighth neural	+	-	+	+	+
11. Scutes of carapace sculptured but not concentrically so	+	-	+	+	+
12. Bridge width broad	+	-	+	+	+
13. Hind edges of carapace flared	+	-	+	+	+

¹The designations + and - indicate the presence or absence respectively of the feature.

emys obviously could not have been derived independently from *M. terrapin* during the Pleistocene.

Adult female *Malaclemys terrapin* and adult females of some species of *Graptemys* (*pseudogeographica*, *pulchra*, *barbouri* and *geographica*) resemble one another closely in general skull shape. The resemblance of *M. terrapin* to those *Graptemys* species is probably not due to common ancestry but rather to the development by each species of similar kinds of anatomical features (e.g., broad heads) as adaptations for feeding on similar kinds of food items (mussels.) *Graptemys pulchra*, *barbouri*, and *geographica* are also farther from the base of the *Graptemys* phylogenetic tree than is *G. pseudogeographica* (a species which is presumed to represent more nearly the ancestral-like stock) and both *G. geographica* and *G. barbouri* appear to be highly specialized, derived terminal end forms with respect to skull features. None of those species appears to be closely related to *Malaclemys terrapin* even though all have broad heads.

Mature females of some of the species of *Graptemys*, *G. nigrinoda*, *G. oculifera*, *G. flavimaculata*, *G. versa*, *G. caglei*, *G. ouachitensis* and some *G. pseudogeographica*, have narrow alveolar surfaces. The genus *Graptemys* cannot be differentiated, therefore, from *Malaclemys* on the basis of wide alveolar surfaces, as O.P. Hay (1908) contended.

The evidence is clearly against the lumping of *Graptemys* and *Malaclemys*. A subsequent paper will clarify the phylogenetic relationships of the *Graptemys* turtles.

ACKNOWLEDGMENTS

I am grateful to Drs. Robert Mount and George Folkerts for their advice on various aspects of this study. Several museums and one individual loaned me specimens and Robert Mount, John Pritchett and Lacy Hyche reviewed this manuscript. Theresa Rodriguez and Dr. Jeanne Stuart did most of the drawings.

SPECIMENS EXAMINED

Chrysemys picta: (74) (AUM 426, 605, 749, 829, 1170, 1553, 1915, 2062, 3827, 3872-73, 3875-76, 3884-85, 3999, 5669, 5885, 7072, 9514, 9747, 10091, 10126, 12587, 12589, 13616, 14133-34, 16231, 17366-67, 17871-72, 18033-34, 18218, 18812-14, 23478, 24109, 25088); (AUMP 132, 1713-23, 1965, 1967, 1983, 1985, 1990, 2117, 2171-76, 2318-20, 2351-54, 2405).

Clemmys guttata: (9) (AUM 21554, 22433, 26741, three classroom specimens); (AUMP 308, 2251); (UF/FSM 41018).

C. insculpta: (5) (AUM 29257); (AUMP 279); (UF/FSM 19016, 41525-26).

C. marmorata: (9) (AUMP 2260-62, 2264-66, 2310-11); (UF/FSM 41523).

C. muhlenbergi: (1) (UF/FSM 14116).

Deirochelys reticularia: (44) (AUM 1705, 1733, 3378, 3898, 8747-48, 9320, 10090, 10109, 10152, 11564, 12394, 13495, 15791, 18236, 18484, 18999, 19729, 22706, 22998, 23001); (AUMP 125-26, 897, 935, 1924, 2315, 2910); (UF/FSM T736, 6530, 7744, 14192, 14244-48, 30348, 34880, 35026, 38433, 40824, 41524, 41533).

Emydoidea blandingi: (17) (AUMP 1724-26, 1959, 1962, 1971, 2014-15, 2017, 2115, 2117, 2119, 2252-54, 2417-18).

Graptemys barbouri: (35) (AUM 3380-81, 5956, 6238, 6326-27, 6329, 6388, 6621, 8793, 8966, 9470-71, 9500, 9548, 9659, 10101, 10104-05, 10276, 11231, 12694-95, 13653-54, 14278, 21606, 22662); (AUMP 297, 325, 328-29, 931, 1733, 2357).

G. caglei: (10) (TNHC) 36066, 36071, 36084, 36088, 36093, 36097, 36103, 36621, 36627-28).

G. flavimaculata: (48) (AUM 5941, 5968-74, 6147, 6387, 8792, 8941-43, 8982-83, 9238-31, 9348, 9492-95, 9538-40, 9542-46, 10150-51, 10294, 10296-98, 13660-61, 23664); (AUMP 925, 940, 998-99, 2129, 2247).

G. geographica: (31) (AUM 5976-77, 6622, 9319, 9446-47, 10858, 11805, 11830, 12410-18, 12240-41, 13002, 21613, 22910, 23111, 23242, 29574); (AUMP 300, 909, 1940, 2355); (NLSC 622).

G. nigrinoda: (33) (AUM 5665, 5939, 5942, 5964, 5983, 5989, 8948, 8968, 8970, 9233, 9235, 9237, 9261-62, 9268, 10127, 10143-44, 10149, 10292, 10301, 12562, 12575, 12630, 12635, 21553, 22988-89); (AUMP 927, 1730, 2255-56, 2419).

G. oculifera: (23) (AUM 5951-53, 5979, 9333, 14289, 23665-69, 25136-39); (AUMP 304, 2125-28, 2215-16, 2248).

G. ouachitensis ouachitensis: (27) (AUM 9136-38, 25983-84, 25988, 26431-34, 26648); (AUMP 278, 309, 1738, 1997, 2131-32, 2136, 2200-04, 2273-75); (NLSC 9383).

G. ouachitensis sabinensis: (32) (AUM 24019, 24022-23, 24239-46, 24253-55, 25129-35); (AUMP 2121-24, 2244-46); (NLSC 10137-39, 10142).

G. pseudogeographica pseudogeographica: (24) (AUM 25985, 27090, 27101, 27113), (AUMP 2905, 2902, 2277-84); (SUSD 1520, 2855, 2860, 2862,

2880-83, two uncatalogued specimens).

G. pseudogeographica kohni: (81) (AUM 6843, 20715, 23985, 23989, 23991-97, 24020, 24191, 24224-25, 24247-52, 24259-60, 24263, 25989, 26385, 26401-02, 26406, 26422-25, 27093-98); (AUMP 305-08, 326-27, 2118, 2133-35, 2161-66, 2185-88, 2191-99, 2221, 2267-72, 2276, 2402, 2901); (KU 1183); (NLSC 2304, 5263).

G. pulchra: (37) (AUM 4997, 5000-01, 5004-06, 5597, 5742, 5961, 6302, 6311, 9467-69, 9532, 9535, 12556, 19898, 23482, 25140-44, 25977); (AUMP 301, 443, 926, 930, 936, 943-44, 989-91, 1000, 1960).

G. versa: (14) (AUM 16653, 22816, 23984, 24202, 24222, 26030-34, 29302); (AUMP 924, 2130 2137).

Malaclemys terrapin: (23) (AUM 8839, 14277, a classroom specimen); (AUMP 706, 932, 954, 963, 1732, 1734-37, 1956, 1980, 2157-58, 2179, 2403); (TU 15194, .2, 15195.1); (UF/FSM 22849a-49b).

Pseudemys alabamensis: (41) (AUM 4840, 9346, 9957, 10072, 11598-99, 11601-02, 11608, 11813-14, 12580, 12591, 16870-71, 17032-33, 19362, 26998, 27003-05, 27007, 27009-10, 27018, 27020, 27023); (AUMP 277, 298, 938, 1706, 1710, 1906, 2285, 2356, 2360-62); (USA 1501-02).

P. concinna: (142) (AUM 4560, 5901, 5994, 7432, 7567, 8918, 10140, 10147, 10396, 11294, 12650, 13553, 13639, 13743, 16906, 17139, 18483, 18975, 19140, 21802-05, 22825, 23248, 24201, 24208, 24214-16, 24223, 24227-28, 24280-81, 25126-28, 26413, 26416, 29298-01); (AUMP 17, 284, 288, 290, 311, 318-19, 693-94, 697, 881, 900-01, 911-12, 917-19, 933-34, 950, 1707-09, 1904-05, 1941, 1976, 1989, 1993, 2000, 2148, 2156, 2167-69, 2181-84, 2189-90, 2221 2286-90, 2292-94, 2316 2410-12); (FMNH 55646, 55649-52); (KU 33526); (SFA 2769, 2803, 2858, 2989, 3460); (TCWC 13735, 13965-67, 42345); (TNHC 536-37); (TU1637, 3605-06, 11940, 13464, 14414, 14421-22, .1-.3, .9-.10, 14441, .2-.3, .10, 14451, .2-.3, 14506.1, 14541, 16030); (UNM465, 30345).

P. floridana: (53) (AUM 1670, 7672, 8976, 9505, 9563, 10102, 10290-91, 10725-29, 11596, 12428, 12430, 12602, 13834, 17133-34, 19000, 19927-29, 21609, 21831, 22658, 23201, 23490, 23703, 27706, 27945); (AUMP 289, 440-42, 447-48, 700, 1703, 1712, 1727-29, 1902, 1948, 1963, 1981, 1998, 2249, 2291, 2309, 2404).

P. nelsoni: (19) (AMNH 80234); (AUM 27948); (AUMP 299, 446, 449, 913, 1702, 1946, 1964, 1982, 1992, 1994, 2200, 2413-16); (USNM 101393, 101398).

P. rubriventris: (25) (AMNH 69909-12, 77114, 77587, 77613, 99145); (AUMP 445, 2116, 2120); (CM 14022-29); (UF/FSM 1821 - six specimens).

P. scripta: (84) (AUM 3828, 6993-97, 7574-76, 7578-80, 11557-58, 11560, 13319, 21540, 24203, 24258, 24261-62, 24264-68, 25125, 27016); (AUMP 11.0-11.21, 12-15, 16.1-.5, 285-87, 317, 692, 1720, 1969-70, 1972-73, 1984, 1988, 1999, 2001, 2149, 2155, 2173, 2214, 2222-24, 2406-09).

LITERATURE CITED

- BAUR, G. 1890. Two new species of tortoises from the South. Science 16: 262-263.
- BJORK, P.R. 1967. Late Eocene vertebrates from northwestern South Dakota. J. Paleontology, 41: 227-436.
- BOULENGER, G.A. 1889. Catalogue of the chelonians, rhynchocephalians, and crocodiles in the British Museum (Natural History). Taylor and Francis, London. 541 pp.
- CAGLE, F.R. 1952. The status of the turtles *Graptemys pulchra* Baur and *Graptemys barbouri* Carr and Marchand with notes on their natural history. Copeia 1952: 223-234.
- . 1953a. Two new subspecies of *Graptemys pseudogeographica*. Occ. Pap. Mus. Zool. Univ. Mich., 546: 1-17.
- . 1953b. The status of the turtle *Graptemys pseudogeographica*. Occ. Pap. Mus. Zool.
- . 1954. Two new species of the genus *Graptemys*. Tulane Stud. Zool., 1: 167-186.
- CARR, A.F. 1949. The identity of *Malaclemys kohnii* Baur. Herpetologica, 5: 9-10.
- . 1952. Handbook of turtles. Comstock Publ. Assoc., Ithaca, New York, 542 pp.
- and C.J. GOIN. 1955. Guide to the reptiles, amphibians, and freshwater fishes of Florida. Univ. Florida Press, Gainesville. 341 pp.
- CLARK, J. 1937. The stratigraphy and paleontology of the Chadron Formation in the Big Badlands of South Dakota. Ann. Carnegie Mus., 25: 261-350.
- CLARK, W.E. 1978. The weevil genus *Sibinia* Germar: natural history, taxonomy, phylogeny, and zoogeography, with revision of the New World species (Coleoptera; Curculionidae). Quaest. Ent., 14: 91-387.
- DOBIE, J.L. and D.R. JACKSON. 1979. First fossil record for the diamondback terrapin, *Malaclemmys terrapin* (Emydidae), and comments on the fossil record of *Chrysemys nelsoni* (Emydidae). Herpetologica, 35: 139-145.
- DUNDEE, H.A. 1974. Evidence for specific status of *Graptemys kohni* and *Graptemys pseudogeographica*. Copeia 1974: 540-542.
- ERNST, C.H. 1974. Observations on the courtship of male *Graptemys pseudogeographica*. Herpetol. 8: 377-378.
- and R.W. BARBOUR. 1972. Turtles of the United States. The Univ. Press of Ky., Lexington, Ky. 347 pp.
- GAFFNEY, E.S. 1972a. An illustrated glossary of turtle skull nomenclature. Am. Mus. Novit., 2486: 1-33.
- . 1972b. The systematics of the North American family Baenidae (Reptilia, Cryptodira). Bull. Amer. Mus. Nat. Hist., 147: 241-319.
- . 1975. A phylogeny and classification of the higher categories of turtles. Bull. Amer. Mus. Nat. Hist., 155: 387-436.

- HAY O.P. 1908. The fossil turtles of North America. Publ. Carnegie Inst. Washington, 75: IV + 568 pp.
- HAY, W.P. 1904. A revision of *Malaclemmys*, a genus of turtles. Bull. U.S. Bur. Fisheries, 24: 1-20.
- HENNIG, W. 1966. Phylogenetic systematics. Univ. IL. Press, Urbana, IL. 263 pp.
- KILLEBREW, F.C. 1977. Mitotic chromosomes of turtles. IV. The Emydidae. Texas J. Sci., 29: 245-253.
- _____. 1979. Osteological variation between *Graptemys flavimaculata* and *Graptemys nigrinoda* (Testudines: Emydidae). Herpetologica, 35: 146-153.
- LOOMIS, F.B. 1904. Two new river reptiles from the Titanotheres Beds. Am. J. Science, 18: 427-432.
- LOVERIDGE, A. and E.E. WILLIAMS. 1957. Revision of the African tortoises and turtles of the suborder Cryptodira. Bull. Mus. Comp. Zool., 115: 163-557.
- MCDOWELL, S.B. 1964. Partition of the genus *Clemmys* and related problems in the taxonomy of the aquatic Testudinidae. Proc. Zool. Soc. London, 143: 239-279.
- McKOWN, R.R. 1972. Phylogenetic relationships within the turtle genera *Graptemys* and *Malaclemys*. Unpublished Ph.D. Dissertation, University of Texas at Austin. 111 pp.
- PARSONS, T.S. 1960. The structure of the choanae of the Emydinae (Testudines, Testudinidae). Bull. Mus. Comp. Zool, 123: 111-127.
- _____. 1968. Variation in the choanal structure of recent turtles. Canadian J. Zool., 46:1235-1263.
- PRITCHARD, P.C.H. 1979. Encyclopedia of turtles. T.F.H. Publ. Inc. of Neptune, N.J. 895 pp.
- SAY, T. 1825. On the fresh water and land tortoises of the United States. J. Acad. Nat. Sciences, Philadelphia, 1: 203-219.
- TINKLE, D.W. 1962. Variation in shell morphology of North American turtles I. The carapacial seam arrangement. Tulane Stud. Zool., 9: 331- 349.
- VOGT, R.C. 1978. Systematics and ecology of the false map turtle complex *Graptemys pseudogeographica*. Ph.D. dissertation. Univ. of Wisconsin - Madison. 375 pp.
- _____. 1980. Natural history of the map turtles *Graptemys pseudogeographica* and *G. ouachitensis* in Wisconsin. Tulane Stud. Zool. and Bot., 22: 17-48.
- _____. and C.J. McCOY. 1980. Status of the emydine turtle genera *Chrysemys* and *Pseudemys*. Ann. Carnegie Mus., 49: 93-102.
- WEAVER, W.G. and F.L. ROSE. 1967. Systematics, fossil history, and evolution of the genus *Chrysemys*. Tulane Stud. Zool., 14: 63-73.
- WIED, PRINZ MAXIMILIAN Z. 1865. Verzeichniss der Reptilien welche auf einer Reise im nördlichen American beobachtet wurden. Nova. Act. Acad. Leopold Carol. Nat. Curios, 32: viii + 143.
- WOOD, R.C. 1977. Evolution of the emydine turtles *Graptemys* and *Malaclemys* (Reptilia, Testudines). J. Herpetol., 11: 415-421.
- ZANGERL, R. 1969. The turtle shell. In: Biology of the reptilia, I. Gans, C., and T.S. Parsons (eds.): Academic Press, pp. 311-339.
- ZUG, G.R. 1966. The penial morphology and the relationships of cryptodiran turtles. Occ. Pap. Mus. Zool. Univ. Mich., 647: 1-24.
- _____. 1971. Buoyance, locomotion, morphology of the pelvic girdle and hind limb, and systematics of cryptodiran turtles. Misc. Publ. Mus. Zool. Univ. Mich., 142: 1-98.

December 30, 1981

ADDENDUM

Tulane Studies in Zoology and Botany Volume 23, number 1

The addendum below is a continuation of the left hand paragraph of page 101 in the article by Dobie. It ends where the right hand paragraph begins LITERATURE CITED.

MUS. COMP. ZOOLOG.
LIBRARY

DEC 20 1982

HARVARD
UNIVERSITY

P. stejnegeri: (5) (AUMP 2363, four uncatalogued specimens).

Rhinoclemmys areolata: (1) (AUMP 2111).

R. pulcherrima: (2) (AUMP 910, uncatalogued specimen).

R. unidentified species: (1) (AUMP 2299).

Terrapene ornata: (AUM 10732); (AUMP 122-23, 962, 1939).

T. carolina: (52) (AUM 551, 1394, 1899, 3909-11, 4998, 5925, 8866, 9414, 11611, 14295, 17634, 20942, 23851, 25096-97); (AUMP 116-20, 124, 128, 130-31, 136-42, 702, 712, 914-16, 2250, 2257, 2312, 2317); (UF/FSM 7570, 14204, 35023, 38341, 40388, 41508-09, 41518, 41521-22).

Unidentified genus and species: (1) (SDSM & T 59187).

Specimens came from the following collections: American Museum of Natural History (AMNH); Auburn University Museum (AUM); Auburn University Museum of Paleontology (AUMP); Carnegie Museum (CM); Field Museum of Natural History (FMNH); University of Kansas Museum of Natural History (KU); The Vertebrate Museum, Northeast Louisiana State College (NLSC); South Dakota School of Mines and Technology (SDSM & T); Stephen F. Austin State University Vertebrate Collection (SFA); State University of South Dakota (SUSD); Texas Cooperative Wildlife Collection, Texas A&M University (TCWC); Texas Natural History Collection, Austin (TNHC); Tulane University Museum (TU); University of Florida, Florida State Museum (UF/FS); Museum of Southwestern Biology, The University of New Mexico (UNM); University of South Alabama (USA); United States Museum of Natural History, Smithsonian Institution (USNM).

TULANE STUDIES IN ZOOLOGY AND BOTANY

Volume 23, Number 2

\$3.50

MSS. DEPT. 2002
LIBRARY

December 15, 1982

DEC 20 1982

HARVARD
UNIVERSITY

CHANGES IN MELANIN MIGRATION INDUCED BY NORADRENERGIC
AND HISTAMINERGIC AGENTS IN THE FIDDLER CRAB, *UCA PUGILATOR*

MUKUND M. HANUMANTE AND MILTON FINGERMAN

p. 103

ADDITIONAL TREMATODES OF MAMMALS IN LOUISIANA
WITH A COMPILATION OF ALL TREMATODES REPORTED FROM
WILD AND DOMESTIC MAMMALS IN THE STATE

WESLEY L. SHOOP AND KENNETH C. CORKUM

p. 109

COMPARATIVE VISCERAL TOPOGRAPHY OF THE
NEW WORLD SNAKE TRIBE
THAMNOPHIINI (COLUBRIDAE, NATRICINAE)

NITA J. ROSSMAN, DOUGLAS A. ROSSMAN

and

NANCY K. KEITH

p. 123



TULANE UNIVERSITY
NEW ORLEANS

TULANE STUDIES IN ZOOLOGY AND BOTANY, a publication of the Biology Department of Tulane University, is devoted primarily to the biology of the waters and adjacent land areas of the Gulf of Mexico and the Caribbean Sea, but manuscripts on areas outside this geographic area will be considered. Each number contains an individual monographic study or several minor studies. Normally two numbers plus an index and a table of contents are issued annually. Preferred citation of the journal is *Tulane Stud. Zool. and Bot.*

INFORMATION FOR AUTHORS: Manuscripts submitted for publications are evaluated by the editors and by an editorial committee selected for each paper. Contributors need not be members of the Tulane faculty. Manuscripts of 20 or more pages, double-spaced, are preferred. We recommend conformance with the principles stated in CBE Style Manual, 4th ed., 1978. Manuscripts should be typewritten and double spaced. Two additional copies should accompany the original to expedite editing and publication. Legends for figures should appear on a separate page and in sequence. Illustrations should be proportioned for one or two column width corresponding to our printed page size, and should allow for insertion of the legend if occupying a whole page. Guidelines for letter and other extraneous markings should be done with a non-photo blue pencil such as Eagle Prismacolor. Photographs should be on glossy paper.

Many tables, if carefully prepared with a carbon ribbon and electric typewriter, can be photographically reproduced, thus helping to reduce publication costs. Lettering in any illustrative or tabular material should be of such a size that no letter will be less than 1 ½ mm high when reduced for publication.

An abstract not exceeding three percent of the length of the article must accompany the manuscript.

Separates of published articles are available to authors at a nominal cost.

Page charges, calculated at \$45/page, are solicited from authors who have funds for this purpose through their institutions or grants. Acceptance of papers is not dependent on ability to underwrite costs but excessive illustrations and tabular matter may be charged to the author.

EXCHANGES, SUBSCRIPTIONS, ORDERS FOR INDIVIDUAL COPIES: Exchanges are invited from institutions publishing comparable series. Subscriptions are billed in advance. A price list of back issues is available on request. Individuals should send their remittance, preferably money order, along with their orders. Remittances should be made payable to "Tulane University." Subscription rates:

Volume 23. \$8.50 domestic, \$9.50 foreign.

Copies of *Tulane Studies in Zoology and Botany* sent to regular recipients, if lost in the mails, will be replaced if the editorial offices are notified before the second subsequent issue is released.

COMMUNICATIONS: Address all queries and orders to: Editor, TSZ&B, Department of Biology, Tulane University, New Orleans, Louisiana 70118, U.S.A.
Harold A. Dundee, *Editor*

CHANGES IN MELANIN MIGRATION INDUCED BY NORADRENERGIC AND HISTAMINERGIC AGENTS IN THE FIDDLER CRAB, *UCA PUGILATOR**

MUKUND M. HANUMANTE AND MILTON FINGERMAN

*Department of Biology, Tulane University
New Orleans, Louisiana 70118 U.S.A.*

ABSTRACT

The effects of the H_1 receptor blocker SA-97, the H_2 receptor blocker cimetidine, the tyrosine hydroxylase inhibitor α -methyl-para-tyrosine and the H_1 receptor and norepinephrine uptake, blocker diphenhydramine on histamine- or 4-methyl histamine-induced inhibition of melanin dispersion in the fiddler crab, *Uca pugilator* undergoing a background transfer from white to black were determined. Only cimetidine significantly antagonized the 4-methyl histamine-evoked decrease in melanin dispersion. α -Methyl-para-tyrosine by itself significantly diminished whereas diphenhydramine by itself significantly potentiated the amount of this centrifugal melanin migration in the fiddler crabs. None of these drugs affected melanin migration *in vitro*. The results are consistent with the hypotheses that norepinephrine triggers release of a melanin-dispersing hormone and that H_1 receptor activation decreases impulse-mediated norepinephrine release in this crab.

INTRODUCTION

Translocation of the melanin in the melanophores of the fiddler crab, *Uca pugilator*, is regulated by antagonistic neurohormones, a melanin-dispersing hormone (MDH) and a melanin-concentrating hormone (Carlson, 1935; Sandeen, 1950; Fingerman, 1956). Norepinephrine (NE) triggers release of MDH in this crab (Fingerman et al., 1981; Hanumante and Fingerman, 1981a,b; 1982a,b,c; Hanumante et al., 1981). Recently histamine (HA) has been shown to inhibit melanin

dispersion in a dose-dependent manner (Hanumante and Fingerman, 1981b). Use of a variety of histaminergic agonists and antagonists led to the hypothesis that two types of HA receptors, called H_1 and H_2 , are present on NE neurons that trigger MDH release and that HA exerts its inhibitory action by stimulating the H_2 receptors. The present investigation was devised to obtain further support for this hypothesis. This objective was carried out by observing the effects of specific mammalian histaminergic and noradrenergic agents not used previously on the inhibitory action of HA and 4-methyl histamine (4-MeHA; a selective H_2 receptor agonist, Owen et al., 1979; Douglas, 1980; Polanin et al., 1981) on melanin dispersion in *Uca pugilator* transferred from a white to a black background.

MATERIALS AND METHODS

Adult male fiddler crabs, *Uca pugilator*, from the vicinity of Panacea, Florida, (Gulf Specimen Company) were used. Their melanophores were staged according to the system of Hogben and Slome (1931) whereby stage 1.0 represents maximal pigment concentration, stage 5.0 maximal pigment dispersion and stages 2.0, 3.0, and 4.0 the intermediate conditions. When intact crabs were used, the melanophores seen through the cuticle on the anteroventral surface of the second walking leg on the right side were staged at the time a sub-

*Supported by Grant PCM-81-08864 from the National Science Foundation.

EDITORIAL COMMITTEE FOR THIS PAPER:

DR. RAY W. FULLER, Research Advisor, Eli Lilly and Company, Indianapolis, Indiana 46206

DR. WILLIAM S. HERMAN, Professor and Head, Department of Genetics and Cell Biology, University of Minnesota, Minneapolis, Minnesota 55108

stance was injected and 15, 30, 60, 90, and 120 minutes thereafter. To facilitate comparison of the responses of the experimental and control crabs, mean differences between the 15 through 120 minute melanophore stages for the control and experimental groups were calculated for use in Table 1. The depicted data are based on the mean melanophore stages of 20 intact crabs (10 experimental and 10 control) or 20 isolated legs (10 experimental and 10 control). When assays were performed on isolated legs, the melanophores were staged only at the time the legs were removed from the crab (at which time the legs were perfused with the test or control solution) and 15, 30, 45, and 60 minutes thereafter. The second and third walking legs from both sides of the crab were removed; the legs from the right served as experimentals and the legs from the left side received control solution; the melanophores on the anteroventral surface of these isolated legs were observed for staging. The assays were performed using isolated legs having initially either maximally concentrated melanin (stage 1.0) or maximally dispersed melanin (stage 5.0). Melanophores in isolated legs of this crab remain responsive for at least 120 minutes (Herman and Dallmann, 1975). The statistical significance of the data was determined using Standard Errors of the Means (SEM) the Student's *t* test with significance set at the 95% confidence interval. None of the data for isolated legs were statistically significant.

The volume of the solution injected into each crab or isolated leg was always 0.05 ml. The experiments with intact crabs and isolated legs were performed at 24°C under an illumination of 1190 lx. 4-MeHA dihydrochloride (Smith, Kline and French), cimetidine (N''-Cyano-N-methyl-N'-{2-(5-methylimidazol-4-yl) methylthioethyl} guanidine) (Smith, Kline and French) and SA-97 (homochlorcyclizine) (Eisai) were generous gifts. In addition, HA, α -methyl-para-tyrosine (α -MPT) and diphenhydramine HCl (all from Sigma) were used. The concentration used for each drug, whether

injected alone or in combination, was 20 ug/dose of the free compound. All drugs except cimetidine were dissolved in Pantin's physiological saline (Pantin, 1934). Cimetidine was dissolved in acidified (a drop of 1.2 M HCl) saline. Consequently, a drop of HCl (1.2 M) was added to control saline for the cimetidine experiments. The rest of the controls received pure saline.

RESULTS AND DISCUSSION

4-MeHA, an H_2 receptor agonist, slowed the rate of melanin dispersion, as observed earlier by Hanumante and Fingerman (1981b), in intact crabs transferred from a white to a black background (Table 1). Cimetidine, which selectively blocks mammalian H_2 receptors (Douglas, 1980; Polanin and McNeill, 1981) significantly antagonized the 4-MeHA. On the other hand, the H_1 receptor blocker SA-97 not only did not antagonize the 4-MeHA but the combination of 4-MeHA plus SA-97 resulted in significantly further inhibition. None of these drugs affect melanin migration *in vitro* nor do SA-97 and cimetidine by themselves have an effect on the rate of melanin dispersion in crabs undergoing a background change from white to black (Hanumante and Fingerman, 1981b), a black background fostering melanin dispersion (Brown and Hines, 1952) which will be effected by MDH.

α -MPT selectively inhibits tyrosine hydroxylase. This enzyme catalyzes the synthesis of dihydroxyphenylalanine from tyrosine. At least in mammals this is the rate-limiting step in the biosynthesis of NE (Terrasawa et al., 1975; Lofström and Backström, 1978). α -MPT by itself significantly decreased melanin dispersion. HA by itself, as reported earlier (Hanumante and Fingerman, 1981b), significantly reduced centrifugal melanin migration in intact crabs transferred from a white to a black background. However, in the crabs that were co-administered either 4-MeHA and α -MPT or HA and α -MPT (Table 1), 4-MeHA and HA were not able to produce further, significant

reduction of the melanin dispersion. Diphenhydramine, a blocker of H_1 receptors and NE uptake, in mammals (Isaac and Goth, 1965; Fantozzi et al., 1975; Marco et al., 1980), by itself significantly enhanced melanin dispersion. However, when HA was co-administered with diphenhydramine, the HA-induced inhibition in melanin dispersion was still evident (Fig. 1).

The present data, in light of our earlier report (Hanumante and Fingerman, 1981b) and the pharmacological actions of noradrenergic and histaminergic agents in mammals, further strengthen the hypothesis that (a) NE serves as a neurotransmitter triggering release of MDH and that (b) activation of H_2 receptors located on NE neurons which control MDH release results in a decrement of melanin dispersion in *Uca pugilator* transferred from a white to a black background. The observations that cimetidine, a selective H_2 receptor blocker, antagonized the 4-MeHA-induced inhibition in melanin dispersion, whereas the H_1 blocker SA-97 did not, reveal that this effect is mediated specifically by activation of HA H_2 receptors. The marked increase in inhibitory effect of 4-MeHA when co-administered with the H_1 antagonist SA-97 was probably due to the fact that excitation of H_1 receptors evokes enhanced melanin dispersion (Hanumante and Fingerman, 1981b), blocking them would prevent any endogenous H_1 stimulation of the crabs. This would enable 4-MeHA, an agonist of H_2 receptors, to produce an even greater inhibition of the melanin dispersion. On the contrary, in the crabs whose H_2 receptors were blocked by cimetidine, 4-MeHA was unable to significantly decrease the action potential-mediated release of NE, which in turn resulted in a near normal quantity of MDH being released into the hemolymph of these crabs transferred to the black background. The fact that metiamide, another H_2 receptor blocker, significantly antagonized the 4-MeHA-stimulated decrease in centrifugal melanin migration (Hanumante and Fingerman,

1981b) *in vivo* further strengthens this conclusion.

NE has been found ($0.51 \mu\text{g/g}$) in the supraesophageal ganglia of male fiddler crabs (Hanumante and Fingerman, 1982b). Also, we have provided evidence that H_1 and H_2 receptors occur on NE neurons because in fiddler crabs pretreated with 6-hydroxydopamine (which presumably destroys NE neuroterminals in *Uca* as it does in vertebrates) (Hanumante and Fingerman, 1982b,c) HA is unable to significantly reduce further the melanin dispersion (Hanumante and Fingerman 1981b). We have not determined (i) the levels of NE in α -MPT injected crabs or (ii) the exact mechanism of action of α -MPT in *Uca puiator*. However, data that we obtained using noradrenergic and histadrenergic agents (Hanumante and Fingerman, 1981b) reveal that 20 MPT clearly interferes with NE neurotransmission. This probably was either by way of its well-established (at least in mammals) pharmacological NE synthesis-inhibiting effect (Terraswawa et al., 1975; Lofström and

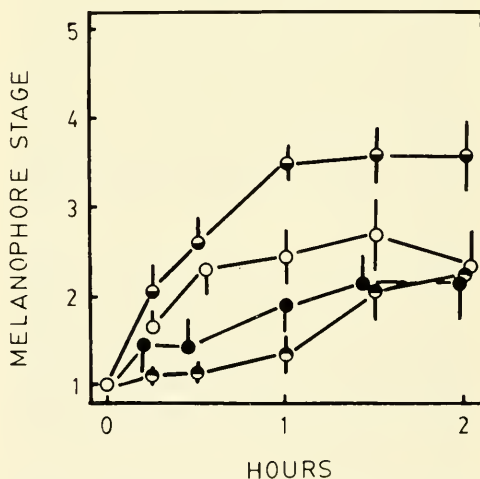


Figure 1. Relationships between melanophore stage and time. Circles with bottom-half darkened, crabs that received diphenhydramine; circles with top-half darkened, crabs that received histamine; solid circles, crabs that received histamine plus diphenhydramine; open circles, saline-injected controls. Vertical bars indicate SEM.

TABLE 1. The means ($\pm$ SEM) of the differences between the melanophore stages determined at 15, 30, 60, 90, and 120 minutes of the intact crabs that received a drug versus the saline-injected controls. The minus sign indicates decreased melanin dispersion relative to the controls. *Statistically significant $p \leq .05$ relative to respective controls.

4-Methyl histamine (4-MeHA)	-0.67* ($\pm$ 0.08)
Cimetidine	-0.17 ($\pm$ 0.01)
4-MeHA plus cimetidine	-0.39 ($\pm$ 0.07)
4-MeHA plus SA-97	-1.43* ($\pm$ 0.12)
α -Methyl-p-Tyrosine (α -MPT)	-1.15* ($\pm$ 0.15)
4-MeHA plus α -MPT	-1.44* ($\pm$ 0.21)
Histamine (HA)	-1.18* ($\pm$ 0.18)
HA plus α -MPT	-1.01* ($\pm$ 0.12)

Backström, 1978; Douglas, 1980) or by stimulating H_2 receptors, thereby leading to the observed decrement in MDH release (Table 1). Hence, the melanin of these α -MPT-treated crabs did not disperse to the extent it did in the control animals.

As stated above, in the crabs co-injected with 4-MeHA and α -MPT or HA and α -MPT, neither 4-MeHA nor HA significantly affected the melanin dispersion compared with that which occurred in response to α -MPT alone (Table 1). This presumably was due to the interference with NE neurons by α -MPT in such a way that the impulse-mediated decrement in NE secretion by the H_2 stimulators 4-MeHA and HA was not large enough to affect significantly the NE-mediated MDH release.

The diphenhydramine-evoked increment in melanin dispersion (Fig. 1) was presumably due to its blocking action on NE uptake₁ (Marco et al., 1980). NE uptake₁ inhibitors like nisoxetine (Koe, 1976) have already been shown to potentiate MDH release (Hanumante and Fingerman, 1981a). Diphenhydramine antagonizes H_1 receptors (Isaac and Goth, 1965; Fantozzi et al., 1975; Marco et al., 1980) also. However, because H_1 receptor blockers do not significantly abolish HA- or 4-MeHA- (an H_2 receptor agonist) mediated inhibition of melanin dispersion, we suggest that the NE uptake₁ blocking action of diphenhydra-

mine is responsible for the potentiation of melanin dispersion. The observation that even when HA is co-administered with diphenhydramine there is still a decrease in melanin dispersion (Fig. 1) indicates that HA does not evoke its effect by stimulating NE uptake₁; uptake₁ being the major mechanism of inactivating the postsynaptic actions of monoamines including NE (Fuller and Wong, 1977). That none of these drugs affect significantly melanin migration in isolated legs (Hanumante and Fingerman, 1981b) is consistent with the hypothesis that these drugs elicit changes in melanin dispersion indirectly by interacting with the neuroendocrine system of *Uca pugilator*.

LITERATURE CITED

BROWN, F.A., JR., and M.N. HINES. 1952. Modifications in diurnal pigmentary rhythm of *Uca* affected by continuous illumination. *Physiol. Zool.* 25: 56-70.

CARLSON, S.P. 1935. The color changes in *Uca pugilator*. *Proc. Nat. Acad. Sci.* 28: 549-551.

DOUGLAS, W.W. 1980. Histamine and 5-hydroxytryptamine (serotonin) and their antagonists, pp. 609-646 In: A.G. Gilman et al., Eds. Goodman and Gilman's The pharmacological basis of therapeutics, 6th ed., Macmillan Publishing Co., New York.

FANTOZZI, R., F. FRANCONI, P.E. MANNAIONI, E. MASINI, F. MORONI. 1975. Interaction of H_1 - and H_2 - receptor antagonists with histamine uptake and metabolism by guinea-pig isolated atrium and mouse neoplastic mast cells

- in vitro*. Br. J. Pharmacol. 53: 569-574.
- FINGERMAN, M. 1956. Black pigment concentrating factor in the fiddler crab. Science 123: 585-586.
- _____, M.M. HANUMANTE, S.W. FINGERMAN, and D.C. REINSCHMIDT. 1981. Effects of norepinephrine and norepinephrine agonists and antagonists on the melanophores of the fiddler crab, *Uca pugilator*. J. Crust. Biol. 1: 16-26.
- FULLER, R.W., and D.T. WONG. 1977. Inhibition of serotonin reuptake. Fed. Proc. 36: 2154-2158.
- HANUMANTE, M.M., and M. FINGERMAN. 1981a. Responses of the melanophores of the fiddler crab, *Uca pugilator*, to drugs affecting noradrenergic neurotransmission: Further evidence for norepinephrine as a neurotransmitter triggering release of melanin-dispersing hormone. Comp. Biochem. Physiol. 70C: 27-34.
- _____. 1981b. Inhibitory effect of histamine on the release of melanin-dispersing hormone in the fiddler crab, *Uca pugilator*. Amer. Zool. 21: 1011.
- _____. 1982a. Additional evidence for norepinephrine as a neurotransmitter triggering release of melanin-dispersing hormone in the fiddler crab, *Uca pugilator*: The effects of alpha₁ and beta adrenoceptor blocking drugs on melanin migration. Comp. Biochem. Physiol. 71C: 15-19.
- _____. 1982b. Further evidence for norepinephrine as a neurotransmitter stimulating release of melanin-dispersing hormone in the fiddler crab, *Uca pugilator*: The changes in the melanophores of the crabs following reserpine, 6-hydroxydopamine and bretylium administration. Gen. Pharmacol. 13: 99-103.
- _____. 1982c. Pharmacological involvement of presynaptic alpha₂ adrenoceptors in norepinephrine neurotransmission triggering the release of melanin-dispersing hormone in the fiddler crab, *Uca pugilator*. J. Crust. Biol. 2: 22-30.
- _____, S.W. FINGERMAN, and M. FINGERMAN. 1981. Antagonism of the inhibitory effect of the polychlorinated biphenyl preparation, Aroclor 1242, on color changes of the fiddler crab, *Uca pugilator*, by norepinephrine and drugs affecting noradrenergic neurotransmission. Bull. Environ. Contamin. Toxicol. 26: 479-484.
- HERMAN, W.S., and S.H. DALLMANN. 1975. *Limulus* chromatophorotropin: action on isolated *Uca* legs and in various crustaceans. Experientia 31: 918-919.
- HOGBEN, L., and D. SLOME. 1931. The pigmentary effector system - VI. The dual character of endocrine co-ordination in amphibian colour change. Proc. R. Soc. Lond. B. 108: 10-53.
- ISAAC, L., and A. GOTH. 1965. Interaction of antihistaminics with norepinephrine uptake: cocaine-like effect. Life Sci. 4: 1899-1904.
- KOE, K. 1976. Molecular geometry of the inhibitors of the uptake of catecholamines and serotonin in synaptosome preparations of rat brain. J. Pharmac. Exp. Ther. 199: 649-661.
- LOFSTRÖM, A., and T. BACKSTRÖM. 1978. Relationship between plasma estradiol and brain catecholamine content in the diestrus female cat. Psychoneuroendocrinology 3: 103-107.
- MARCO, E.J., G. BALFAGON, J. MARIN, B. GOMEZ, and S. LLUCH. 1980. Indirect adrenergic effect of histamine in cat cerebral arteries. Naunyn-Schmiedeberg's Arch. Pharmacol. 312: 239-243.
- OWEN, D.A.A., C.A. HARVEY, and R.W. GRESTWOOD. 1979. Cardiovascular studies with impromidine (S. K. and F. 92676), a new very potent and specific histamine H₂-receptor agonist. J. Pharm. Pharmacol. 31: 577-582.
- PANTIN, C.P.A. 1934. The excitation of crustacean muscle. J. Exp. Biol. 11: 11-27.
- POLANIN, A., and J.H. McNEILL. 1981. Characterization of the histamine receptors in rabbit left atria. Can. J. Physiol. Pharmacol. 59: 19-24.
- _____, T.E. TENNER, JR., and J.H. McNEILL. 1981. The characterization of cardiac histaminergic chronotropic receptors in the rabbit. Can. J. Physiol. Pharmacol. 59: 14-18.
- SANDEEN, M.I. 1950. Chromatophorotropins in the central nervous system of *Uca pugilator*, with special reference to their origins and actions. Physiol. Zool. 23: 337-352.
- TERRASAWA, E., W.E. BRIDSON, J.W. DAVENPORT, and R.W. GAY. 1975. Role of brain monoamines in release of gonadotropin before proestrus in the cyclic rat. Neuroendocrinology 18: 345-359.

ADDITIONAL TREMATODES OF MAMMALS IN LOUISIANA WITH A COMPILATION OF ALL TREMATODES REPORTED FROM WILD AND DOMESTIC MAMMALS IN THE STATE

WESLEY L. SHOOP AND KENNETH C. CORKUM

Department of Zoology and Physiology, Louisiana State University
Baton Rouge, Louisiana 70803

ABSTRACT

The following trematodes were collected from hunter-trapped mammals in the Atchafalaya basin of Louisiana during the winters of 1981 and 1982: *Alaria alarioides* (Dubois, 1937) Dubois, 1970 from mink, *Mustela vison* Schreber, and river otter, *Lutra canadensis* (Schreber); *Alaria marcianae* (La Rue, 1917) Walton, 1949 from raccoon, *Procyon lotor* (Linn.) and bobcat, *Lynx rufus* (Schreber); *Alaria mustelae* Bosma, 1931 from raccoon and mink; *Amphimerus speciosus* (Stiles and Hassal, 1896) Barker, 1911 from raccoon and the domestic cat, *Felis domesticus* Linn.; *Baschkirovitrema incrassatum* (Dies., 1850) Skrjabin, 1944 from mink and river otter; *Brachylaima virginiana* Dickerson, 1930 from opossum, *Didelphis virginiana* Kerr; *Carneophallus basodactylophallus* Bridgman, 1969 from raccoon; *Cryptocotyle concava* (Creplin, 1825) Luhe, 1899 from mink; *Fibricola cratera* (Barker and Noll, 1915) Dubois, 1932 from mink, opossum, and raccoon; *F. lucida* (La Rue and Bosma, 1927) Dubois and Rausch, 1950 from mink and opossum; *Gyrosoma singulare* Byrd, Bogitsh, and Maples, 1961 from raccoon and mink; *Hasstilesia texensis* Chandler, 1929 from muskrat, *Ondatra zibethica* (Linn.); *Heterobilharzia americana* Price, 1929 from mink, raccoon, and bobcat; *Isthmiophora melis* (Schrunk, 1788) Luhe, 1909 from raccoon and mink; *Linstowiella szidati* (Anderson, 1944) Anderson and Cable, 1950 from opossum and raccoon; *Maritreminoides nettae* (Gower, 1938) Rankin, 1939 from raccoon and mink; *Microphallus opacus* (Ward, 1894) Ward, 1901 from raccoon and mink; *Paragonimus kellicotti* Ward, 1908 from opossum; *Pharyngostomoides procyonis* Harkema, 1942 from raccoon; *Quinqueserialis quinqueserialis* (Barker and Laughlin, 1911) Harwood, 1939 from muskrat; *Rhopalias macracanthus* Chandler, 1932 from opossum; and *Sella-cotyle vitellosa* Sogandares-Bernal, 1961 from mink.

Alaria alarioides, *A. marcianae*, *Amphimerus speciosus*, *Cryptocotyle concava*, *Isthmiophora melis*, *Microphallus opacus*, *Paragonimus kellicotti*, and *Quinqueserialis quinqueserialis* have not been previously reported from Louisiana mammals. Diagnoses are presented for the species representing state records along with pertinent notes on the biology of each. New host records include *Heterobilharzia americana*, *Cryptocotyle concava*, and *Maritreminoides nettae* from mink; *Alaria marcianae*, *Amphimerus speciosus*, and *Linstowiella szidati* from raccoon; and *Hasstilesia texensis* from muskrat. A compilation of trematodes previously reported from Louisiana mammals is presented.

INTRODUCTION

Recently, we reported some trematodes collected from mammals in south Louisiana (Shoop and Corkum, 1981a). Since that time we have continued our examination of hunter-trapped mammals from the Atchafalaya basin of Louisiana during the winters of 1981 and 1982. The following mammals were examined for trematodes: 42 minks, *Mustela vison* Schreber; 37 raccoons, *Procyon lotor* (Linn.); seven river otters, *Lutra canadensis* (Schreber); five muskrats, *Ondatra zibethica* (Linn.); three bobcats, *Lynx rufus* (Schreber); four domestic cats, *Felis domesticus* Linn.; two opossums, *Didelphis virginiana* Kerr; and three red foxes, *Vulpes fulva* (Desmarest). The red foxes were found uninfected with trematodes.

Trematodes were fixed in steaming 10%

EDITORIAL COMMITTEE FOR THIS PAPER:

DR. BERT B. BABERO, Professor of Biological Sciences, University of Nevada, Las Vegas, Las Vegas, Nevada 89154

DR. WALTER E. WILHELM, Associate Professor of Biology, Memphis State University, Memphis, Tennessee 38152

formalin and stained in Semichon's acetocarmine. All measurements are in micrometers unless otherwise stated; means are followed by the ranges in parentheses. Line drawings were prepared with the aid of a microprojector. Representative specimens of the species for which diagnoses are given were deposited in the Manter Laboratory, University of Nebraska State Museum, Lincoln, Nebraska.

Table I lists the trematodes recovered from the eight species of mammals. Lumsden and Zischke (1961) reported and diagnosed *Fibricola cratera*, *F. lucida*, *Hasstilesia texensis*, *Brachylaima virginiana*, and *Rhopalias macracanthus* from Louisiana mammals. Our specimens agree in all respects with Lumsden and Zischke's (1961) diagnoses. Our specimens of *Hasstilesia texensis* from the muskrat represent a new host record. Shoop and Corkum (1981a) reported and diagnosed *Alaria mustelae*, *Baschkirovitrema incrassatum*, *Gyrosoma singulare*, *Maritreminoides nettae*, and *Pharyngostomoides procyonis* from Louisiana mammals. In that report we noted *M. nettae* in raccoons; it is herein reported from the mink as well (new host record). In a more recent note, we (Shoop and Corkum, 1982) commented further on the status of *G. singulare* in this state. *Heterobilharzia americana* has been reported from Louisiana mammals by Malek et al. (1961) and Kaplan (1964). Our collections of *H. americana* from mink represent a new host record. *Carneophallus basodactylophallus* was originally described by Bridgman (1969) from raccoon in Louisiana as was *Sellacotyle vitellosa* from mink by Sogandares-Bernal (1961). Lumsden and Winkler (1962) reported *Linstowiella szidati* from opossum. We have found it in opossum as well as in raccoon. In addition to these trematodes, we identified eight other species that have not been previously reported from Louisiana mammals and that are of importance from epidemiological or zoogeographical standpoints. Table II compiles all trematodes reported heretofore from mammals in the state of Louisiana.

Family DIPLOSTOMIDAE Poirier, 1886
Alaria alarioides (Dubois, 1937)
 Dubois, 1970
 (Figure 1)

Synonyms: *Diplostomum alarioides* Dubois, 1937; *Enhydrodiplostomum alarioides* (Dubois, 1937) Dubois, 1944.

Hosts: *Mustela vison* Schreber and *Lutra canadensis* (Schreber).

Location: Small intestine.

Locality: Belle River, Assumption Parish, Louisiana.

Deposition: Univ. Nebraska State Mus., Manter Lab. Coll. No. 21367.

Diagnosis (based on ten mature specimens): Body elongate, distinctly bisegmented, 1650 (1400-1800) long by 540 (450-650) at the widest point. Forebody spathulate, 777 (640-940) long by 540 (450-650) wide; pseudosuckers present as depressions on either side of the oral sucker, never observed evaginated. Hindbody claviform, 907 (760-1050) long by 430 (400-480) wide, containing reproductive organs. Forebody tegument covered with small spines; hindbody smooth. Oral sucker terminal, 92 (80-100) long by 106 (90-120) wide; acetabulum weak, spherical, 75 (60-80) long by 76 (60-90) wide, often covered by the tribocytic organ; tribocytic organ broadly elliptical when evaginated, 348 (240-400) long by 280 (240-330) wide, with a longitudinal cleft.

Prepharynx and esophagus extremely short or absent; pharynx usually in contact with oral sucker, 77 (70-90) long by 65 (50-80) wide; paired ceca extend to the posterior end of body. Testes tandem, not equal; anterior testis asymmetrical, laterally disposed on either side of midline, 215 (200-250) long by 317 (290-350) wide; posterior testis symmetrical, dumbbell-shaped, much wider than anterior testis, 218 (190-250) long by 394 (350-410) wide, with a ventro-median groove to allow passage of ceca, uterus, and vitellaria; ejaculatory duct opens into the genital atrium; genital atrium opens posterior, subterminally on the dorsal surface. Ovary spherical, located in hindbody just in front of

TABLE 1. Trematodes recovered from hunter-trapped mammals in Louisiana during the winters of 1981 and 1982.

Trematode	Hosts	No. Examined	No. Infected	%	Location
<i>Alaria alarioides</i> (Dubois, 1937)	otter	7	2	29	Sm. Int.
Dubois, 1970	mink	42	24	57	"
<i>A. marcianae</i> (La Rue, 1917)	raccoon	37	2	5	"
Walton, 1949	bobcat	3	2	67	"
<i>A. mustelae</i> Bosma, 1931	raccoon	37	1	3	"
	mink	42	1	2	"
<i>Amphimerus speciosus</i> (Stiles and Hassal, 1896) Barker, 1911	raccoon	37	1	3	Liver
	domestic cat	4	1	25	"
<i>Baschkirovitrema incrassatum</i> (Dies., 1850) Skrjabin, 1944	otter	7	2	29	Sm. Int.
	mink	42	21	50	"
<i>Brachylaima virginiana</i> Dickerson, 1930	opossum	2	1	50	"
<i>Carneophallus basodactylophallus</i> Bridgman, 1969	raccoon	37	2	5	"
<i>Cryptocotyle concava</i> (Creplin, 1825) Luhe, 1899	mink	42	22	52	"
<i>Fibricola cratera</i> (Barker and Noll, 1915) Dubois, 1932	mink	42	4	10	"
	raccoon	37	12	32	"
	opossum	2	2	100	"
<i>F. lucida</i> (La Rue, and Bosma, 1927) Dubois and Rausch, 1950	mink	42	26	62	"
	opossum	2	2	100	"
<i>Gyrosoma singulare</i> Byrd, Bogitsh, and Maples, 1961	raccoon	37	7	19	"
	mink	42	2	5	"
<i>Hasstilesia texensis</i> Chandler, 1929	muskrat	5	1	20	Cecum
<i>Heterobilharzia americana</i> Price, 1929	raccoon	37	20	54	Mes. Ven.
	mink	42	2	5	"
	bobcat	3	1	33	"
<i>Isthmiophora melis</i> (Schrank, 1788) Luhe, 1909	raccoon	37	6	16	Sm. Int.
	mink	42	2	5	"
<i>Linstowiella szidati</i> (Anderson, 1944) Anderson and Cable, 1950	raccoon	37	1	3	"
	opossum	2	1	50	"
<i>Maritreminoides nettae</i> (Gower, 1938) Rankin, 1939	mink	42	3	7	"
	raccoon	37	6	16	"
<i>Microphallus opacus</i> (Ward, 1894) Ward, 1901	raccoon	37	5	14	"
	mink	42	4	10	"
<i>Paragonimus kellicotti</i> Ward, 1908	opossum	2	1	50	Lungs
<i>Pharyngostomoides procyonis</i> Harkema, 1942	raccoon	37	31	84	Sm. Int.
<i>Quinqueserialis quinqueserialis</i> (Barker and Laughlin, 1911) Harwood, 1939	muskrat	5	2	40	Cecum
<i>Rhopalias macracanthus</i> Chandler, 1932	opossum	2	1	50	Sm. Int.
<i>Sellacotyle vitellosa</i> Sogandares-Bernal, 1961	mink	42	2	5	"

the anterior testis, 103 (90-120) long by 114 (110-120) wide; uterus courses anteriorly into the forebody and turns immediately posteriorly where it opens in the genital atrium; vitellaria penetrate the forebody and extend in two bands through the ventro-medial grooves of the testes to the level of the genital atrium; vitelline reservoir median, intertesticular. Eggs large, operculate, 101 (90-110) long by 55 (50-60) wide. Excretory system not observed.

Discussion: Dubois (1937) originally described *Diplostomum alarioides* from a Brazilian otter. He (Dubois, 1944) subsequently purged the genus *Diplostomum* of all mammalian parasites, retaining it for avian parasites, and erected the new genus *Enhydrodiplostomum* for *D. alarioides* and a second otter parasite, *D. fosteri*. Chandler and Rausch (1946) assigned two additional species, *Alaria clathrata* and *A. pseudoclathrata*, both also parasites of the otter, to the genus *Enhydrodiplostomum*. In a later revision, Dubois (1970) agreed that these four species are closely related, but reassigned them to the genus *Alaria* where additional mustelid parasites are found.

Sawyer's (1961) collection of *A. alarioides* from river otter in Georgia was the first report from North America. Since then, Miller and Harkema (1964, 1968) reported *A. alarioides* from both mink and river otter in North Carolina, and Fleming et al. (1977) reported it from river otter in Alabama. *A. alarioides* is also a common parasite of mink and river otter in Louisiana. Measurements of *A. alarioides* from the two hosts compare favorably with the descriptions of Dubois (1937, 1970).

Alaria marcianae (La Rue, 1917)

Walton, 1949

(Figure 2)

Synonyms: *Cercaria marcianae* La Rue, 1917; *Agamodistomum marcianae* (La Rue, 1917) Cort, 1918; *Alaria americana* Hall and Wigdor, 1918; *Alaria canis* La Rue and Fallis, 1934; *Alaria minnesotae* Chandler, 1954.

Hosts: *Lynx rufus* (Schreber) and *Procyon lotor* (Linn.).

Location: Small intestine.

Locality: Pierre Part, Assumption Parish, Louisiana.

Deposition: Univ. Nebraska State Mus., Manter Lab. Coll. No. 21368.

Diagnosis (based on ten mature specimens): Body elongate, distinctly bi-segmented, 1375 (1000-1600) long by 478 (350-600) at the widest point. Forebody spathulate with lateral margins folded ventrally where they meet at the midline, the entire forebody serving as an organ of attachment, 883 (650-1050) long by 478 (350-600) wide; ear-like appendages present on either side of the oral sucker, rarely observed invaginated to form pseudo-suckers. Hindbody conical, 535 (400-650) long by 363 (280-500) wide, containing reproductive organs. Forebody tegument covered with small spines, hindbody tegument smooth. Oral sucker terminal 90 (60-105) long by 73 (60-81) wide; acetabulum weak, spherical, 74 (60-95) long by 75 (60-95) wide, rarely covered by the tribocytic organ; tribocytic organ elongate when evaginated, 453 (310-550) long by 200 (155-225) wide, with a longitudinal cleft. Prepharynx present, 5 (4-6) long; pharynx pyriform, 102 (75-215) long by 64 (55-85) wide; esophagus 6 (4-10) long; paired ceca extend to the posterior end of the body. Testes tandem, not equal; anterior testis asymmetrical, typically wedge-shaped, laterally disposed on either side of the midline, 160 (128-215) long by 225 (175-300) wide; posterior testis symmetrical, dumbbell-shaped much wider than anterior testis, 210 (165-276) long by 340 (275-425) wide, with a ventro-medial groove to allow passage of ceca and uterus; muscular ejaculatory pouch lies posterior to the testes and empties into the genital atrium; genital atrium located in the posterior end of the body, opening on the dorso-subterminal side. Ovary reniform, located in front of the anterior testis on either side of midline, 72 (60-99) long by 167 (100-180) wide; Mehlis' gland opposite

the ovary; uterus courses briefly into the forebody and turns immediately posteriad where it empties into the genital atrium; vitellaria located only in the forebody, from just in front of the acetabulum to the forebody-hindbody juncture; vitelline reservoir prominent, located in the hindbody at the level of the anterior testis. Eggs few, large, operculate, 122 (110-128) long by 65 (60-75) wide. Excretory pore terminal, remainder of excretory system not observed.

Discussion: Apparently, adult *Alaria marcianae* have not previously been reported from Louisiana. A single specimen of *A. americana* (= *A. marcianae*) from a dog from Baton Rouge was deposited by G. Dikmans (USNM Helm. Coll. No. 25159). We examined that specimen and identify it as *A. marcianae*, being similar to our material from the bobcat.

In a previous report, the epidemiology of *A. marcianae* mesocercariae was studied in Louisiana and evidence was presented that this species was responsible for an autochthonous human infection (Shoop and Corkum, 1981b). In experimental infections only juvenile raccoons served as definitive hosts for *A. marcianae*. Adult raccoons proved to be refractory to the development of the mesocercarial stage, which remained undifferentiated in the subcutaneous fat. These findings were corroborated in the present study because no adult raccoons were found infected. Two yearlings, however, harbored several adult *A. marcianae* in their duodena. This is the first report of raccoon naturally infected with this species. Though these worms from the yearlings exhibited no morphological anomalies, they were smaller than specimens from the bobcat.

The known definitive hosts for *A. marcianae* in Louisiana now include the domestic dog, bobcat, and juvenile raccoons. In experimental laboratory infections we have found that the domestic cat is a suitable definitive host and that it, as well as feral cats, may play a significant role in the maintenance of *A. marcianae* in Louisiana.

Family OPISTHORCHIIDAE

Braun, 1901

Amphimerus speciosus

(Stiles and Hassal, 1896) Barker, 1911

(Figure 3)

Synonyms: *Amphimerus caudalitestis* Caballero, Grocott, and Zerecero, 1953; *A. guayaquilensis* (Rodriguez, Gomez, and Montalvan, 1948) Caballero, Grocott, and Zerecero, 1953; *A. interruptus* (Braun, 1901) Barker, 1911; *A. minimus* Thatcher, 1970; *A. neotropicalis* Caballero, Montero-Gei, and Caballero, 1963; *A. parciotatus* Franco, 1967; *A. pricei* (Foster, 1939) Yamaguti, 1958; *A. pseudofelineus* (Ward, 1901) Barker, 1911.

Hosts: *Felis domesticus* Linn. and *Procyon lotor* (Linn.).

Location: Liver and bile ducts.

Locality: Ramah, Iberville Parish, Louisiana.

Deposition: Univ. Nebraska State Mus., Manter Lab. Coll. No. 21369.

Diagnosis (based on ten mature specimens): Body elongate, sharply tapered anterior to the acetabulum, 10.25 (8.0-12.25) mm long by 2010 (1150-2400) at the widest point. Tegument beset with small, stout spines. Oral sucker 268 (240-300) long by 313 (270-340) wide; acetabulum 200 (150-240) long by 218 (170-250) wide. Prepharynx absent; pharynx 183 (160-200) long by 173 (150-190) wide; esophagus 170 (120-200) long; paired ceca extend to the posterior end of body. Testes tandem, in posterior $\frac{1}{3}$ of body, transversely elongate, slightly lobed; anterior testis 498 (410-600) long by 925 (550-1150) wide; posterior testis 573 (450-720) long by 925 (550-1150) wide; seminal vesicle elongate, coiled, opens into the genital atrium which is immediately preacetabular. Ovary oval to reniform, may be slightly lobed, 325 (240-450) long by 470 (370-610) wide; seminal receptacle large, lying immediately postovarian, 525 (200-700) long by 473 (320-600) wide; Laurer's canal present, opening on dorsal surface; Mehlis' gland preovarian, sinistral to midline; uterus forming transverse, intercecal coils between the ovary and ace-

tabulum; vitellaria lateral, extracecal, consisting of two pairs of disjunct bundles on each side, each pair separate at level of the ovary; four vitelline ducts fuse mesially at the level of the ovary to form a vitelline reservoir. Eggs small, 28 (25-32) long by 12 (11-14) wide. Excretory pore terminal or slightly subterminal; excretory vesicle sigmoid, coursing anteriorly between the testes and bifurcating immediately posterior to the seminal receptacle.

Discussion: Reports of species of *Amphimerus* from North American mammals have almost exclusively been *A. pseudofelineus* and this name has become well entrenched in veterinary literature. However, Nasir and Diaz (1972) synonymized the following species with *A. speciosus*: *A. caudalitestis*; *A. guayaquilensis*; *A. interruptus*; *A. minimus*; *A. neotropicalis*; *A. parciotatus*; *A. pricei*; and *A. pseudofelineus*.

Lumsden and Zischke (1963) reported *Amphimerus interruptus* from a yellow-crowned night heron, *Nyctanassa violacea*. Their measurements fall within the ranges we recorded and the specimen figured is remarkably similar to ours, indicating that they are the same species. Lumsden and Zischke also noted similarities between their specimens and the description of *A. speciosus*. These observations corroborate, in part, Nasir and Diaz's (1972) synonymies and further indicate the ability of these organisms to live in both avian and mammalian hosts.

A. speciosus has been reported in cats and dogs from several states in the United States (Rothenbacher and Lindquist, 1963). Chronic morbidity associated with infection includes liver and biliary cirrhosis and pancreatitis. Also, Thatcher (1970) commented on the unassessed possibility of human infection with this species. *A. speciosus* was collected from the liver and bile ducts of one of four domestic cats and two of 37 raccoons in Louisiana. The raccoon apparently is a new host record for this species.

Family HETEROPHYIDAE
(Leiper, 1909) Odhner, 1914

Cryptocotyle concava (Creplin, 1825)
Luhe, 1899
(Figure 4)

Synonyms: *Distoma concava* Creplin, 1825; *Tocotrema concava* Looss, 1899; *Cryptocotyle echinata* Linstow, 1878.

Hosts: *Mustela vison* Schreber.

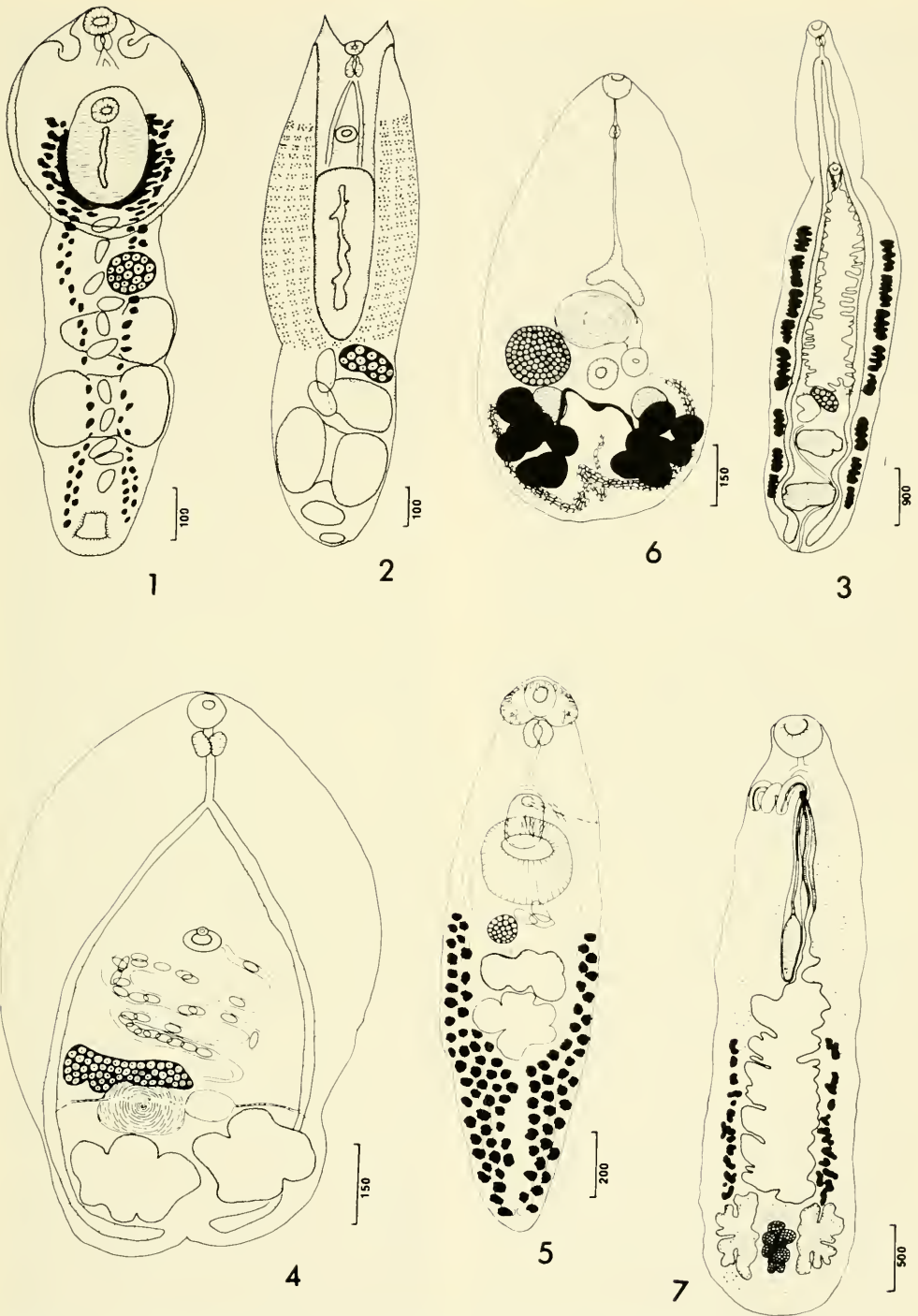
Location: Small intestine.

Locality: Belle River, Assumption Parish, Louisiana.

Deposition: Univ. Nebraska State Mus., Manter Lab. Coll. No. 21370.

Diagnosis (based on ten mature specimens): Body foliate, 904 (780-1050) long by 612 (560-680) wide. Tegument beset with small spines. Oral sucker terminal, 47 (35-55) long by 54 (40-65) wide; acetabulum 41 (35-50) in diameter, found within the genital atrium and comprising a part of the acetabulogenital apparatus; acetabulogenital apparatus 67 (60-75) long by 91 (70-125) wide, located medially and equatorially. Prepharynx 10 (5-15) long; pharynx 49 (40-55) long by 48 (45-60) wide; esophagus 76 (65-100) long; paired ceca extend to the posterior end of body where they turn medially just posterior to the testes. Testes opposite, distinctly lobate, 152 (125-175) long by 233 (210-250) wide, located in posterior end of body; seminal vesicle courses from testes to the acetabulogenital apparatus; cirrus pouch absent. Ovary wedge-shaped, lobate, 93 (70-115) long by 138 (100-175) wide, located dextral to the midline, between the ovary and right testis; uterus makes 3-4 intercecal loops before opening into the acetabulogenital complex; vitellaria mostly lateral, commence behind the level of the cecal bifurcation and extend to the posterior end of body where they meet at the midline; vitelline reservoir is located medially, at the level of the seminal vesicle. Eggs small, operculate, 36 (33-40) long by 15 (13-20) wide.

Discussion: Wootton (1957) first reported *Cryptocotyle concava* from North America and elucidated the life cycle. It included an operculate snail, *Amnicola longiqua*, in which rediae gave rise to pleurolophocercous cercariae; these penetrated and



Figures 1-7. 1. *Alaria alarioides* from mink and river otter. 2. *Alaria marcianae* from bobcat and raccoon. 3. *Amphimerus speciosus* from raccoon and the domestic cat. 4. *Cryptocotyle concava* from mink. 5. *Isthmiophora melis* from raccoon and mink. 6. *Microphallus opacus* from raccoon and mink. 7. *Quinqueserialis quinqueserialis* from muskrat. Scales in micrometers.