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## Evolution and Fossil Relationships of Slider Turtles

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### Abstract

Slider turtles belong to the genus *Trachemys*, which includes *T. scripta* and four insular species endemic to the Caribbean region. Based on overall comparisons of morphology, biochemistry, and ecology, sliders appear most similar to map turtles, genus *Graptemys*. However, phylogenetic analysis suggests that sliders, map turtles, cooters (*Pseudemys*), and terrapins (*Malaclemys*) are all closely related and form a monophyletic group (clade). This relationship, as well as similarities between sliders and painted turtles (*Chrysemys*), is supported by electrophoretic evidence. Fossil skulls recently assigned to *Trachemys* have contributed to our knowledge of the evolutionary history of sliders. Based on available fossil material, three extinct species of *Trachemys* are tentatively considered to be valid: *T. idahoensis* Gilmore from late Pliocene, and *T. inflata* Weaver and Robertson and *T. hillii* (Cope) from the Upper Miocene. *Trachemys inflata* is a highly specialized form that appears divergent from the lineage leading to extant *Trachemys*. The progenitor of modern trachemyne species was probably an early Pliocene form similar to *T. idahoensis* or *T. hillii*. The relationship of this ancestor to *Chrysemys*, *Graptemys*, and *Pseudemys* remains undetermined.

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### Introduction

Although the taxonomy of slider turtles has received considerable attention (see Chapter 4), most work has focused on the alpha level, with emphasis on descriptions of new subspecies or generic identifications. Theories on the evolution of *Trachemys scripta* are few. This is, in part, due to the uncertain relationships of many Mesoamerican populations and the often confused taxonomy of closely related species in the West Indies. Recently, however,

some of these taxonomic problems have been resolved (Seidel and Inchaustegui Miranda, 1984; Seidel and Adkins, 1987; Seidel, 1988; also see Chapter 7). The extensive variability of diagnostic characters in sliders makes it difficult, and in some cases nearly impossible, to identify homologies or homoplasies (convergent character states). Morphological convergence resulting from similar feeding strategies (herbivory versus omnivory) and habitat selection (fluvial versus lentic) appears to be common in *Trachemys* and related forms (Jackson, 1977, 1978a). Unfortunately, much more work is needed in this area, and there remain more questions than answers. Nevertheless, the following discussion presents theories on the origin and phylogeny of sliders, based on our current understanding of their taxonomy and fossil record.

### *Trachemys* and Related Extant Genera

As noted by Ernst (see Chapter 4), slider turtles are assigned to the subfamily Emydinae, genus *Trachemys* (formerly and occasionally still included in *Pseudemys* sensu lato or *Chrysemys* sensu lato), which includes *T. scripta*, *T. decussata*, *T. decorata*, *T. terrapen*, and *T. stejnegeri* (Seidel and Smith, 1986). *Trachemys scripta dorbigni* (South America) and *T. s. gaigeae* (Texas and New Mexico) have been elevated to species by some recent authors (Dixon, 1987; Ernst, pers. com.). *Trachemys scripta* is the only extant mainland species and is widely distributed from the United States to lower South America. The other four species are endemic to the Greater Antilles and adjacent West Indian islands. The taxonomic position of trachemyne turtles has been controversial for the past 20 years, resulting in their inconsistent assignment to the genus *Pseudemys* (which includes cooters and red-bellied turtles) or the composite genus *Chrysemys* (which also includes painted turtles). Recently, Seidel and Smith (1986) reviewed these genera and presented evidence that sliders (*Trachemys*) are a natural, monophyletic group. The following combination of shared character states distinguishes them from cooters (*P. concinna* and *P. floridana*), red-bellied turtles (*P. rubriventris*, *P. nelsoni*, and *P. alabamensis*), and painted turtles (*C. picta*): adult carapace rugose, notched and serrated posteriorly (sensu Weaver and Robertson, 1967), and usually keeled; ventral surface of lower jaw rounded, and upper (alveolar) surface usually narrow and without a conspicuous symphyseal ridge; tuberculate denticles absent from alveolar surface of upper jaw; cutting surface of upper jaw uncusped and medially forming an angle or shallow notch; cranium shallow anterior to basisphenoid (30% to 40% of condylobasal length); and zygomatic arch and narial opening relatively narrow. In addition to finding close relationships among *Trachemys*, *Pseudemys*, and *Chrysemys*, a number of authors have recognized affinities of these genera with *Graptemys* (*Malaclemys* sensu lato) and *Deirochelys* (Loveridge and

Williams, 1957; McDowell, 1964; Zug, 1971; Bramble, 1974; Jackson, 1978a; Dobie, 1981; Frair, 1982; Ckhikvadze, 1984). A survey of shared-unshared character states in these turtles (including morphology, biochemistry, and ecology) is presented in Table 5.1. A strictly phenetic comparison based on these characters indicates that sliders (*Trachemys*) and map turtles (*Graptemys*) are most similar, with 19 character states in common. No karyologic variation has been observed in the Emydinae (Bickham and Baker, 1976a,b; Killebrew, 1977).

In the past decade there has been a major shift in systematics from the evolutionary and phenetic approaches to the phylogenetic (or cladistic) approach. Rather than defining genealogical relationships by overall similarity, phylogenetics involves the identification of homologous structures and the evolutionary direction (polarity) of characters from a primitive (plesiomorphic) to a derived (apomorphic) state (for a review, see Wiley, 1981). Those groups that share the greatest number of derived character states (synapomorphies) are presumed to have an exclusive common ancestor and are thus joined as sister taxa in a branching tree. In determining polarity, character states are sometimes identified as primitive if they are the most common or if they appear in fossils. More often, however, primitive states are identified by their presence in a closely related, extant taxonomic out-group (see Watrous and Wheeler, 1981). This purely phylogenetic approach has seldom been applied in systematic studies of *Trachemys*, in spite of the relatively large suite of characters reported (Table 5.1). Based on fossil evidence and extant morphology, *Deirochelys* (the chicken turtle) is a logical out-group for analyzing the phylogeny of *Trachemys*, *Pseudemys*, *Chrysemys*, and *Graptemys*. Although aspects of the head and neck morphology of chicken turtles are highly derived for specialized feeding, *Deirochelys* presumably diverged from a *Chrysemys-Pseudemys-Trachemys*-like ancestor (perhaps in the Oligocene) and has retained a number of characters shared with extant species of that group (Jackson, 1978a). Electrophoretic data also support a close relationship among *Deirochelys*, *Trachemys*, *Pseudemys*, *Chrysemys*, and *Graptemys* (Frair, 1982; Seidel, pers. obs.). Most of the character states identified in *Deirochelys* (Table 5.1) are also present in *Clemmys*, a genus of emydines often considered generalized and primitive (Bramble, 1974; Ward, 1980). When *Deirochelys* is the designated out-group, nine characters are synapomorphic between *Trachemys* and *Graptemys*, and nine are synapomorphic between *Trachemys* and *Pseudemys* (Table 5.1). *Trachemys* and *Chrysemys*, which have often been viewed as closely related (congeneric) taxa, are joined by only two synapomorphies. A phylogenetic tree based on these character polarities indicates an unresolved trichotomy among *Trachemys*, *Pseudemys*, and *Graptemys* (Fig. 5.1). *Chrysemys*, which has a greater number of plesiomorphic states (18, Table 5.1), appears as an earlier divergent lineage. This agrees with

Table 5.1. Adult character states of some emydine turtles

Character state	<i>Graptemys</i> ( <i>Malaclemys</i> )	<i>Trachemys</i>	<i>Chrysemys</i>	<i>Pseudemys</i>	<i>Deirocheilus</i>
Cranium and mandible (McDowell, 1964)					
1. Cranium short and deep	-	-	-	+	-
2. Thick anterior border of inferior parietal process	+	-	-	-	-
3. Mandible flattened ventrally	-	-	-	+	-
4. Tuberculate denticles prominent on alveolar surface	-	-	-	+	-
5. Alveolar surfaces nearly flat (median ridge absent)	+	-	-	-	+
6. Alveolar surface of lower jaw usually narrow	-	+	+	-	+
7. Anterior cusp absent from median ridge of upper jaw	+	+	-	-	+
8. Posterior palatine foramen large relative to nasopalatine fenestra	-	-	+	-	+
9. Posterior pterygoid near to or contacting exoccipital	+	+	-	-	+
Carapace and appendages (Hay, 1908; McDowell, 1964; Zug, 1971; Ernst and Barbour, 1972; Dobie, 1981)					
10. Carapace with median keel	+	+	-	+	-
11. Carapace with longitudinal rugosities	+	+	-	+	+
12. Posterior marginals (peripherals) usually serrate and/or notched	+	+	-	+	-
13. Vertebral scute I usually not constricted anteriorly	+	-	+	-	+
14. Lateral edges of nuchal bone usually overlapped broadly by first pleural scutes	+	+	-	+	-
15. Anterolateral border of vertebral scute I confined to nuchal bone	+	+	-	+	-
16. Female carapace length < 250 mm	-	-	+	-	+
17. Adult females often larger than twice the size of males	+	-	-	-	-
18. Never more than three phalanges on fifth toe	-	+	+	-	+
Penial morphology (Zug, 1966)					
19. Plica media spade-shaped	-	+	+	+	+
20. Lateral folds of plica media thick and sulcus weakly defined	-	-	+	-	+
Isozymes (Vogt and McCoy, 1980)					
21. Slow (cathodal) electromorphs for lactate dehydrogenase	-	-	+	-	-
22. Medium-fast (anodal) electromorph for plasma protein	-	-	+	+	-
Choanal structure (Parsons, 1960)					
23. Flap (rarely a ridge) along lateral choanal margin	+	+	+	-	-
Endoparasites (Ernst and Ernst, 1980)					
24. High diversity of monogenetic trematodes	-	+	+	+	-
25. High diversity of acanthocephalans	-	+	-	+	-
26. Cestodes present	+	+	-	+	-
Ecology (Cagle and Chaney, 1950; Jackson, 1978a; Bury, 1979)					
27. Feeding habits mostly herbivorous	-	-	-	+	-
28. Often demographically dominant to sympatric emydines	+	+	-	-	-
Frequency of shared character states					
<i>Trachemys</i>	19				
<i>Chrysemys</i>	7	12			
<i>Pseudemys</i>	12	17	9		
Frequency of presumptive synapomorphies					
<i>Trachemys</i>	9				
<i>Chrysemys</i>	1	2			
<i>Pseudemys</i>	9	9	3		
Frequency of presumptive plesiomorphies					
	9	12	18	6	

Note: Matrix summarizes the numbers of character states shared between genera (modified from Seidel and Smith, 1986). Character states indicate what is typical of most, but not necessarily all, species in a genus, and polarities are determined by out-group comparisons with *Deirocheilus*. Abbreviations: +, present; -, absent.

the phylogenetic position of *C. picta* illustrated by Weaver and Rose (1967) and with the conclusion of Ward (1980) that *Chrysemys* preceded the appearance of *Pseudemys* and *Trachemys*.

Obviously there are alternative phylogenetic theories if different taxonomic out-groups are designated, if characters are weighted, or if subsets of characters are used. For example, if only cranial characters are considered, *Trachemys* and *Chrysemys* appear to be closely related (sister taxa) because they are more generalized (Loveridge and Williams, 1957; McDowell, 1964). The cranium of *Pseudemys* is deep, with large orbits and broad, tuberculate, alveolar surfaces for processing vegetation. Pritchard and Trebbau (1984) implied that the specialized feeding

apparatus of *Pseudemys* is derived from a generalized ancestral stock of *Trachemys*. Skulls of adult female *Graptemys* may be even more specialized. In some species the crania are disproportionately large and very wide, with broad alveolar surfaces adapted for molluscivory. McDowell (1964) proposed that *Graptemys* (= *Malaclemys* auct.) is a highly derived genus, perhaps from trachemyne stock. Dobie (1981) proposed that *Graptemys* and *Malaclemys* arose from a pseudemyne-trachemyne stock. Dryden (1985) reported that *Malaclemys* and *Graptemys* form a monophyletic unit based on cranial and postcranial characters, as do *Chrysemys*, *Trachemys*, and *Pseudemys*. If fossil *Graptemys* from the Oligocene reported by Loomis (1904) and Clark (1937) are correctly assigned, the origin (diver-

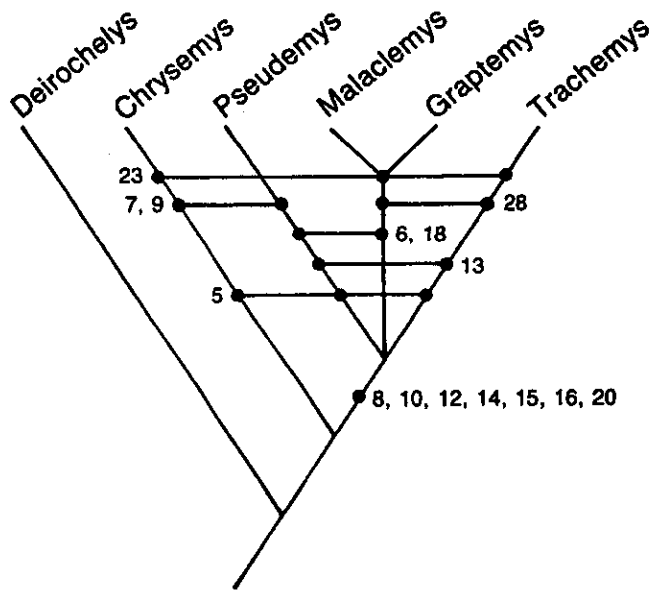


FIGURE 5.1. A theory on the phylogeny of *Trachemys* and related genera of emydines. Numbers (identified in Table 5.1) refer to synapomorphies or possible homoplasies (convergent states), as indicated by lines cutting across lineages.

gence) of this genus would have occurred quite early, probably before the origin of a trachemyne line. Some of the trophic-related character states as well as others (e.g., notched marginal scutes and underlying peripheral bones) in these turtle genera may be homoplasious. However, if all available characters are considered equally (Table 5.1 and Fig. 5.1), the precise relationship of *Trachemys* to *Graptemys* and *Pseudemys* is unclear.

**Trachemys Fossils**

A major limitation of the fossil record in defining the evolutionary history of *Trachemys* has been the absence of skulls of extinct forms. Until recently, only two fossil emydid skulls from North America had been reported (Hay, 1908; Gilmore, 1933), and the identities of these were ambiguous. The conclusions drawn by McDowell (1964) almost entirely from cranial characters have, therefore, been nearly impossible to apply to fossil species whose taxonomy has been based primarily on shell morphology. However, the report by Jackson (1988) of previously unrecognized skull material from the Florida Pliocene has allowed reanalysis of some of these problems. Probably owing to their abundance in the Pleistocene of Florida and Texas and their ease of recognition, fossils of the *T. scripta* group have been known longer and studied more extensively than those of most other emydine turtles (Table 5.2). Hay (1908, 1916) assigned eight extinct species from Florida and Texas Pleistocene deposits to this group: *T. euglypha* (Leidy), *T. sculpta* Hay (1908), *T. jarmani* Hay (1908), *T. petrolei* (Leidy), *T. bisornata* (Cope),

*T. trulla* Hay (1908), *T. delicata* Hay (1916), and *T. nucho-carinata* Hay (1916). Weaver and Robertson (1967) correctly placed six of these names in synonymy with *T. scripta* and incorporated them, as well as other Florida material, in their new combination, *T. s. petrolei*. However, the validity of *T. s. petrolei* and subspecific designation of fossil *Trachemys* in general is questioned by Jackson (1988). The remaining two names represent fossils incorrectly assigned to *Trachemys*: *T. nucho-carinata* = *Terrapene carolina* (Auffenberg, 1958) and *T. jarmani* = *Pseudemys nelsoni* (Jackson, 1978b). The only other *Trachemys* recognized by Hay (1908) was *T. hillii* (Cope), presumably from the Upper Miocene of Kansas (exact stratigraphic position uncertain). This species was expanded by Adler (1968b) to include Galbreath's (1948) *Chrysemys limnodytes*. Two Pliocene (Blancan) fossils, believed to be in the *Trachemys* group, have been described: *T. platymarginata* from Florida (Weaver and Robertson, 1967) and *T. idahoensis* from Idaho (Gilmore, 1933; Zug, 1969; Jackson, 1988). Finally, the oldest stratigraphically fixed fossil turtle that can be definitely assigned to *Trachemys* is *T. inflata*, reported from the Upper Miocene of Florida (Weaver and Robertson, 1967).

Whereas the Pleistocene may provide information on the former distribution of *T. scripta* and development of geographic variation (subspeciation), we must look back to the Pliocene for information on the evolution of *Trachemys*. Weaver and Robertson (1967) correctly assigned *T. platymarginata* to the *T. scripta* complex, but they believed that no skull material of *T. platymarginata* was available. Jackson (1988) recently reported cranial fragments identifiable to this species. The skull of *T. platymarginata* shares many features of *Trachemys* with *T. scripta*, its probable descendant. However, Jackson noted that some morphological features of *T. platymarginata* suggest a more exclusively herbivorous diet than that of the omnivorous *T. scripta*. The discovery of skulls of *T. platymarginata* allows analysis of its relationships to other species. Aside from the report by Rogers (1976) of fossil *Trachemys* shell fragments from Texas, the only other Blancan turtle that

Table 5.2. Geologic timetable of Upper Cenozoic era, with occurrence of fossil and extant forms of *Trachemys*

Epoch	Time, beginning of period to present (millions of years)	Species
Recent	0.01	<i>T. scripta</i> <i>T. decussata</i> <i>T. decorata</i> <i>T. stejnegeri</i> <i>T. terrapen</i>
Pleistocene	2	<i>T. scripta</i> <i>T. stejnegeri</i>
Pliocene	4	<i>T. idahoensis</i>
Upper Miocene	7	<i>T. hillii</i> <i>T. inflata</i>

is potentially a member of the *T. scripta* group is *T. idahoensis* Gilmore (1933) from the Pliocene of Idaho. The holotype of this species is an entire (though partially crushed) shell, a well-preserved skull, and much of the postcranial skeleton. The shape of the nuchal scute underlap (longer than wide) and the absence of bosses on the carapace clearly distinguish the shell from that of *Graptemys*. Previous authors (Gilmore, 1933; Rose and Weaver, 1966) associated *T. idahoensis* with the *P. rubriventris* lineage on the basis of similarly broad alveolar surfaces of jaws. However, broad triturating surfaces have occurred in the *T. scripta* lineage in the past as well, specifically in *T. platymarginata*. Zug (1969) correctly noted that other cranial characteristics, as well as the geographic distribution of *T. idahoensis*, are actually more similar to *T. scripta*'s than to those of the *P. rubriventris* lineage. From such lines of evidence, Jackson (1988) concluded that *T. platymarginata* is synonymous with *T. idahoensis*, which is viewed as a widespread species of Pliocene *Trachemys*.

Clearly *T. idahoensis* could not have been the progenitor of the *Trachemys* line. It appears too late in the fossil record and already shows most of the diagnostic characteristics of northern populations of modern *T. scripta*, such as the doubly toothed peripheral bones. *Trachemys hillii* (Cope), as expanded by Adler (1968b), presumably is known from Upper Miocene strata in Oklahoma and Kansas (Cope's collections were subject to little stratigraphic control). Adler (1968b) noted a number of similarities between *T. hillii* and *T. scripta*, including slight notching of the posterior peripheral bones, and speculated that the fossil may be ancestral or closely related to *T. scripta*. The Upper Miocene *T. inflata* (Weaver and Robertson, 1967), still known only from peninsular Florida, remains ambiguous. Until contradictory material is discovered, the interpretation by Weaver and Robertson (1967) that "it was a specialized or aberrant species characterized by an extreme development of *Trachemys* features and not representative of the main evolutionary sequence leading to recent *T. scripta*" must stand. *Trachemys inflata* may represent a pre-Blancan isolate from *T. idahoensis* stock that, perhaps in response to unique environmental circumstances, developed a massive, highly sculptured shell. It seems reasonable to assume that the progenitor of all trachemyne was a form similar to *T. idahoensis* and *T. hillii*. Whether this ancestor shared a closer relationship with the *Chrysemys*, *Graptemys*, or *Pseudemys* line remains undetermined. Of further interest are the relationships of these modern genera to possibly ancestral turtles assigned to the early Cenozoic North American genus *Echmatemys*.

Little or no information on the origin of *Trachemys* in the West Indies, Mesoamerica, or South America can be obtained from the fossil record. Tertiary remains of terrestrial and freshwater vertebrates are virtually absent from the Caribbean islands. Whether this implies that habitation did not occur until the Quaternary period

(Pregill, 1981a) or simply reflects a lack of conditions suitable for fossilization is subject to controversy (Poinar and Cannatella, 1987). The only report of fossil *Trachemys* in the West Indies is that of a plastral fragment, presumably *T. stejnegeri*, from the late Pleistocene of Puerto Rico (Pregill, 1981b). This supports the belief (Seidel, 1988) that *Trachemys* did not occur in the Greater Antilles until late Pliocene or early Pleistocene. The fossil record of *Trachemys* from Central and South America consists of a single late Pleistocene specimen from Panama (Gazin, 1957). This is congruent with theories, based on reproductive cycles and nesting habits, that *T. scripta* is a recent (perhaps Pleistocene) colonizer of the tropics (Moll and Legler, 1971; Pritchard and Trebbau, 1984).

For information on the evolution of modern *T. scripta* and its northern races, we can look again at fossils from the Pliocene of Florida and Idaho (*T. idahoensis*). Jackson (1988) noted that additional series of fossil *Trachemys* from the Pliocene of Nebraska (J. A. Holman, pers. com.), Kansas (Zug, 1969), and Texas (Rogers, 1976) share many characteristics with *T. idahoensis* and proposed that all Pliocene trachemyne fossils represent a single widespread species. With regard to subtle morphological differences, *T. idahoensis* from Idaho through Texas more closely resembles the northern and western *T. s. elegans*, whereas *T. idahoensis* from Florida shows more similarities to the southeastern *T. s. scripta* (Jackson, 1977). Thus the inclusive chronospecies, *T. idahoensis*, exhibits a pattern of geographic variation not unlike that of modern *T. scripta*.

A look at early Pleistocene fossils of *T. scripta*, presumably descended from and possibly conspecific with *T. idahoensis*, shows a similar pattern of geographic variation. Unfortunately, the diagnoses for modern subspecies of *T. scripta* rely mostly on color pattern, making comparisons with the fossils difficult. However, the osteological characters used by Preston (1966) to distinguish temperate forms have some value, particularly the development of a middorsal keel and relief of the nuchal lamina (though some intrasubspecific variation is evident). It is also difficult to ascertain subspecific differences when the two most widespread North American subspecies, *T. s. scripta* and *T. s. elegans*, have a broad range of intergradation (Davidson, 1971; Conant, 1975). Nonetheless, carapaces of *T. scripta* from Irvingtonian deposits in Florida and Texas appear to differ osteologically in the same way that the subspecies *T. s. scripta* and *T. s. elegans* differ in these regions today (Jackson, 1988). It appears that these two modern subspecies became established no later than early Pleistocene, a process that may have begun in the Pliocene.

### Biochemical Evidence

Electrophoretic analyses of *Trachemys* have been reported by Dessauer et al. (1957), Ramirez and Dessauer (1957),

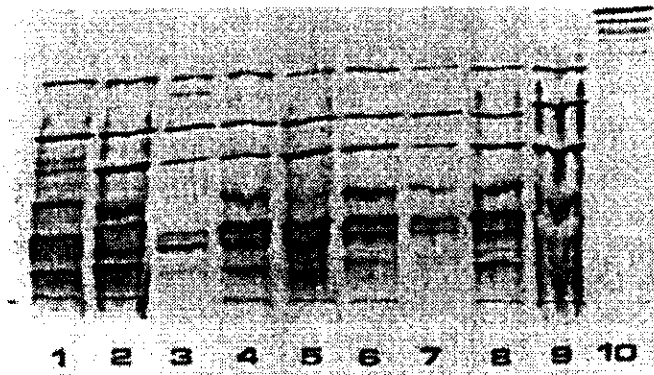


FIGURE 5.2. Electrophoregram of skeletal muscle proteins from *Pseudemys concinna* (1), *Chrysemys picta* (2), *Graptemys geographica* (3), *Trachemys scripta elegans* (4, 5, 6), *T. s. scripta* (7), *T. s. venusta* (8, 9), and protein standard (10) separated by isoelectric focusing.

Zweig and Crenshaw (1957), Kaplan (1960), Bueker (1961), Leone and Wilson (1961), Dozy et al. (1964), Sheeler and Barber (1965), Manwell and Schlesinger (1966), Masat and Dessauer (1968), Vogt and McCoy (1980), Frair (1982), Rose and Dobie (1983), Scribner et al. (1984a, 1986), Sites et al. (1984), Alonso Biosca et al. (1985), and Seidel and Adkins (1987). On cellulose acetate, electrophoretic protein patterns of *Deirochelys*, *Trachemys*, *Chrysemys*, and *Graptemys* were found to be more similar to each other (*Pseudemys* was not examined) than to other emydines (Frair, 1982). Starch gel analysis of polymorphic lactate dehydrogenase and general protein indicated no variation between *Graptemys* and *Trachemys*, whereas unique bands appeared in *Chrysemys* and *Pseudemys* (Vogt and McCoy, 1980). Profiles of protein banding patterns separated by isoelectric focusing also reveal greater similarities among *Pseudemys*, *Chrysemys*, *Graptemys*, and *Trachemys* (Fig. 5.2) than among other members of the Emydinae (Seidel, pers. obs.). Although previous biochemical studies confirm the close relationship of these genera, they add relatively little to the understanding of the phylogeny of *Trachemys*. There is clearly a need for a broad electrophoretic analysis of the Emydinae based on a large number of protein systems and genetic loci.

Some information on biochemical relationships within *Trachemys* is presented by Seidel and Adkins (1987). From isoelectric focusing, these authors described relationships among several subspecies of *T. scripta* and trachemyne species from the West Indies. They detected variation in the occurrence of nine protein bands (electromorphs in liver, heart, kidney, or skeletal muscle), eight of which were identified as apomorphies by out-group comparisons to *P. nelsoni*. No electrophoretic character was found to be synapomorphic among all West Indian species examined, whereas *T. decussata* and *T. terrapen* shared a unique apomorphy with *T. scripta*. This suggests that the insular

forms of *Trachemys* may not be monophyletic and have perhaps originated independently from more than one *T. scripta*-like ancestor. *Trachemys s. callirostris* (from South America) appeared highly divergent from West Indian species as well as from the races of North American *T. scripta* examined. On morphological grounds, Williams (1956) defined *T. s. callirostris* as a very distinct form and recognized two major groups in *T. scripta*: a *scripta* group including the northern races and an *ornata* group of Middle and South America. Weaver and Rose (1967) also separated Middle American forms (which they elevated to *T. ornata*, *T. callirostris*, and *T. gaigeae*) from northern races of *T. scripta*. However, that interpretation has been criticized by Legler (see Chapter 7) and Moll and Legler (1971), who consider all mainland *Trachemys* to be conspecific. Preliminary biochemical observations suggest that both the West Indian species complex and *T. scripta* are paraphyletic or polyphyletic groups. The phylogeny and taxonomy of the former are discussed in detail by Seidel (1988). One could argue that several races of *T. scripta* should be elevated to species rank, but the existence of 16 modern species of trachemyines, as suggested by Ward (1984), seems unlikely. Additional comparisons of *Trachemys* throughout Central and South America (see Chapter 7) are necessary before a thorough taxonomic revision or phylogeny of the *T. scripta* complex can be proposed.

### Concluding Remarks

Our present knowledge of the origin and evolutionary relationships of slider turtles remains incomplete. Available morphological, paleontological, and biochemical information indicates that *Trachemys* arose during or prior to the Miocene from a generalized *Chrysemys-Pseudemys*-like ancestor. Subsequent radiation resulted in several Miocene and Pliocene forms broadly distributed in temperate North America. Multiple dispersals, followed by isolation of *Trachemys* in the neotropics during the early Pleistocene, have resulted in divergence of Central and South American *T. scripta* as well as several species in the West Indies.

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