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A Systematic Review of the Turtle Family Emydidae

MICHAEL E. SEIDEL[1] & CARL H. ERNST[2]

[1] 4430 Richmond Park Drive East, Jacksonville, FL, 32224, USA and Department of Biological Sciences, Marshall University, Huntington, WV, USA; seidel@marshall.edu — [2] Division of Amphibians and Reptiles, mrc 162, Smithsonian Institution, P.O. Box 37012, Washington, D.C. 200137012, USA; chernst@frontiernet.net

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Abstract

Family Emydidae is a large and diverse group of turtles comprised of 50–60 extant species. After a long history of taxonomic revision, the family is presently recognized as a monophyletic group defined by unique skeletal and molecular character states. Emydids are believed to have originated in the Eocene, 42–56 million years ago. They are mostly native to North America, but one genus, *Trachemys*, occurs in South America and a second, *Emys*, ranges over parts of Europe, western Asia, and northern Africa. Some of the species are threatened and their future survival depends in part on understanding their systematic relationships and habitat requirements. The present treatise provides a synthesis and update of studies which define diversity and classification of the Emydidae. A review of family nomenclature indicates that RAFINESQUE, 1815 should be credited for the family name Emydidae. Early taxonomic studies of these turtles were based primarily on morphological data, including some fossil material. More recent work has relied heavily on phylogenetic analyses using molecular data, mostly DNA. The bulk of current evidence supports two major lineages: the subfamily Emydinae which has mostly semi-terrestrial forms (genera *Actinemys*, *Clemmys*, *Emydoidea*, *Emys*, *Glyptemys*, *Terrapene*) and the more aquatic subfamily Deirochelyinae (genera *Chrysemys*, *Deirochelys*, *Graptemys*, *Malaclemys*, *Pseudemys*, *Trachemys*). Within subfamilies, some generic relationships have become well defined, supporting sister group relationships (e.g. *Emydoidea* + *Emys*, *Malaclemys* + *Graptemys*, and *Trachemys* + *Graptemys*/*Malaclemys*). There is also strong evidence that *Glyptemys* and *Deirochelys* are outgroups (early sister lineages) to all of the other taxa in their respective subfamilies. The phylogenetic position of other genera (e.g. *Clemmys*, *Chrysemys*, *Actinemys*) remains enigmatic or controversial. Similarly, many species relationships have been clarified within recent decades, but several remain poorly resolved such as those belonging to *Pseudemys*, *Trachemys*, and *Terrapene*. Overall, our systematic knowledge of emydid turtles has rapidly progressed and ongoing studies are targeting broader and more comprehensive sampling of populations.

Key words

Emydidae, Turtles, Systematics, Phylogeny, Taxonomy, *Actinemys*, *Chrysemys*, *Clemmys*, *Deirochelys*, *Emydoidea*, *Emys*, *Glyptemys*, *Graptemys*, *Malaclemys*, *Pseudemys*, *Terrapene*, *Trachemys*.

Contents

Prologue 2
Introduction 3
Early Taxonomic Recognition and Family Assignments 3
Nomenclatural History of the Family Emydidae 8
Birth of a Modern Restricted Family Emydidae RAFINESQUE, 1815 12
The Relationship Between *Deirochelys* and *Emydoidea* 18
Two Major Phyletic Lines of Emydids 20

ISSN 1864-5755

Subfamily Emydinae Rafinesque, 1815. The Semiterrestrial Emydids 20
- *Emys* Duméril, 1805 30
- *Actinemys* Agassiz, 1857 36
- *Clemmys* Ritgen, 1828 38
- *Emydoidea* Gray, 1870 40
- *Glyptemys* Agassiz, 1857 41
- *Terrapene* Merrem, 1820 45

Subfamily Deirochelyinae Agassiz, 1857. The Aquatic Emydids 49
- *Deirochelys* Agassiz, 1857 54
- *Chrysemys* Gray, 1844 54
- *Graptemys* Agassiz, 1857 57
- *Malaclemys* Gray, 1844 67
- *Pseudemys* Gray, 1856a 68
- *Trachemys* Agassiz, 1857 77

Epilogue 91

Acknowledgments 92

References 93

Table 1. Extant Taxa Assigned to the Family Emydidae 117

Glossary of Currently Used Scientific Names for Living Turtles in the Family Emydidae 120

Prologue

Defining diversity and developing a reliable classification system for organisms is more important today than ever before. Natural habitats throughout the World are threatened by expanding human populations and industrialization. Stability of our ecosystems depends on maintaining species diversity, which can only be measured by a reliable taxonomy. As a group of vertebrate animals, turtles (order Testudines) have been especially impacted (Turtle Taxonomy Working Group, 2014). Turtle populations are declining throughout the World, primarily due to habitat loss and human exploitation. Many turtle species are extremely vulnerable due to their restricted geographic distribution, small population size, long generation time, and low fecundity. Understanding systematic relationships and developing a stable taxonomy for turtles is crucial to promoting their protection and survival.

In modern times, the discipline of systematics entails the study of diversity and relationships among organisms, reflecting the results of evolution. Taxonomy is the theory and practice of describing, naming, and ordering groups of organisms (taxa). It is often viewed as the product of systematics. The collective discipline of taxonomy and systematics has advanced tremendously over the last several decades. This is primarily due to the advent of phylogenetic or cladistic methodology and the development of molecular (DNA) technology. Genetic data bases of nucleotide sequencing are expanding at a rapid pace, providing new insight to relationships among turtle species (Shaffer et al., 2007; Thomson & Shaffer, 2010; Wiens et al., 2010; Fritz et al., 2012; Parham et al., 2015; Spinks et al., 2016). Nevertheless, morphology continues to be important in classifying organisms, considering that the vast majority of taxa are diagnosed by their phenotypic structures. Systematists now rely heavily on phylogenetic methods, and certainly turtle taxonomists are no exception. It is clear that defining ancestral relationships is critical to the development of a natural classification system.

The family Emydidae is the largest group of turtles in the New World. It has a rich history of classification over the last two centuries, including extensive revision of species and genera. Thus it provides a good example of the challenges turtle systematists face. As authors (M.E.S. and C.H.E.), we have research experience with historical and current taxonomic problems of this group. In reviewing the systematics of Emydidae, we provide an account of how approaches to classification have developed over the years, and an update on the current taxonomic status of these turtles. Thus, our goal is to provide a historical perspective and summary for future investigators and students of emydid classification. We have not included formal synonymies, detailed species descriptions, or geographic distributions, thus avoiding duplication of the emydid accounts published in the Catalogue of American Amphibians and Reptiles (CAAR) and Conservation Biology of Freshwater Turtles and Tortoises (CBFTT). For that information, we refer to those accounts and to published accounts of the Old World genus *Emys* compiled by Uwe Fritz, Director of the Senckenberg Natural History Collections, Dresden, Germany. Current taxonomic literature up to 1 June, 2016 is included.

Introduction

Emydid turtles are small to moderately large aquatic or semi-aquatic species with a well-developed bony shell and prominent dorsal rib heads. The carapace has a cervical scute, five vertebrals, four pleurals, and twelve pairs of marginals. The terminal posterior pair of marginal scutes do not extend forward to contact the suprapygal bone. A broad bridge usually unites the carapace and plastron. The relatively large plastron is covered with six pairs of ventral scutes: gular, humeral, pectoral, abdominal, femoral, anal. The abdominal scutes are not enlarged; and intergular and inframarginal scutes are not usually present except in the genus *Chrysemys*. Mesoplastral bones are also absent and there is no raised bony ridge on the visceral surface of the entoplastron. The relatively small bony skull is well developed except for the roof which is posteriorly emarginated in the temporal region. This may also involve reduction of the zygomatic arch by absence of the quadratojugal or reduction of the jugal bone (e.g. genus *Terrapene*). The basioccipital bone of the cranium does not have prominent lateral projections and there is no contact between the pterygoid bone and basioccipital. On the lower jaw, the angular bone usually contacts Meckel's cartilage. The Karyotype consists of 50 chromosomes.

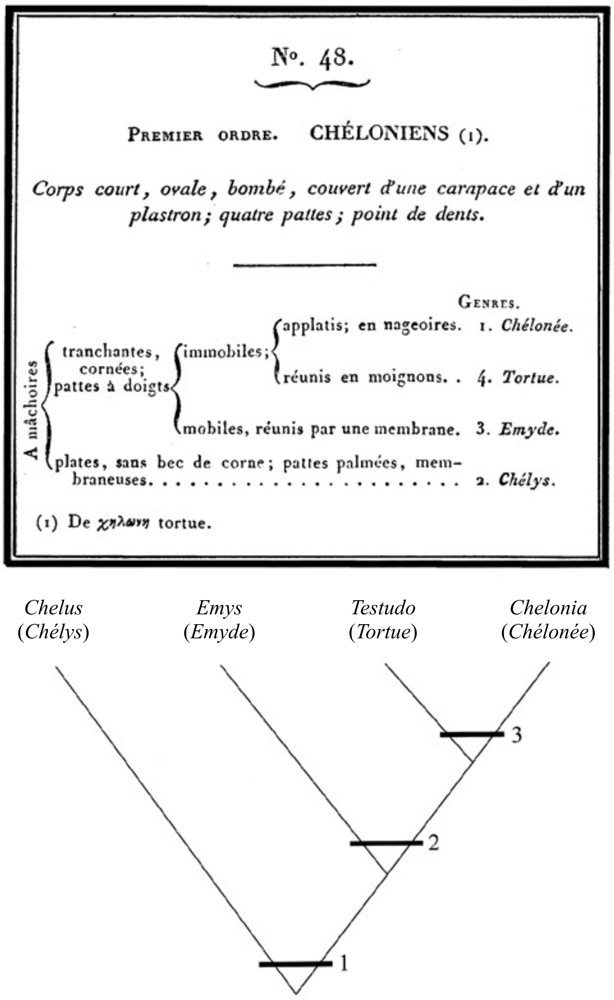
Our current concept of the turtle family Emydidae (order Testudines, suborder Cryptodira) now appears to be relatively stable. It is a distinct taxonomic unit of approximately 52 extant species (Table 1) which are here classified into 12 genera: *Actinemys*, *Chrysemys*, *Clemmys*, *Deirochelys*, *Emydoidea*, *Emys*, *Glyptemys*, *Graptemys*, *Malaclemys*, *Pseudemys*, *Terrapene*, and *Trachemys.* All of them are restricted to North America except *Trachemys* which ranges into South America and the West Indies, and *Emys* which occurs in southern Europe, northern Africa, and western Asia. Relationships among the 12 genera in Emydidae remain somewhat controversial, as does their species composition. The present treatise defines the earliest formal recognition of emydids and traces their taxonomic history through multiple stages of revision. Classification of these turtles has been influenced by a wide variety of systematic techniques and philosophies which are discussed and evaluated. Specific attention is aimed at the rationale workers have used, documenting their methods, and detailing the evidence upon which they based their decisions.

Early taxonomics recognition and family assignment

During the 18th and 19th centuries, pioneers of herpetology were busy practicing alpha taxonomy: naming new species and classifying them according to the Linnaean system. Often they did not document their criteria for assignments to family and genus. Formal recognition of turtles (four species) dates back to the classic work "Systema Naturae" (1735) by Carolus Linnaeus, a Swedish naturalist who applied the Aristotelian system of logic to classification. He believed that nature, including all plants and animals, was the product of divine creation. In his monumental classification of the world's living things (tenth edition, 1758: 197), he recognized 11 turtle species, all of which were placed in the genus *Testudo*. This composite genus continued to be used by many subsequent authors (Walbaum, 1782: 95; Schneider, 1783: 348, 1792: 264; Lacépède, 1788: 135; Bonnaterre, 1789: 25; Gmelin, 1789: 1042; Schoepff, 1792: 25, 1793: 64, 1801: 132; Daudin, 1801: 144 [1802]; Latreille *in* Sonnini & Latreille, 1802: 124; Shaw, 1802: 43; Link, 1807: 52; Le Conte, 1830: 112) as a large taxon representing turtles we now classify in a broad diversity of families.

Description of type species for the modern genera of emydid turtles began with Linnaeus (1758: 198) who described the Old World *Testudo* (currently = *Emys*) *orbicularis* and the New World *Testudo* (now *Terrapene*) *carolina*. Subsequently, Schneider (1783: 348 and 1792: 264) described *Testudo* (now *Chrysemys*) *picta* and *Testudo* (now *Clemmys*) *guttata*, respectively. In 1788: 135, Lacépède described *Testudo flava* (= *Emydoidea blandingii*), which may have been based on a mixed series of *Emys orbicularis* and *Emydoidea blandingii.* Lacépède's (1788) *Testudo flava* and Shaw's [in Shaw & Nodder 1793: 44] *Testudo meleagris* have been suppressed by ICZN 1963 for the purpose of the Law of Priority but not for those of the Law of Homonymy, and, as the work of Bonnaterre (1789) has been overlooked, has left us with Holbrook's (1838: 35) *Cistudo blandingii* [conserved in ICZN 1963] as the nominotypical (type species) of the genus *Emydoidea* Gray 1870: 19 (by monotypy; see Loveridge & Williams 1957: 202 and McCoy 1973: 2 for comments). Both *T. flava* and *T. meleagris* are now considered senior synonyms of *Emydoidea blandingii.* Schoepff described *Testudo* (now *Malaclemys*) *terrapin* in 1793: 64, and *Testudo* (now *Glyptemys*) *muhlenbergii* in 1801: 132. Latreille (1802: 124) (*in* Sonnini & Latreille, 1802) described *Testudo* (now *Deirochelys*) *reticularia*, Le Sueur (1817: 86) described *Testudo* (now *Graptemys*) *geographica*, and Le Conte (1830: 106) described *Testudo* (now *Pseudemys*) *concinna*. The only presently recognized type species of emydid which was not associated with Linnaeus's genus *Testudo* is *Actinemys marmorata*. This turtle was originally described by Baird & Girard (1852: 177) as *Emys marmorata*.

Following Linnaeus, Duméril (1805) published what appears to be the oldest hierarchical classification of turtles [the 1805 date of the original French publication is often confused with that of the 1806 German edition by Froriep; Gregory, 2010]. Gaffney (1984) transferred this to a cladogram (Fig. 1), with *Emys* and *Testudo* represented as composite genera. August Friedrich Schweigger (1812 and 1814) is often credited with publishing the



N°. 48.

Premier ordre. CHÉLONIENS (1).

Corps court, ovale, bombé, couvert d'une carapace et d'un plastron; quatre pattes; point de dents.

Genres.

A mâchoires { tranchantes, cornées; pattes à doigts { immobiles; { applatis; en nageoires. 1. *Chélonée.*
réunis en moignons. 4. *Tortue.*
mobiles, réunis par une membrane. 3. *Emyde.*
plates, sans bec de corne; pattes palmées, membraneuses. . . . . 2. *Chélys.*

(1) De χηλώνη tortue.

Fig. 1. (Upper) A classification of turtles by Duméril (1805), which appears to be the oldest hierarchical classification of the group. (Lower) A cladogram representing the relationships expressed in Duméril's classification (from Gaffney 1984, fig.1).

first truly scientific account of turtles (Adler 2007: 140). Schweigger studied at the Muséum d'Histoire Naturelle in Paris (now MNHN), and thus had the largest collection of turtles at that time available to him. He partitioned Linnaeus's composite genus *Testudo* into six genera, one of which (*Emys*) included the emydids *Emys pulchella* (p. 303, not Schoepff 1801: 113, a homonym of *Testudo pulchella* (= *Emys orbicularis*), but sensu Schweigger 1814: 34 (= *Glyptemys insculpta*); *Emys clausa* (p. 315), *Emys schneideri* (p. 317), and *Emys virgulata* (p. 316), all now *Terrapene carolina*; *Emys centrata* (p. 281, now *Malaclemys terrapin centrata*); and *Emys lutaria* (p. 35) and *Emys europaea* (p. 36), both now *Emys orbicularis*; as well as other North American emydids. Based mostly on external morphological characters, Schweigger's genus *Emys* also included Old World geoemydids (aquatic and semi-terrestrial turtles) as well as New World kinosternids (Mud and Musk Turtles). In an effort to define natural groups, he divided *Emys* into two subgroups, those having a movable plastron and those with a fixed plastron. It is evident now that a hinged plastral condition in turtles has evolved multiple times, independently in different families, which is clearly an example of homoplasy or parallel evolution (see Bramble, 1974 and Hutchison & Bramble, 1981). In 1826, Fitzinger presented the oldest branching diagram (illustrated in Gaffney 1984: 285) which showed relationships among genera of turtles (Fig. 2). However, Fitzinger's (1826) genera *Emys* and *Terrapene* included some species which are not currently recognized as emydids.

In 1830 John Le Conte, co-founder of the New York Academy of Sciences, rejected contemporary revisions of turtle taxonomy, including those of Schweigger (1812, 1814) and Gray (1825), and reverted back to a system similar to that of Linnaeus (1758). In his "Description of the Species of North American Tortoises" he returned all emydids to the composite genus *Testudo*, including all turtles except trionychids (Softshells). Referring to the contemporary revisions of turtle classification, Le Conte (1830: 92) stated "The monstrous absurdity which runs through these is as shocking to all natural method, as it is insulting to common sense." Richard Harlan, a contemporary of LeConte, did not follow Gray's (1825) arrangement (Emydidae; including *Emys*, *Terraphene* [sic] = *Cistula* [sic], *Kinosternom* [sic], and *Sternotherus*); but included in his own 1827 and 1835 listings *Testudo* and *Cistula* in his first family, Land Tortoises, lacking a familial scientific name, and *Emys*, *Kinosternon* and *Sternothaerus* (= *Sternotherus*) in a second family, Fresh Water Tortoises, or Emydidae, and only mentioned Gray (1831a) in his 1835 synopsis of North American turtle genera and species.

The next major systematic arrangement of turtles, based on the large collection in Paris (MNHN), was compiled by Duméril & Bibron (1835). These authors went beyond comparisons of external morphology by including descriptions of skeletal material and soft anatomy based on dissection. They are sometimes credited as the first to recognize "natural" taxonomic groups of turtles (above the genus level) using analytical methods (Gaffney, 1984; Adler, 2007). Following Wagler's 1830 discovery, they separated turtles into two major groups (pleurodires and cryptodires) based on cervical biomechanics. Within the cryptodires, they recognized four families by vernacular names which referred to their general habitats. Emydids were placed in "Elodites ou Tortues Paludines" (freshwater and land turtles). The family was very large and included all known species (at that time) of cryptodires except Softshell Turtles (trionychids), Sea Turtles (cheloniids, dermochelyds), and Tortoises (testudinids).

In 1838, the study of New World turtles came of age with the publication of John Edwards Holbrook's "North American Herpetology." Holbrook (1838) included emydids in two families: Chersites (p. 23), which is mostly terrestrial, and Elodites (p. 43), which is mostly aquatic. Chersites contained the genus *Cistuda* (now*Terrapene* and *Emydoidea*) as well as the Gopher Tortoises in genus *Testudo* (now *Gopherus*). He characterized the

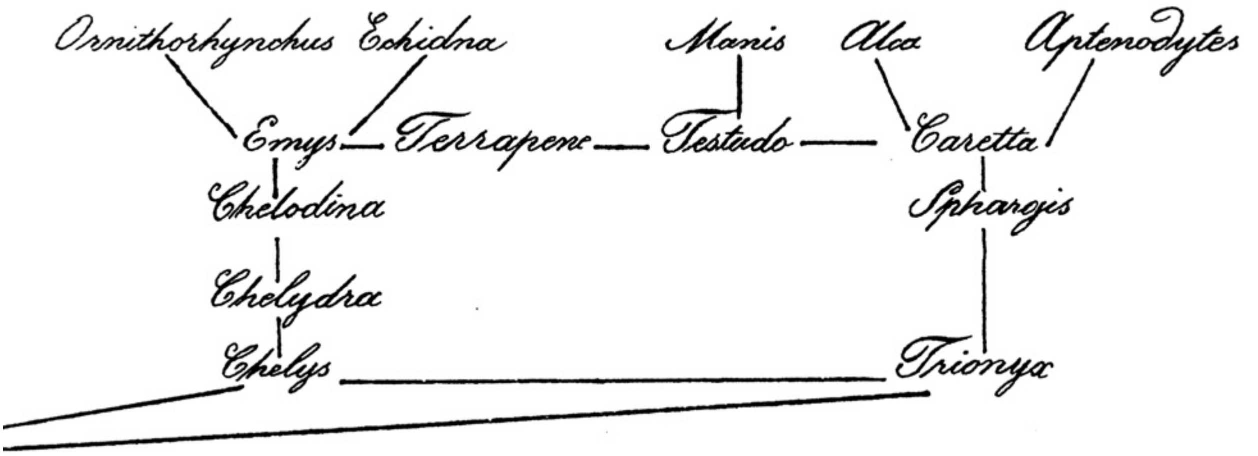


Fig. 2. The oldest branching diagram (Fitzinger 1826) relating a series of turtle genera.

genus *Cistuda* as: "Shell gibbous, strong; marginal plates twenty-five; sternum oval, covered with twelve plates, bivalve, both valves movable on the same axis, and joined to each other and to the shell by ligamento-elastic tissue; anterior extremities with five, posterior with four nails." Holbrook's family Elodites was comprised of Mud (*Kinosternon*), Musk (*Sternothaerus*), and Snapping turtles (*Chelonura*, = *Chelydra*), as well as the large genus *Emys* which included all of the other 17 species of emydids described to that date. This was a departure from Schweigger (1812) and Harlan (1835) who included the Mud and Musk Turtles in *Emys*. Holbrook characterized the genus *Emys* as having a "Shell depressed, solid; sternum broad, solid, immovably joined to the shell, and covered with twelve plates…" Thus Holbrook's arrangement avoided, at least in part, the unnatural grouping of all turtles with a hinged plastron. On the other hand, he assigned "solid-plastron" taxa to a genus whose type species has a modestly kinetic plastron.

During the next 50 years, collections in the British Museum of Natural History (BMNH) were growing rapidly and came to house the World's most representative assemblage of turtles. British scientist John Gray, its founder and curator (Adler 2007: 140), published a large number of papers (1825–1873) dealing with taxonomic revisions of turtles, including several checklists in 1825, 1831a, 1831b, 1844, 1856b [although this publication is dated "1855" on its cover page, Webb, 1995, has shown that it was actually published in 1856], 1870, and 1873. Also during this time, Louis Agassiz established the Museum of Comparative Zoology (MCZ) at Harvard University, Cambridge, Massachusetts. He was a Swiss-born American naturalist and compiled a substantial number of turtle specimens. Agassiz believed in "special creation," and opposed Darwin's theory on origin of species by natural selection. In his classic work "Contributions to the Natural History of The United States of America" (1857), Agassiz placed emydid turtles in the family Emydoidae which included "… over 60 well known species." This group exclusively contained emydids and geoemydids (batagurines), but his descriptions and classifications dealt primarily with the New World forms.

Agassiz (1857: 351, 430) described the family Emydoidae in detail from skeletal anatomy (vertebrae, ribs, appendages, and skull) and external morphology (scutes, shell, head, and limbs). Based on variation among species, he suggested the Emydoidae could be partitioned into five subfamilies described as follows:

1. Nectemydoidae, pp. 355, 431 (= *Chrysemys*, *Graptemys*, *Malaclemys*, *Pseudemys*, *Trachemys*). "The body is rather flat. The bridge connecting the plastron and carapace is wide, but flat. The hind legs are stouter than the fore legs, and provided with a broad web, extending beyond the articulation of the nail joint. The representatives of this group are the largest and the most aquatic of the whole family."
2. Deirochelyoidae, pp. 355, 441 (= *Deirochelys*). "The body is higher and more elongated; the bridge connecting the plastron and carapace is not only wide, but at the same time high. The plastron itself is narrower than in the preceding tribe. The neck is remarkably long and snake-like, and recalls that of the Chelodinae among the Pleuroderes. The feet are webbed."
3. Evemydoidae, pp. 356, 441 (*Emys*, *Emydoidea*). "Differ chiefly from the preceding by the great width and flatness of the plastron, the narrowness of the bridge which unites the plastron and carapace, and the movability of the plastron, at its junction with the carapace, and upon itself, owing to a transverse articulation across its middle. The feet are webbed."
4. Clemmydoidae, pp. 356, 442 (*Actinemys*, *Clemmys*, *Glyptemys*). "Their chief peculiarity consists in their more arched though elongated form, and the more compact structure of their feet, the front and hind pairs of which are more nearly equal, and the toes united by a smaller web. They are less aquatic, and generally smaller than the preceding."
5. Cistudinina, pp. 356, 444 (*Terrapene*). "The body is remarkably short and high, slightly oblong, and almost round. The plastron which is movable upon itself and upon the carapace, as in the Evemydoidae, is also con-

nected with the carapace by a narrow bridge; but the feet are very different, as in the Testudinina [= Testudinidae], being nearly free of web. Their habits are completely terrestrial." Surprisingly these subfamilies, with the exception of Clemmydoidae (due to recent revision of the genus *Clemmys*) have been recognized as monophyletic clades of species or subspecies defined by modern phylogenetic methods (Iverson et al. 2007). This is especially ironic considering Agassiz's opposition to evolutionary theory.

In 1862: 107 a Russian herpetologist, Alexander Strauch, placed 62 species of emydids and geoemydids in a large composite genus *Clemmys*. The only emydids which he did not include in *Clemmys* were *Terrapene carinata* (= *carolina*), *Emys blandingii*, and *Emys lutaria* (= *orbicularis*). Gray (1863) disregarded Strauch's arrangement and argued vigorously with Agassiz regarding species identification in the family Emydidae (= in part Emydoidae sensu Agassiz). Curiously, however, Gray (1863: 178) used the adjective "Emydoids" and followed generic assignments similar to Agassiz: *Callichelys* (= *Trachemys*, in part), *Chrysemys*, *Deirochelys*, *Emys*, *Graptemys*, *Malaclemmys* (= *Malaclemys*), *Pseudemys*, and *Trachemys*. Although the generic name *Clemmys* is mentioned, Gray, following his 1855b: 18–19 designations, assigned the Spotted Turtle (*Clemmys guttata*), the Bog Turtle (*Glyptemys muhlenbergii*), and the Wood Turtle (*Glyptemys insculpta*) to the composite species *Glyptemys pulchella.* In 1870: 27 Gray assigned species *marmorata*, *guttata* and *muhlenbergii* to the genus *Geoclemmys.* In that same paper (p. 16) he placed emydids in the suborder Steganopodes (which also included geoemydids, chelydrids, *Platysternon*, and *Dermatemys*) separate from the suborder Tylopoda which included testudinid land tortoises. Gray partitioned Steganopodes into eight families, four of which were comprised of a combination of emydids and geoemydids: Cistudinidae (e.g. *Cistuda carolina*, *Emydoidea blandingii*, and *Emys orbicularis* [as *Lutremys europaea*]), Malaclemmydae (e.g. *Malaclemys* and *Graptemys*), Pseudemydae (e.g. *Pseudemys* and *Trachemys*), and Emydidae (e.g. *Chrysemys*, *Deirochelys*, *Emys*, *Geoclemmys* [= *Clemmys*], *Actinemys*, and *Glyptemys*).

In his 1877 checklist of Nearctic Batrachia and Reptilia, Edward Drinker Cope mostly followed Agassiz (1857) in his interpretation of the New World genera belonging to the family Emydidae (see McCoy 1973: 2): *Chrysemys*, *Cistuda* (= *Terrapene*), *Emys* (*E. meleagris*, = *Emydoidea blandingii*; the first appearance of *Testudo meleagris*), *Malacoclemmys* (= *Graptemys* and *Malaclemys*), and *Pseudemys* (including *Trachemys scripta*); but proposed the new genus *Chelopus* (p. 53) for *Actinemys*, *Clemmys*, and *Glyptemys*. This generic arrangement was adopted by Yarrow (1882) in the first catalog of turtle specimens in the Smithsonian Institution.

Following John Gray at the BMNH, George A. Boulenger published his monumental "Catalogue of the Chelonians, Rhynchocephalians, and Crocodiles in the British Museum (Natural History)" in 1889. This work is often regarded as the first modern summary of living turtles (Adler 2007: 141). Boulenger (1889: 48) dispensed with the Emydidae (sensu Gray 1825, 1855b) and redefined the Testudinidae of Gray (1825: 210) as a composite group including the land tortoises *Homopus*, *Kinixys*, *Pyxis*, and *Testudo*; as well as the then recognized aquatic or semiterrestrial Old World genera *Batagur*, *Bellia*, *Callagur*, *Chaibassia*, *Cyclemys*, *Damonia*, *Emys*, *Geomyda*, *Hardella*, *Kachuga*, *Morenia*, and *Ocadia*; and the New World genera *Chrysemys* (including *Deirochelys*, *Pseudemys*, and *Trachemys*), *Cistuda* (= *Terrapene*), *Clemmys* (including *Actinemys*, *Glyptemys*, and most of the Old World genus *Mauremys*), *Emys* (= *Emydoidea*), *Malacoclemmys* (*Graptemys* and *Malaclemys*), and *Nicoria* (the geoemydid Neotropical *Rhinoclemmys* and part of the Old World *Mauremys*). He stated (footnote p. 48) that "A recent writer [presumably Gray] suggests to separate the Land-Tortoises from the Emyds [sic] on the ground of the presence in the former and the absence in the latter of dermal ossifications on the limbs. But the absence of such ossifications in the gigantic Land-Tortoises destroys the value of that character." Boulenger (1889: 48) defined Testudinidae with the following morphological characters: "Nuchal plate without well-developed costiform processes. Plastral bones nine. Shell covered with epidermal shields. Caudal vertebrae procoelous. Neck completely retractile within the shell. Lateral temporal arch usually present; no parieto-squamosal arch. Digits short or moderately elongate; phalanges with condyles; claws four or five."

In 1908b, Oliver P. Hay, a noted American herpetologist and paleontologist, published his landmark work on "The Fossil Turtles of North America." His application of the family Emydidae included all New World and some Old World forms of geoemydids (= batagurids) as well as the broad fossil genus *Echmatemys*. Not surprisingly, his description of Emydidae, pp. 284–285 was based almost entirely on skeletal characters. Other than turtles now in the Geoemydidae, he recognized the following extant genera of emydids: *Chrysemys*, *Clemmys*, *Deirochelys*, *Emys*, *Graptemys*, *Malaclemys*, *Pseudemys*, *Terrapene*, and *Trachemys*. In *Emys* he included *Emys orbicularis* and *Emydoidea blandingii* as congeners. Based on plastral hinging, Hay stated *Terrapene* was derived from an *Emys* ancestor. Based on skull similarities, he stated that *Graptemys* was derived from *Malaclemys*. Hay (1908b) further suggested that the genus *Clemmys* could be ancestral to all of the other emydids. He presented the most explicit phylogenetic diagram to that time and illustrated a "sister group" relationship between the Emydidae and tortoises, Testudinidae (Fig. 3).

In 1909, Friedrich Siebenrock, a naturalist at the Hofmuseum in Wien (Vienna, Austria), in his "Synopsis der rezenten Schildkroten, mit Berücksichtigun der historischer Zeit ausgestorbenen Arten" considered the Emydinae a subfamily of the family Testudinidae (p. 429). He included in Emydinae not only emydid genera and species, but turtles now relegated to the family Geoemydidae. His genus *Geoemyda* included *Cuora*, *Cyclemys*, *Geoemyda*, *Heosemys*, *Mauremys*, *Melanochelys*, *Notochelys*, and

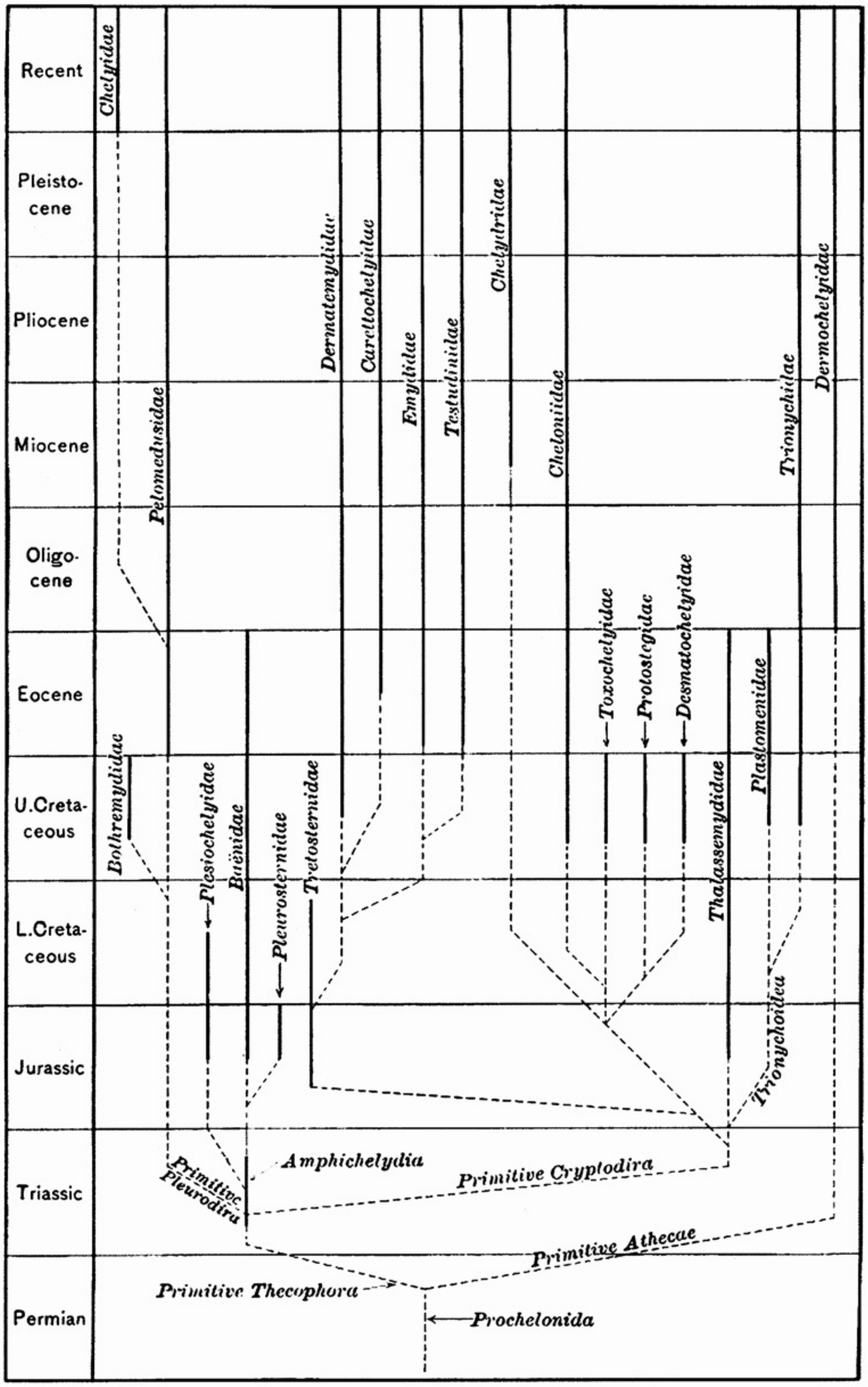


Fig. 3. Turtle family relationships as illustrated by Hay (1908b: 27).

Rhinoclemmys. Other Old World genera included in his Emydinae were *Batagur*, *Callagur*, *Kachuga*, *Morenia*, *Orlitia*. He placed several taxa of the modern genera *Pseudemys* (*alabamensis*, *concinna*, *floridana*, *rubriventris*, *texana*) and *Trachemys* (*callirostris*, *dorbigni*, *grayi*, *nebulosa*, *ornata*, *scripta*, *terrapen*, *venusta*) in the genus *Chrysemys*; current species *Graptemys pseudogeographica*, in the genus *Malaclemys*; the geoemydid genus *Mauremys*, along with the American species *Clemmys guttata*, *Glyptemys insculpta*, *Actinemys marmorata*, and *G. muhlenbergii* in the genus *Clemmys*; *Emydoidea blandingii* in the Old World genus *Emys* along with *E. orbicularis*; recognized the American Box Turtle genus *Terrapene*; and considered *Deirochelys* monotypic.

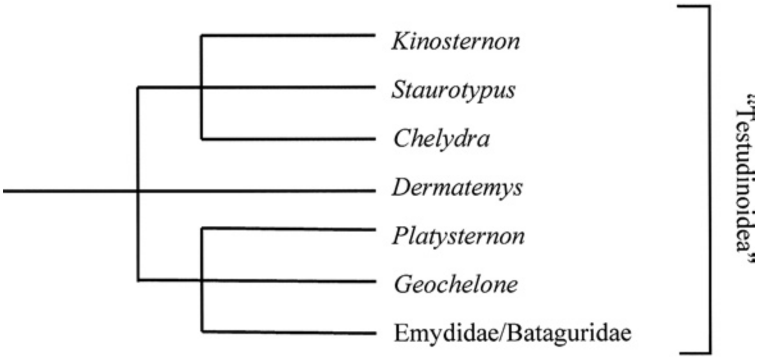


Fig. 4. Hypothesis of chelonian relationships based on the classification of Williams (1950). Modified from Shaffer et al. (1997, fig. 1).

Although Siebenrock's rendition of the subfamily Emydinae represented the prevailing thoughts of the day, its mixture of geoemydids and emydids retarded understanding of the true composition of Emydinae.

For the next 30 years there was relatively little activity in chelonian taxonomy, partly due to World War I. In their influential checklists of North American amphibians and reptiles, Stejneger & Barbour (1917, 1923, 1933, 1939, 1943) used the composite family Testudinidae (sensu Boulenger 1889: 48). Nevertheless, they recognized the same genera as Hay (1908b) except for placement of *Trachemys* in the synonymy of *Pseudemys*. Clifford Pope, in his book "Turtles of the United States and Canada" (1939) recognized a restricted group of aquatic turtles in his family Emydidae. Pope designated Chapter VI (p. 146) to a group formed of *Malaclemys*, *Graptemys*, *Chrysemys*, *Pseudemys*, *and Deirochelys*, commenting that they "… do not comprise a complete systematic group, … [but it] … is clear that the grouping is not entirely one of convenience." Archie Carr, professor and curator of herpetological collections at the University of Florida, used the family Emydidae in his acclaimed Handbook of Turtles (1952). Schmidt in his 1953 checklist applied the families Emydidae and Testudinidae for the extant North American genera listed by Hay (1908b: 284, 285) and the tortoises, respectively; and also included the modern recognized species of *Trachemys* in the genus *Pseudemys.*

Early in his career, Ernest E. Williams (former curator of amphibians and reptiles at the MCZ) studied the cervical anatomy of turtles. A hypothesis of relationships based on his data (Williams 1950) was presented by Shaffer et al. 1997 (Fig. 4). It indicates a tritomous clade of Platysternidae, *Geochelone* (Testudinidae), and Emydidae/Bataguridae. In a subsequent work Loveridge & Williams (1957) used the composite family Testudinidae (p. 181) but recognized three subfamilies: Emydinae (p. 183, the aquatic and semiterrestrial forms), Testudininae (p. 209, the land tortoises), and Platysterninae (p. 182, the monotypic Asian genus *Platysternon*). The Emydinae was divided into two lineages based on carapace morphology (p. 185): a tricarinate group (*Emys*, *Terrapene*, *Clemmys*, and Asian batagurines) and a unicarinate group (*Emydoidea*, *Deirochelys*, *Pseudemys*, *Malaclemys*, *Graptemys*, and *Chrysemys*) (Fig. 5). Wermuth & Mertens (1961, 1977) recognized the family Emydidae which included only the emydines and "batagurines." During the mid 20th century, application of Testudinidae (sensu lato) or Emydidae became very inconsistent. Mertens (1939), Bourret (1941), Carr (1952), Mertens & Wermuth (1955), Pritchard (1967), Parsons (1968), Bellairs (1969), Moll & Legler (1971), Ernst & Barbour (1972, 1989), Gaffney (1975), Mlynarski (1976), Jackson (1978a, 1978b), and Ernst & Lovich (2009) used Emydidae for the aquatic and semi-terrestrial forms. Cahn (1937), Pope (1939), Williams (1950), Romer (1956), Loveridge & Williams (1957), McDowell (1964), Stebbins (1966), Zug (1966, 1971), Zangerl (1969), Goin & Goin (1962, 1971), Porter (1972), McCoy (1973), Dowling (1974), Frair (1977), Dowling & Duellman (1978), and DeSmet (1978) used Testudinidae (sensu lato).

Nomenclatural history of the familiy Emydidae

Authorship of family "Emydidae" has remained uncertain for nearly two centuries. The name has most often been attributed to either Rafinesque (1815: 75, "Analyse de la nature …") or Gray (1825: 210, "A synopsis of the genera of reptiles and Amphibia …"), but five other scientists have dealt with the freshwater family-group of emydids at either the genus or subfamily level and could be considered possible authors of the name. Several of the proposed authors of Emydidae have serious problems associated with their publications, making determination of which is the valid author very confusing.

The earliest treatment was by Brongniart (1805: 27) who used the name *Emydes* as a genus for the European Pond Turtles, now recognized as a senior synonym of the genus *Emys* Duméril (1805: 76). The spelling of the generic name *Emys* was not used by Brongniart, and he included in his term "Emyde (*emydes*)" turtles of families other than the now recognized hard-shelled cryptodiran Emydidae: i.e., the pleurodiran family Chelidae

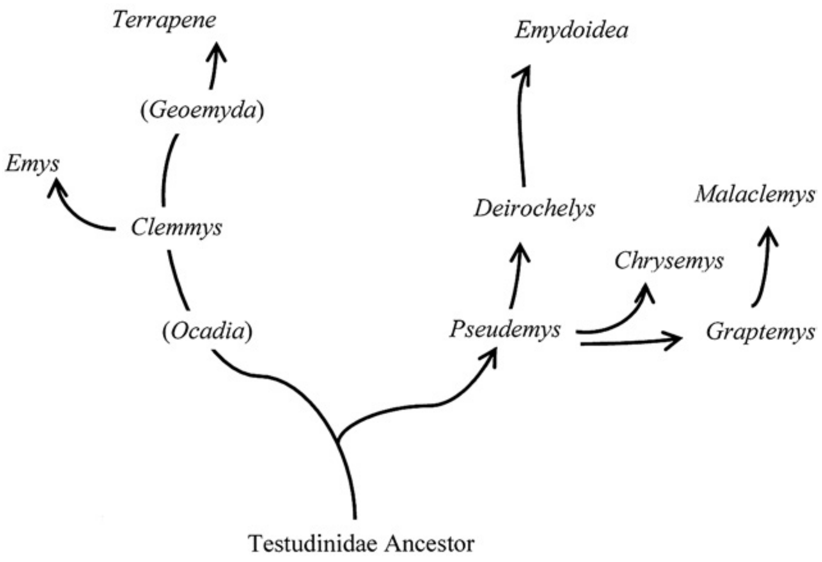


Fig. 5. Relationships of emydine genera described by Loveridge and Williams (1957: 185, fig. 2). As here modified, their batagurine (= geoemydid) genera are not included except those in parentheses which they believed to be ancestral to the emydines. Characters evaluated include size of shell buttresses, degree of plastral hinging, length (position) of entoplastron, and width/ presence of ridges on the triturating (jaw) surfaces.

(*E. matamata* = *Chelus fimbriatus*) and the soft-shelled family Trionychidae (*E. rostrata* = *Pelodiscus sinensis*). In addition, Brongniart's *Emydes* was apparently based on Duméril's (1804: 233) use of the French vernacular name "Les émydes" and hence, not available for either a genus or family name. Furthermore, the name *Emyda*, from which *Emydes* apparently is derived, was previously occupied, having been first used by Lacépède (1788: 171) as a genus of Asian softshelled turtles (see discussion below). In 1995 (Opinion 1800: 111, Bulletin of Zoological Nomenclature 52: 111 – 112) the International Commission on Zoological Nomenclature [ICZN] suppressed under its plenary powers (delineated in the International Code of Zoological Nomenclature [Code]; Article 81) the name *Emydes* Brongniart (1805: 27) for the Principle of Priority, but not for those of the Principle of Homonymy (see Webb's 1993 petition and detailed discussion of *Emydes* as used by Brongniart, upon which the ICZN made its decision).

Duméril (1805: 76) was the first to correctly use *Emys* as a genus name. He also provided a short description of the species *Emys orbicularis* (Linnaeus, 1758: 198), beginning his narrative as "Les Émydes (*emys*) forment un genre …" while placing other turtles in recognizable genera, such as "Les tortues (*testudo*)." On the next page, in a taxonomic key, Duméril referred to the genus by "Emyde," a vernacular name he had used in 1804 (Traité élémentaire d'histoire naturelle), and did not list a nominal species. Bell (1828: 29) listed *Emys picta* (currently *Chrysemys picta*) as the type species of *Emys*, and Fitzinger (1843: 29) later designated *Emys europaea* Schneider, 1783: 323 [= *Emys orbicularis orbicularis* (Linnaeus, 1758: 198)] its type-species. Neither is valid (see Webb, 1993). Duméril, 1895 (p. 76) first made the name *Emys* available by giving a brief description.

In 1993, Webb petitioned the ICZN to preserve *Emys* Duméril, 1805, as a valid name, and to suppress the name *Emydes* Brongniart, 1805: 27 for the purposes of the Principle of Priority but not for those of the Principle of Homonymy. Webb noted that Brongniart's *Emydes* had not been used as a valid name. In 1995, the ICZN (Opinion 1800) ruled in favor of Webb's petition, and conserved *Emys* Duméril, 1805: 76 as an acceptable genus; thus making it available for the stem root of the family name Emydidae. It suppressed the name *Emydes* Brongniart 1805 for the Principle of Priority, but not for the Principle of Homonymy.

Schmid (1819: 11, "Naturhistorische Beschreibung der Amphibien …") adopted Brongniart's (1805) use of *Emydes*, and was later mistakenly championed by Smith & Smith (1980: 364) as the original proposer of the emydid family-group name. Schmid (pp. 9 – 10) used only one genus name for all turtles, "*Testudo*," and created new "Unterabtheilungen" of *Testudo*, including *Emydes* into which he placed *Testudo eruopaea* [sic] (= *Emys orbicularis*) and *T. picta* (= *Chrysemys picta*). Schmid mixed his terms "Familien" and "Hauptfamilien" when referring to the division of the genus *Testudo*, and this confusion possibly has caused some later authors to consider *Emydes* as the family-group name. In addition, Schmid's *Emydes* fails to meet the nomenclatural criteria of the Code, Articles 5.1 and 11.4. First, as Schmid recognized only the genus *Testudo*, his *Emydes* is not formed from the stem of the accepted genus name *Emys* Duméril, 1805 (Code, Article 11.7.11); a name Schmid did not use (see the previous discussion of Duméril's genus name *Emys*). Second, although Schmid's subdivision of *Testudo* clearly amounts to the legitimate creation of subgenera (Code, Article 10.4), he did not use *Emydes* as a suprageneric taxon (Code, Article 11.7.1.2), but instead as a subgenus of *Testudo*. Because of these Code violations, Schmid's *Emydes* can not be considered a valid family-group name.

Constantine Samuel Rafinesque [sometimes addended with his mother's maiden name; i.e., C. S. Rafinesque "Schmaltz"] was one of the most prolific of all scientists of the early 19th Century (Fitzpatrick, 1911). Although known mostly for his North American travels and biological studies, from 1805–1815 he was in Sicily focusing on taxonomy of the family Emydidae. While there, Rafinesque published both his 1814 "Specchio delle Scienze …" and 1815 "Analyse de la Nature …" The most recent modern turtle family synopses (Iverson, 1992; David, 1994; Bonin et al., 2006; and Fritz & Havaš, 2007) have credited Rafinesque (1815) with the authorship of the family name Emydidae based on his apparent use of Emidania (see below), a derivative of the genus name *Emyda* Rafinesque (1815: 75), as an earlier name for the family-group. There have been several questions raised concerning this interpretation. First, in (1814: 66) "Specchio delle Scienze …" Rafinesque used the generic name *Hydrone* for *Testudo orbicularis* (Linnaeus, 1758: 198), but subsequently *Testudo orbicularis* Linnaeus, 1758: 198 was designated the type-species of Rafinesque's 1814: 66 *Hydrone* by Loveridge & Williams (1957: 201). This seems to have provided Rafinesque's 1815: 75 ("Analyse de la Nature …") use of "S. F. [subfamily]. EMIDANIA — *Les Emydiens … Emyda R*[*afinesque*]"; which lists both a genus and a family-group name, and has priority over Gray's (1825: 210) Emydidae. Unfortunately, Rafinesque's (1814: 66) *Hydrone* does not supply a proper stem-root for either the type-genus or the family name Emydidae (Code, Article 11.7.11), and must be rejected. Also, Presl's 1822: 127 *Emysina* is likely a misinterpreted spelling of *Emidania* Rafinesque, 1815: 75; and, as such, is unavailable for the family name (Peter Havaš, personal communication).

Rafinesque (1815: 75) used his newly created name *Emyda* as one of five genera under the subfamily "Emidania" of the family Chelonidia. On what was his name *Emyda* based? The turtle generic name *Emyda* was occupied. It was first used by Lacépède (1788: 171) as *Emyda punctata*, referring to *Testudo punctata* = *Lissemys punctata*, and thus unavailable for the type-genus of Emydidae. Rafinesque (1815), however, did not include any trionychid turtles in his Emydidae. His *Emyda* was apparently used as a new genus derived from *Emys* Duméril, 1805: 76, which immediately follows it on p. 75 in the list of genera included in Emidania (*Emys* Duméril, 1805: 76, was conserved in 1995 by the ICZN as the name of the type genus of the family Emydidae, see previous discussion). This legitimizes Rafinesque's genus name *Emyda*, and makes Emidania available for the group-name of emydine turtles (indicated by his use of the French vernacular "Les *Emydiens*" to denote the turtles concerned). Rafinesque's (1815: 75) group-name "EMIDANIA. Les *Emydiens*" has been used to denote his authorship of Emydidae. This name, however, is apparently based on the French vernacular name "Les *Émydes*," used by Duméril (1805: 76). Thus, Rafinesque's *Emyda* is an unjustified emendation (misspelling) of *Emys* Duméril, 1804, and a junior synonym and *nomen novum* of *Emys* Duméril, 1805: 76 (but see the discussion under the subfamily Emydinae). It is also an original misspelling of Emydania Rafinesque (1815: 75), not specifically formed from a recognized genus name, and should not be considered valid (Code, Article 33.3.1). Nevertheless, Rafinesque's inaccurate spelling of Emidania was corrected to "Emydidae" by Bell (1828: 514) and later by Cope (1870: 123). Their corrections apparently made Emidania a justified emendation (Code; Articles 32.5.3.2, and 35.4.1), and available as the valid family group-name. Rafinesque (1815: 36) stated his usage for the creation of names as "Les Families, les Ordres, et les Classes doivant aussi avoir des noms sustantifs singuliers" [The Families, Orders, and Classes must also have unique names]. This does not agree with Article 11.7.1.1 of the Code, which states that the name must be a "noun" in the "nominative plural" (Rafinesque's subfamily rank for emydid turtles is discussed later under Emydinae).

The name *Emyda* was often used after 1815 (Anderson, 1876: 514, Annandale, 1912: 171–173, Boulenger, 1889: 267, Siebenrock, 1909: 590, Smith, 1931: 154–156–159, etc.). Malcom Smith (1931: 154) realized that Gray's (1831a: 19) *Emyda* (Trionychidae) was a homonym for Rafinesque's (1815: 75) *Emyda*, and proposed the name *Lissemys* (p. xxviii) for the Asian Soft-shelled Turtle *Testudo punctata* Lacépède (now *Lissemys punctata punctata* Smith, 1931: *xxviii*) based on Lacépède (1788: 171). Therefore, it is unavailable as a valid alternate spelling for either Duméril's 1805: 76 genus *Emys* or the stem root of the family name Emydidae.

But what of John Edward Gray's (1825: 210) later use of the family name Emydidae? Gray is probably Great Britain's most famous herpetologist, and served as curator at the British Museum (of Natural History; now "The Natural History Museum," London). He published more than 3,000 herpetological papers, many concerning turtle taxonomy.

In September, 1825, Gray (Annals of Philosophy [New Series 3], 10: 210) first introduced the properly spelled family name Emydidae, which he cited as "*Fam.* II. Emydid*ae*, *Bell MSS*"; clearly indicating that the name was borrowed from Thomas Bell, a British corresponding contemporary. Gray also coined and provided an anatomical definition of what possibly can be interpreted as a subfamily name, Emydina, which he described as having the "*Beak horny*; *sternum entire*," and included the genus *Emys* on the next line. Unfortunately, he copied Bell's manuscript by erroneously listing the author of *Emys* as "*Brogn*. [= Brongniart, 1805: 27; see previous discussion on the availability of this name]. Gray, however, provided an acceptable description of the genus *Emys*. He included only two currently recognized emydid genera in his newly created family Emydidae: *Emys* (pp. 210–211, with only the emydid species *E*[*mys*]. *centrata*, *T*[*estudo*] *concentrica* (= *Malaclemys terrapin*); and *Terraphene* [sic] (= *Terrapene*) with the species *T*[*estudo*]. *clausa* (=

Terrapene carolina) and *Testudo Europea* [sic] (= *Emys orbicularis*). At the end of his brief discussion of the genus *Terraphene*, Gray adds that "Mr. Bell observes, that *Testudo Europea* [sic] is a species of this genus; if so the name of it should be changed, as that was certainly the *Emys* of ancients." Bell (1825a) also published the family name Emydidae, but as a *nomen nudum* and after Gray's 1825 publication.

A nomenclatural roadblock to Gray's (1825: 210) authorship of the family Emydidae is his reversed subfamily descriptions. He stated on p. 210 that the "*sternum* [plastron] *entire*" (presumably meaning "not hinged or moveable") was a characteristic of his subfamily Emydina based on the genus *Emys*; but the currently recognized species in this genus have a hinged, moveable plastron. Gray's description of Emydina more closely matches the currently recognized subgenera Deirochelyinae Agassiz, 1857: 355, in which the species have an immoveable, hingeless plastron. This eliminates the genus *Emys*. Then on the p. 211, he described his subgenera Terraphenina as having the "*sternum transversely sutured*" [immoveable], listing species now assigned to the genera *Emys* and *Terrapene* of the current subfamily Emydinae. Therefore, his description of *Emys*, the type genus of both his family Emydidae and subfamily Emydina, is misidentified (Code; Articles 41 and 65.2.1), and not available.

In October of that same year, Bell (1825b: 302) published his paper using the family name Emydidae. The Emydidae and *Emys* of both Gray and Bell were apparently based on the invalid genus name *Emydes* Brongniart, 1805: 27 and not on Duméril (1805: 76) (Code, Articles 11.7.1.1, and 12.2.4). Authorship of Emydidae has been credited to Gray by Kuhn (1966) and Smith & Smith (1980), but to Bell by Bour (2002). Also, Bell's 1825b: 302 use of Emydidae is a *nomen nudum*, as the family was not properly described. As such, Bell's authorship is not legitimate. Although Bell (1825b) mentioned the name *Emydes* several times, the earliest author he credits with that name is Brongniart 1805 (declared invalid by the ICZN in 1995, see above), and he used the plural *Emydes* to collectively refer to the species of the genus, not as the genus name. Smith & Smith (1980) considered Duméril's *Emys* a senior synonym of *Emydes* Schmid, 1819: 11, but *Emydes* is also unavailable for the proper stem of Emydidae; see previous discussion).

Gray followed Bell's unpublished manuscript in ending the species-group name with the ligature "*ae*." Their misspelled names needed correction (Code; Article 32.5.2). In 1828: 515, Bell published a justified emendation where the name Emydidae is defined correctly; but he significantly paraphrased Gray's (1825) species arrangement and descriptions which he later acknowledged (1832, 2: *x–xi*) in "A Monograph of the Testudinata."

In 1831a: 7 ("A synopsis of the species of the Class Reptilia"), Gray corrected his 1825: 210 mistaken description of the genus *Emys*. He not only adequately described the genus, but also broadened it on p. 7 to include: the "*American Box Terrapin*. E. (*Cistuda*) *Carolinae* ..." (= *Terrapene carolina*) and the „*European Box Terrapin*. E, (*Cistuda*) *Europea* ..." (= *Emys orbicularis*). On following pages, Gray assigned to Emydidae several American species presently considered to belong to the family: p. 9 — *Emys Occulifera* (= *Graptemys oculifera*); p. 10 — *Emys Muhlenbergii* (= *Glyptemys muhlenbergii*), *Emys Guttata* (= *Clemmys guttata*), *Emys Picta* (= *Chrysemys picta*), and *Emys Speciosa* (= *Glyptemys insculpta*); p. 11 — *Emys Concentrica* (= *Malaclemys terrapin*), *Emys Reticulata* (= *Deirochelys reticularia*), *Emys Decussata* (= *Trachemys scripta elegans*), *Emys Scripta*, and *Emys Serrata* (= *Trachemys scripta*); and p. 12 — *Emys Ornata* (= *Trachemys ornata*, original description), *Emys Rugosa* (= *Trachemys scripta elegans*), *Emys Lesueurii* (= *Graptemys geographica*), *Emys Bellii* (= *Chrysemys picta bellii*, original description), and *Emys Annulifera* (= *Pseudemys concinna*). Additionally, Gray included several species of batagurine turtles now assigned to the family Geoemydidae (Theobald, 1868: 9), and some species of other families.

One other 19th Century British scientist has occasionally been suggested as the author of the family name, Emydidae; the British paleontologist Richard Lydekker (1889a, *in* Nicholson & Lydekker, Manual of Palaeontology 2: 1117). Much later, Kuhn (1966; followed by Smith & Smith, 1980, and King & Burke, 1989) proposed Lydekker as the first author to use the rank and spelling of the subfamily Emydinae and, as such, a possible author of the family name Emydidae. This is in error for several reasons, including the observation that Cope (1870, Trans. Am. Philos. Soc. 14: 123) preceded Lydekker in the proper spelling of Emydinae. Additional problems arise from the interpretation of Lydekker's (1889a) authorship of Emydinae. Lydekker proposed the replacement name Cyclanorbinae, a subfamily of softshelled turtles, for the preoccupied name Emydinae, and, as such, was not referring to hard-shelled emydid turtles. Also, Emydinae was misspelled Emydin*ae* in Nicholson & Lydekker (1889a); the italicized "*ae*" attached makes this unavailable as the subfamily name (Code, Article 32.5.2). In an addendum (Volume 2: *xi*) to the same publication, Lydekker corrected his use of Emydin*ae*, stating that it was preoccupied (but did not list the author), and repeated this on p. 22. Lydekker corrected this same mistake (p. *x*) in his 1889b "Catalogue of the fossil Reptilia and Amphibia in the British Museum (Natural History) Part III …" Therefore he clearly should not be considered the author of the family name Emydidae.

The papers of all seven potential previously-discussed authors of the family name Emydidae contain problems and Code violations. However, based on the ICZN's ruling conserving *Emys* Duméril, 1805: 76, which now can officially be considered the type-genus of the family Emydidae; we believe that this eliminates the availability of Gray's (1825: 210) authorship of the family based on "Emys, *Brogn.*" an emendation of Brongniart's (1805) genus *Emydes* (ICZN, 1995). We conclude that neither Gray (1825) nor Bell (1825b) is the legitimate author of the family name Emydidae. Hence, Rafinesque (1815: 75) apparently was the first to accurately group

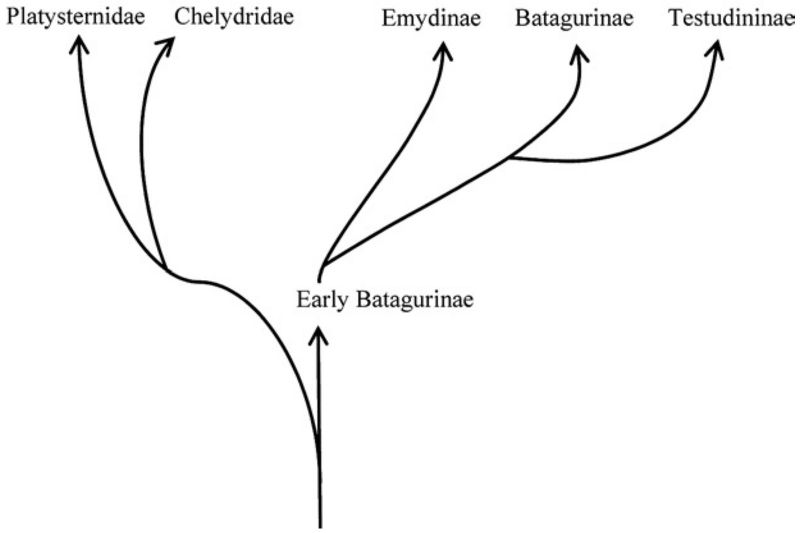


Fig. 6. A tree showing relationships of emydid turtles to other families as theorized by McDowell (1964).

the genera under a subfamily name, Emidania, based on *Emys* Duméril, 1805: 76. Rafinesque's authorship of the family has priority over those who later used the family name Emydidae (Code, Article 23); and he should be credited with the family name Emydidae.

Birth of a modern restricted family Emydidae Rafinesque, 1815

Some of the early revisers of North American turtle taxonomy applied a version of the family Emydidae in a seemingly restricted sense, similar to our present concept of the family. Nevertheless, it was inferred in their works (Schweigger, 1814; Gray, 1856b, 1870; Lindholm, 1929) that the family also included a diversity of turtles we now classify as geoemydids (batagurines) or testudinids. In 1964 Samuel B. McDowell, a professor at Rutgers University and research associate at the American Museum of Natural History, New York, published an important but controversial revision of emydid turtles based on osteological comparisons. The title of McDowell's paper "Partition of the genus *Clemmys* and related problems in the taxonomy of the aquatic Testudinidae" somewhat obscured his decision to change nomenclature throughout the family. This could explain why some of his suggested revisions were not promptly adopted. In the text, McDowell (1964) does not define the content of family Testudinidae, but it appears he followed Williams (1950, study on cervical vertebrae variation) who included *Platysternon*, terrestrial tortoises (subfamily Testudininae) and the "aquatic Testudinidae" (subfamily Emydinae). McDowell split Emydinae into the subfamilies Batagurinae (p. 254) (including the Old World emydids and *Rhinoclemmys* in the New World) and Emydinae (p. 173) (including only the New World emydids *Chrysemys*, *Clemmys*, *Deirochelys*, *Emydoidea*, *Malaclemys*, and *Terrapene*; and *Emys* in the Old World). By doing so, his revised Emydinae sensu stricto became the first taxonomic system to represent what we recognize today as the family Emydidae.

McDowell's (1964) descriptions of the two subfamilies were based on osteological characters which he inferred as primitive or advanced. Because cladistic methodology (sensu Hennig 1950) had not yet become popular, the polarities of McDowell's character states were not tested by a global outgroup. Nevertheless, he observed that the character states of Testudininae (land tortoises) were also shared by batagurines, and concluded that the former descended from the latter. In fact he stated "…it is nearly certain" that the entire family Testudinidae (sensu lato, but presumably not including *Platysternon*) is descended from a batagurine ancestor. A phylogenetic diagram can be liberally constructed from his character states and conclusions (Fig. 6). A decade later, Auffenberg (1974) also suggested that the batagurines are ancestral to both the emydines and testudinids. The character states by which McDowell (1964) identified the Emydinae (sensu stricto) and distinguished it from the Batagurinae are: 1. Angular bone of the lower jaw forms the floor of the canal for meckel's cartilage and does not contact it (Fig. 7A). 2. Basiooccipital bone of the cranium without strong lateral tuberosity; not extending laterally to the lagena (floor of sacculus of inner ear) and not forming the floor of the scalae tympani (Fig. 7B, may reverse in some *Graptemys*, *Malaclemys*, and *Trachemys*). 3. Joint between the centra of the fifth and sixth cervical vertebrae double, joined by a pair of condyles. 4. On the carapace, the posterior pair of marginal scutes, M12 (= post centrals or supracaudals), do not extend forward to contact or overlay the suprapygal bone. Gaffney (1979), based on skull characters, also split the family Emydidae, combining the classifications of Wermuth & Mertens (1961) and McDowell (1964).

In 1966 George Zug, who later became curator of amphibians and reptiles at the National Museum

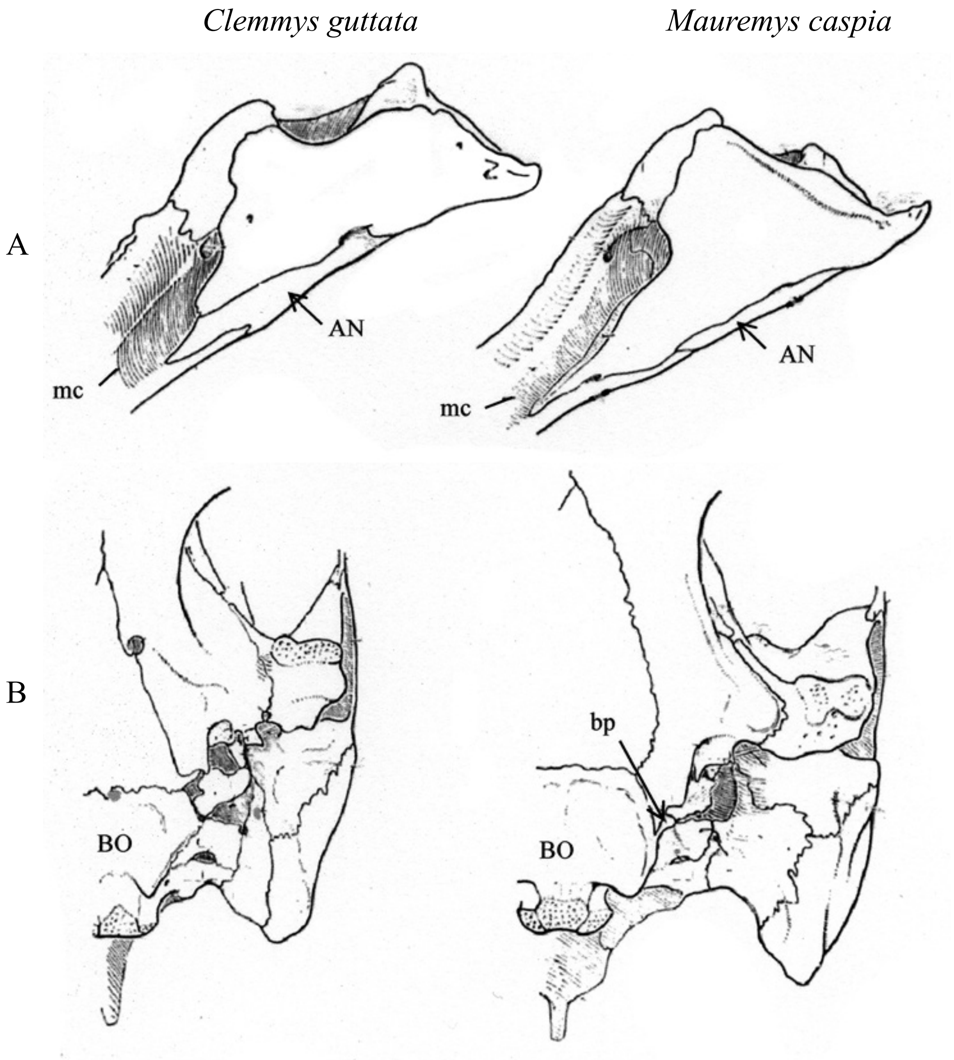


Fig. 7. Skull comparisons between *Clemmys guttata* and *Mauremys caspica*. A. Illustration of lower jaw, indicating that the angular bone (AN) of *C. guttata* comes in contact with Meckel's cartilage (mc). B. Illustration of the basiocranium indicating that the basioccipital bone (BO) of *C. guttata* does not extend laterally to form a "batagurine process" (bp). Modified from McDowell (1964, figs. 1-2)

of Natural History of the Smithsonian Institution in Washington, D.C., published his analysis of the penial morphology of turtles. He found suggestive evidence to support McDowell's splitting off of the Batagurinae. Nevertheless, Zug (1966) presented a tree (p. 18) showing a sister relationship between emydines and batagurines which were included in his family Testudinidae along with the land Tortoises and *Platysternon* (Fig. 8). Pritchard (1967: 18) presented a phylogenetic diagram of turtle families which depicted the Emydidae (including batagurines) sharing a common ancestor with tortoises, Testudinidae (Fig. 9). Gerald Waagen (a graduate student of John M. Legler, Professor of Biology at the University of Utah) described variation in turtle musk gland morphology (unpubl. Master's thesis 1972). Waagen found that batagurines have musk glands in the inguinal region of the shell which are lacking in emydines. Robert Winokur, another student of Legler's, found that mental glands (presumably primitive) are common in batagurines but not in emydines (Winokur & Legler, 1975). In contrast, Thomas Parsons at the Museum of Comparative Zoology (Harvard University) published a detailed study of choanal morphology (1968) which did not provide evidence supporting McDowell's splitting of the Emydinae. Comparing skull morphology, Claude et al. (2004) only found differences in small independent units (e.g. posterior expansion of the pterygoids, length of postorbital) between batagurines and emydines rather than gross cranial shape. Most of the shape variation they reported was related to diet and habitat which apparently represents parallel evolution in the two groups.

Concordant with splitting off the Old World emydids into the subfamily Batagurinae, it was necessary for McDowell (1964) to partition the genus *Clemmys*. Otherwise, species of the same genus would be represented in two subfamilies. He retained the name *Clemmys* for the New World emydine species (*C. guttata*, *C. insculpta*, *C. marmorata*, and *C. muhlenbergii*), while the Old World batagurine species of *Clemmys* were reassigned to other genera. Merkle (1975) applied starch gel electrophoresis (analysis of 17 protein systems) to test McDowell's splitting of *Clemmys*. He identified 12 proteins which differ-

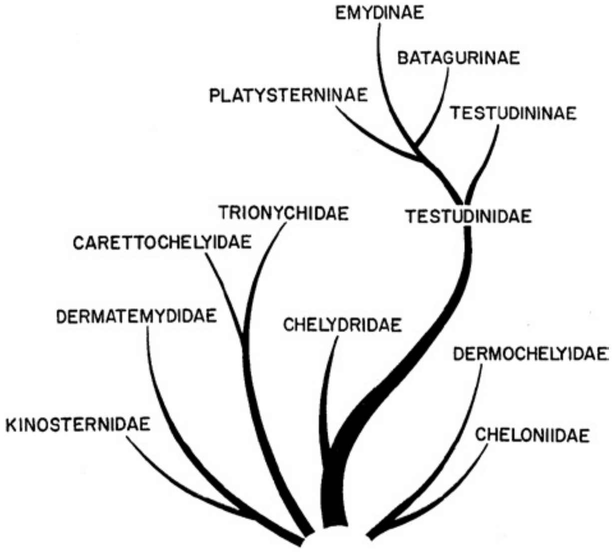


Fig. 8. Diagram of proposed familial relationships of cryptodiran turtles as determined by penial morphology. Neither primitiveness nor the degree of divergence is directly implied except for divergences within each of the four basal lines (Zug 1966, fig. 4).

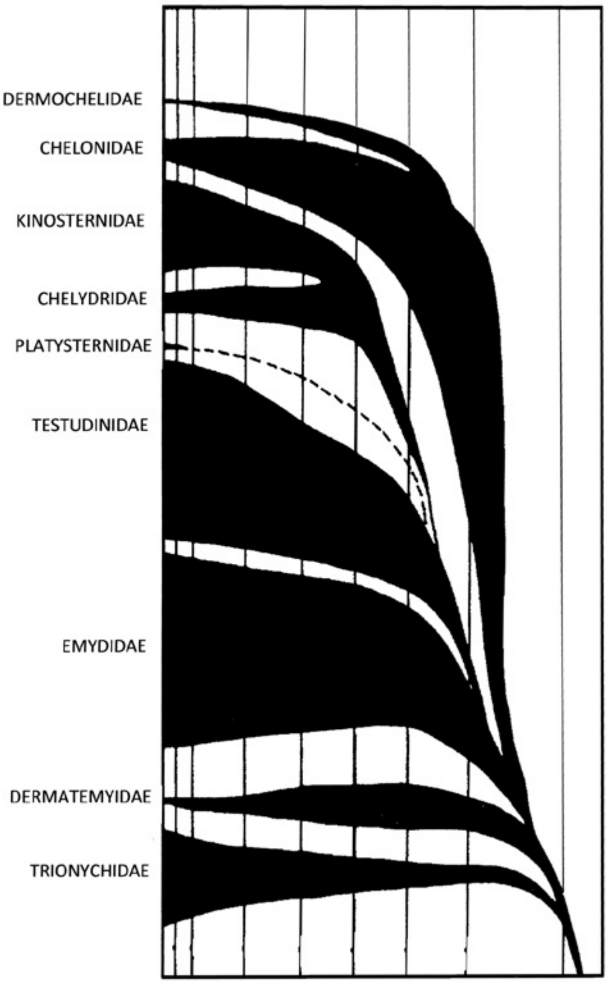


Fig. 9. An early theory on the phylogeny of cryptodiran turtles. The width of the column gives an approximation of abundance and variety within the group. Modified from Pritchard (1967: 18).

entiate the New World *Clemmys* from the two Old World batagurine genera he tested, *Mauremys* and *Sacalia* (both formerly *Clemmys*). Therefore, based on biochemical divergence, he provided support for McDowell's revision. Bickham (1975) provided additional evidence from his analysis of emydid karyotypes; chromosome number and centromeric position. He found that the New World *Clemmys* have 50 chromosomes which show no morphological variation among the four species; *C. guttata*, *C. insculpta*, *C. marmorata*, and *C. muhlenbergii*. In contrast, both of the batagurines which Bickham tested, *Sacalia* and *Mauremys*, have 52 chromosomes which are morphologically divergent from New World *Clemmys*. This distinction was upheld by later karyotypic reports in Killebrew (1977), Haiduk & Bickham (1982), and Bickham & Carr (1983). Nevertheless, these studies considered batagurines a confamilial sister group to emydids (Fig. 10). In a molecular (immunological) analysis of turtle relationships, Chen et al. (1980) reported a sister group relationship between Emydidae and Testudinidae (Fig. 11). Within the Emydidae, it is noteworthy that the only emydine tested (*Terrapene*) showed the greatest immunological divergence compared to the four batagurines examined.

McDowell's (1964: 273) subfamily Emydinae, comprised of New World genera plus *Emys*, remained a stable taxonomic unit followed by most subsequent authors (Mlynarski, 1976; Wermuth & Mertens, 1977; Pritchard, 1979; Smith & Smith, 1980; Iverson, 1985, 1986; Obst, 1986; Ernst & Barbour, 1989; King & Burke, 1989). However, systematic revision of its "sister" subfamily, Batagurinae (p. 254), resulted in re-evaluation of the Emydinae. Hirayama (1985, but dated 1984) examined 86 morphological characters (36 skull and 24 shell) of emydid turtles in his systematic analysis of the Batagurinae. He applied cladistic methodology, polarizing characters and following the principle of parsimony. Hirayama's 1985 results suggested that some of the terrestrial batagurines (e.g. *Geoemyda*) are the sister group of land tortoises, Testudinidae (sensu stricto). This conclusion was based on the presence of a primary palate, reduced hyoid ossification, and reduced webbing between digits, all interpreted as derived character states shared by both groups. Hirayama recognized that this rendered the family Emydidae (sensu Carr 1952; Mertens & Wermuth, 1955; Pritchard, 1979; and Iverson, 1985) poly- or paraphyletic. To further assess relationships, Hirayama (1985) examined paleomaterial of *Echmatemys*, one of the best known fossil genera of emydids (Hay 1908b: 295), and found that it shares derived character states with batagurines and testudinids, but not emydines. Therefore it is evident that *Echmatemys*

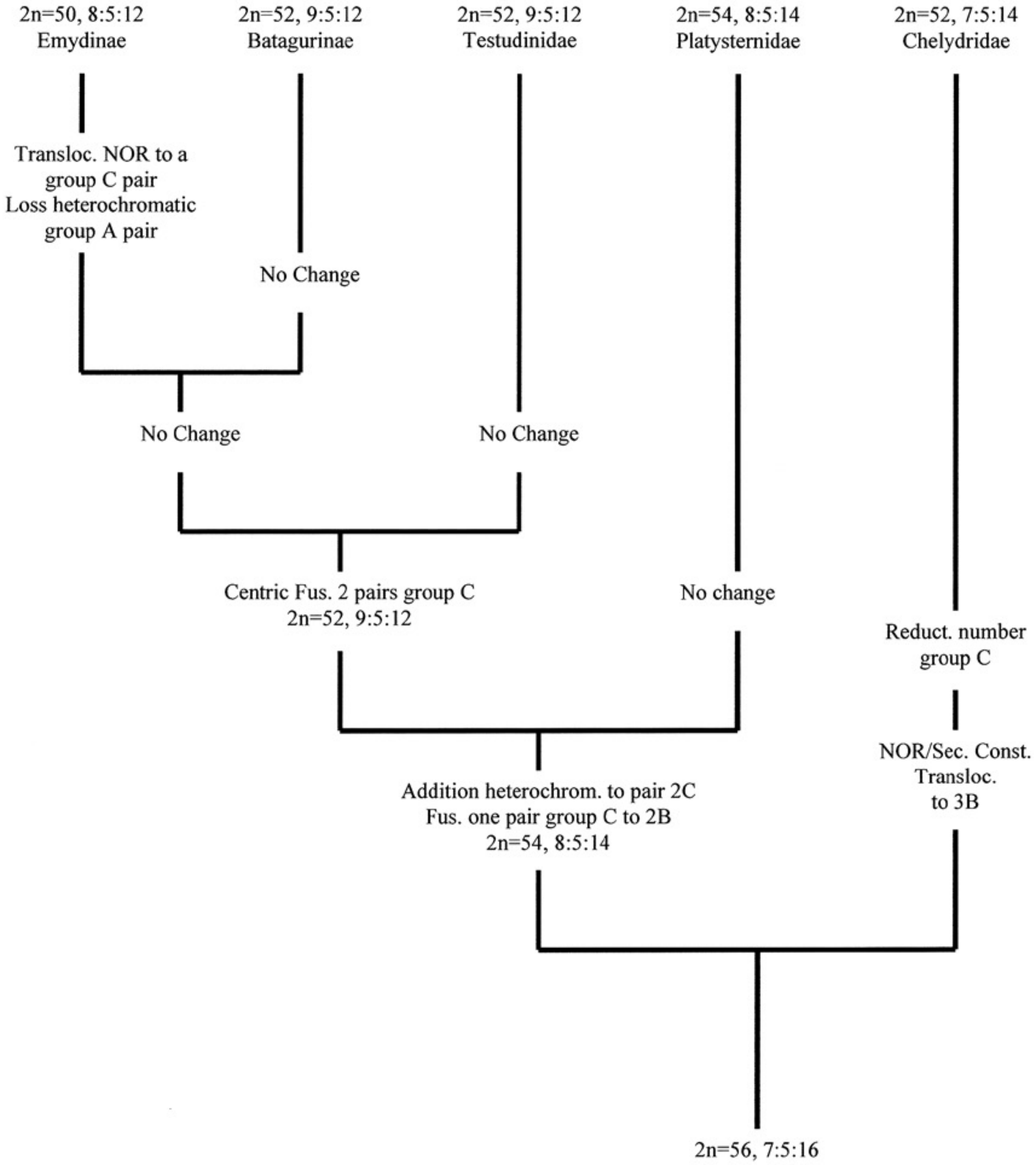


Fig. 10. Cladistic relationships based on karyotypes of the four families of testudinoid turtles (Haiduk and Bickham 1982, fig. 6).

is not ancestral to the entire family, as previously thought by Hay (1908b). Instead it appears that the subfamily Emydinae represents a separate monophyletic lineage. Based on published data and additional morphological analysis, Hirayama (1985) defined it as the sister group to *Echmatemys*, Batagurinae, and Testudinidae; which collectively (with the emydines) formed the sister group to *Platysternon* (Fig. 12). Bour & Dubois (1984: 82) recognized Batagurinae as a subfamily of Emydidae, but considered *Platysternon* to comprise the subfamily Platysterninae within the family Chelydridae. Based on the morphology of extant and fossil turtles, it is clear that Hirayama (1985) believed the Batagurinae (sensu McDowell 1964) was an unnatural taxon and disagreed with the previously hypothesized phylogenetic position of emydines. Nevertheless, he refrained from proposing familial revision. If Hirayama (1985) had chosen to revise the taxonomy he would have had two options: 1. Split the Emydinae off as a separate family, or 2. Revert back to a composite Testudinidae by including emydines, batagurines, and testudinines, excluding *Platysternon* (sensu Mertens et al. 1934). At about the same time, Chkhikvadze (1984), examined fossil material of emydids and also arrived at the conclusion that Batagurinae (sensu McDowell 1964) is polyphyletic. Chkhikvadze attempted to resolve the taxonomic problem by splitting the Batagurinae into subfamilies. Subsequently, Batagurinae and Bataguridae have been documented to be younger, and therefore synonymized under Geoemydidae (Bour & Dubois, 1986: 88).

Gaffney (1984), in his Figure 9, was the first to elevate McDowell's (1964: 240) restricted subfamily Emydinae to the full family Emydidae, sensu stricto, as we recognize it today (comprised of the genera *Chrysemys*, *Clemmys*

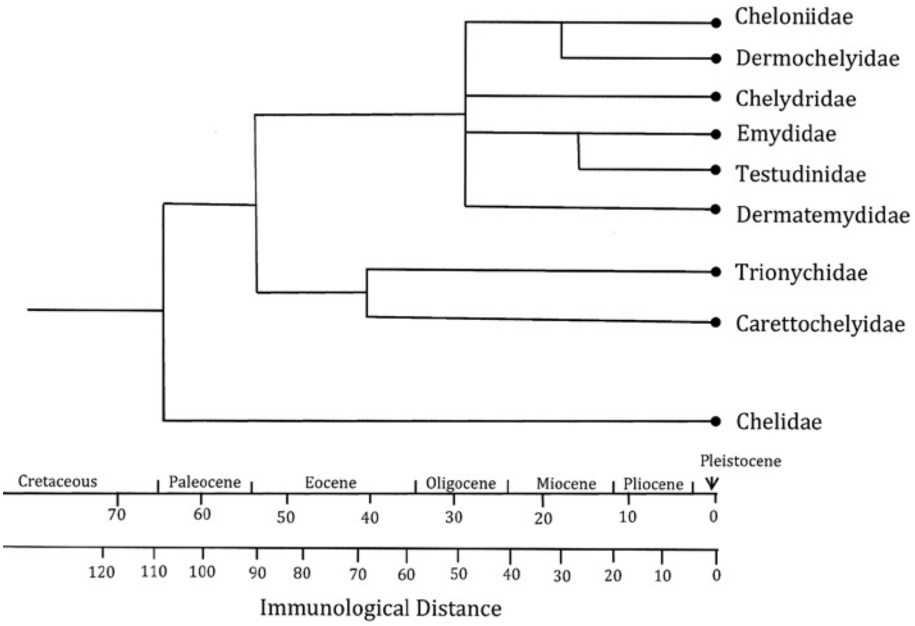


Fig. 11. Phylogeny of Testudine families suggested by albumin structural differences (Chen et al. 1980, fig. 1). Branch points represent averages of immunological distances. The time scale was calculated by assuming that 60 million years is equivalent to an immunological distance of 100 units.

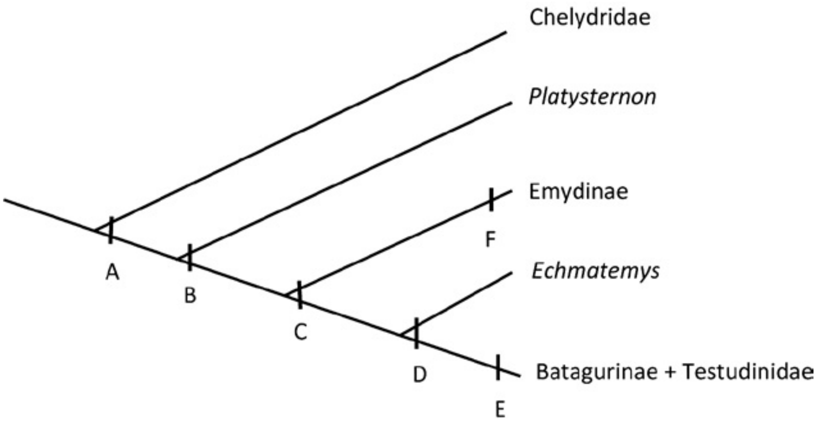


Fig. 12. Cladogram showing hypothesized relationships among selected testudinoid turtles (Hirayama 1985, fig. 1). Character states which support nodes and branches are: A- chromosomal number decreased to 52 or 54, presence of a cloacal bursa; B- biconvex 8th cervical vertebra; C- hypoplastron reaching the pleural plates, iliac blade with outward curvature and the double origin of iliotibialis muscle, loss of inframarginal scutes exclusive of axillary and inguinal; D- axillary and inguinal musk duct foramina enclosed within peripheral plates or between peripherals and plastral buttresses; E- Sixth marginal scute often reaching third costal scute, loss of postorbital-squamosal contact; F- loss of pterygoid-basioccipital contact, double articulation between 5th and 6th cervical centrum, chromosomal number reduced to 50, elongate epipterygoid.

[including *Actinemys* and *Glyptemys*], *Deirochelys*, *Emydoidea*, *Graptemys*, *Malaclemys*, *Pseudemys*, *Terrapene*, *Trachemys*, and the Old World *Emys*). As illustrated in a cladogram (our Fig. 13), his decision was apparently based on Hirayama's (1985) results, which he cited as 1984 in press. In doing so, Gaffney strengthened the nomenclatural status of these genera and salvaged the family Emydidae as a "natural" monophyletic taxon. The decision to elevate Emydinae was not adopted by Ernst & Barbour (1989), King & Burke (1989), Iverson (1992), and Rogner (1995) in their influential accounts and checklists of turtles of the world. Nevertheless, subsequent analyses, based on nucleotide sequence data using cladistic methodology, corroborate the characterization of Emydidae (sensu stricto Gaffney 1984) as a well-defined monophyletic assemblage (Shaffer et al., 1997; Cervelli et al., 2003; Spinks et al., 2004; Krenz et al., 2005). The extant family is entirely New World except for the genus *Emys*.

Establishment of a restricted Emydidae (= McDowell's subfamily Emydinae) was followed by additional theories on relationships of this group to other families or subfamilies. McDowell (1964: 241) indicated a close affinity between the Asian Big-headed turtle,

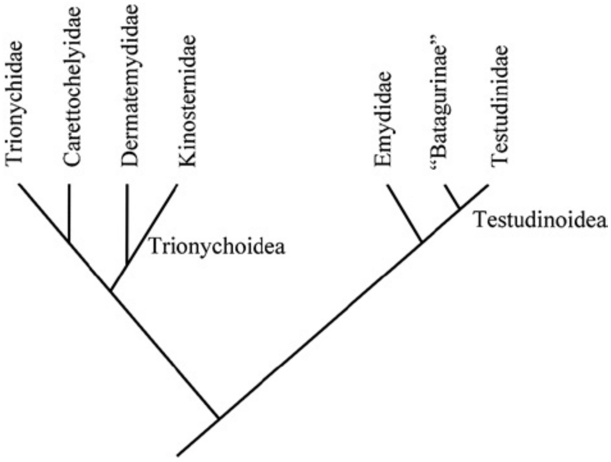


Fig. 13. Diagram of emydid relationships based on osteology; extracted from a cladogram presented in Gaffney (1984, fig. 9).

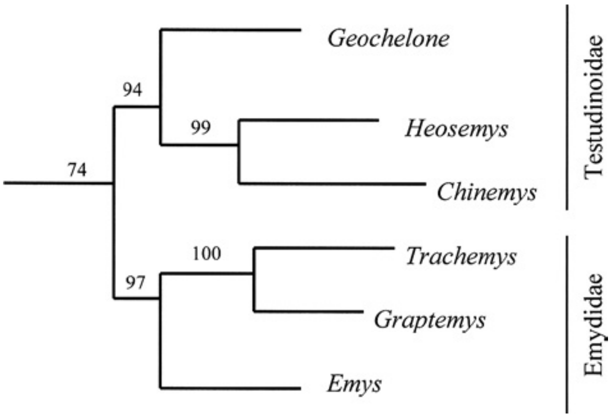


Fig. 14. Relationships of emydid and testudinoid turtles. Modified from a tree of Pleurodira and Cryptodira (Shaffer et al. 1997; Krenz et al. 2005, fig. 1) based on 892 nucleotides from cytochrome *b*, 325 nucleotides from 12S ribosomal DNA, and 115 morphological characters. Numbers at branches indicate bootstrap percentages out of 1000 replicates.

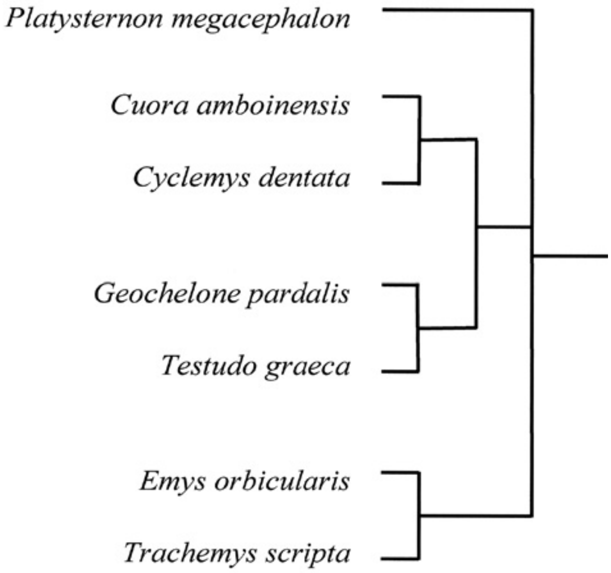


Fig. 15. Maximum parsimony topology (phylogenetic position of *Emys* and *Trachemys*) based on RNA sequencing. Modified from Cervelli et al. (2003, fig. 7).

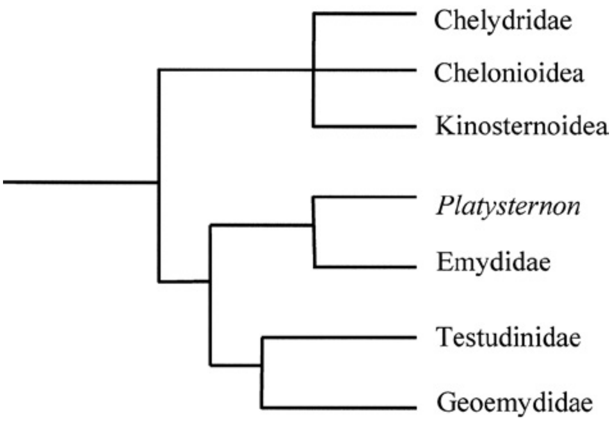


Fig. 16. Phylogenetic tree which illustrates a theory on the position of family Emydidae. Modified from the combined molecular results of Parham et al. (2006), Barley et al. (2010), and Thomson and Shaffer (2010).

Platysternon, and emydines based on cranial structure. Curiously though, on that same page, he went on to state "I hope to show in a later paper that the affinities of *Platysternon* are with the North American genera *Chelydra* and *Macroclemys*." Indeed, subsequent data sets suggested that *Platysternon* shares a close relationship (sister group) to the snapping turtles, family Chelydridae (Gaffney & Meylan, 1988: 174, 182). Phylogenies derived mostly from morphological characters (Hirayama, 1985; Gaffney & Meylan, 1988) indicated that emydids are the sister group to batagurines and testudinids collectively. This relationship (Fig. 14) was later supported by morphology and molecular analysis of 12s ribosomal DNA (Shaffer et al., 1997 and Krenz et al., 2005). However, based on sequence data of nuclear RNA, Cervelli et al. 2003, in their Figure 7, reported an unresolved trichotomy among emydids, *Platysternon*, and a clade formed of testudinids and geoemydids (Fig. 15). More recent analyses of DNA sequence data (Fig. 16) have provided strong evidence for a sister group between Emydidae and *Platysternon* (Parham et al., 2006; Barley et al., 2010; Thomson & Shaffer, 2010). Thus, McDowell's (p. 241) initial observation regarding *Platysternon* appears to have

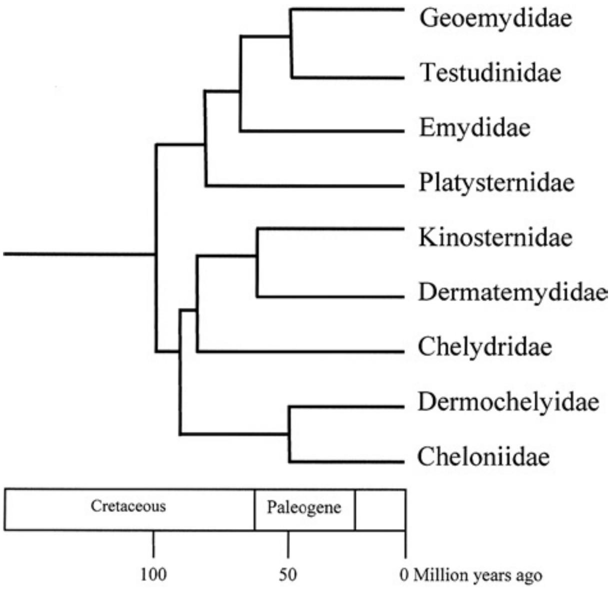


Fig. 17. A timetree for origin of turtle families; modified from Shaffer (2009a, fig. 2).

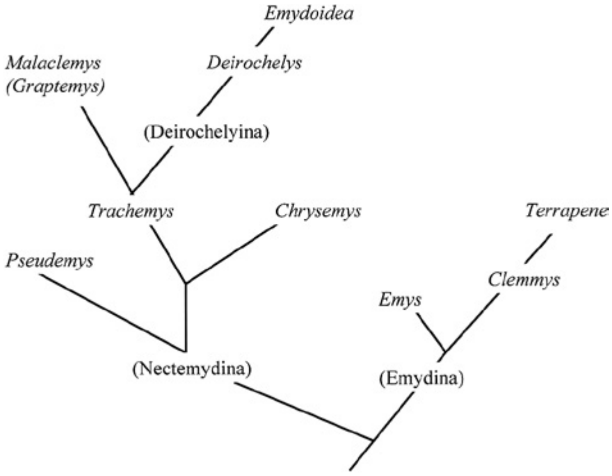


Fig. 18. Phylogenetic tree derived from the theories and classification presented by McDowell (1964).

been correct. The geological time period of origin for Emydidae (Fig. 17) has been estimated by assessing concordance of fossil calibration points in molecular clock studies. The family was reported to date back to the late Cretaceous Period, 70–75 million years ago (Ma) (Near et al., 2005; Shaffer, 2009a, 2009b). Meanwhile, Spinks et al. (2016) reported estimates for the origin of "crown" Emydidae ranging 42–56 Ma (Eocene). From a morphological perspective, McLaughlin & Stayton (2016) have demonstrated that much convergent evolution has occurred in shell shape between turtles in the families Emydidae and Geoemydidae.

The relationship between *Deirochelys* and *Emydoidea*

Within his proposed subfamily Emydinae (sensu stricto, now = Emydidae) McDowell (1964: 273–277) recognized two major lineages partitioned into three generic complexes. One branch consisted of the *Emys* complex (i.e. *Emys*, *Terrapene*, and *Clemmys* including *Actinemys* and *Glyptemys*). His second major branch was comprised of a more aquatic complex, *Chrysemys* (i.e. *Chrysemys*, *Pseudemys*, *Trachemys* and *Malaclemys* including *Graptemys*), as well as the *Deirochelys* complex (i.e. *Deirochelys* and *Emydoidea*). Smith & Smith (1980: 414) later applied formal nomenclature to these complexes by designating them as subtribes Emydina, Nectemydina, and the paraphyletic Deirochelyina, respectively (Fig. 18). McDowell's two evolutionary branches (aquatic and semi-terrestrial) were widely accepted by turtle systematists, except for his position of *Emydoidea*. Prior to this time, most authors recognized an affinity between *E. blandingii* and the Old World species *Emys orbicularis* by placing them exclusively in the genus *Emys* (Agassiz, 1857; Strauch, 1862; Boulenger, 1889; Hay, 1908b; Stejneger & Barbour, 1917, 1943; Pope, 1939; Williams, 1950; Carr, 1952; Schmidt, 1953; and Wermuth & Mertens, 1961). In contrast, McDowell (1964: 275) followed Baur's (1889) original suggestion that Blanding's and Chicken Turtles are closely related (sister taxa) based on their similar, very specialized, elongate cervical vertebrae and skull. McDowell stated "I have been unable to find significant cranial differences between *Deirochelys* and *Emydoidea*" and he did not seem to attach much significance to their differences in shell kinesis. Tinkle's (1962) analysis of scute arrangement and Zug's (1966) description of penial morphology provided further evidence for a close relationship between these two genera; and several authors expressed their support (Pritchard, 1967; Milstead, 1969; Ernst & Barbour, 1972).

During the next decade, evidence began to accumulate demonstrating a different evolutionary relationship for *Deirochelys* and *Emydoidea*. Waagen (1972) found that musk glands are absent in the more aquatic emydids, including *Deirochelys*. In contrast, *Emydoidea* has one pair of musk glands in the axillary region, a feature it shares with *Clemmys*, *Emys*, and *Terrapene*. In 1974, Bramble re-examined the relationship of *Deirochelys* and *Emydoidea* based on the biomechanics and evolution of shell kinesis. Although he did not specifically apply a cladistic methodology by determining the polarity of character states, Bramble (1974) took a phylogenetic approach and identified cases of convergent evolution (homoplasy). He observed that *Emys*, *Emydoidea*, and *Terrapene* (the only emydids with a hinged plastron) share a specialized, segmented scapula with a unique bone, the suprascapula (Fig. 19). It allows these emydids

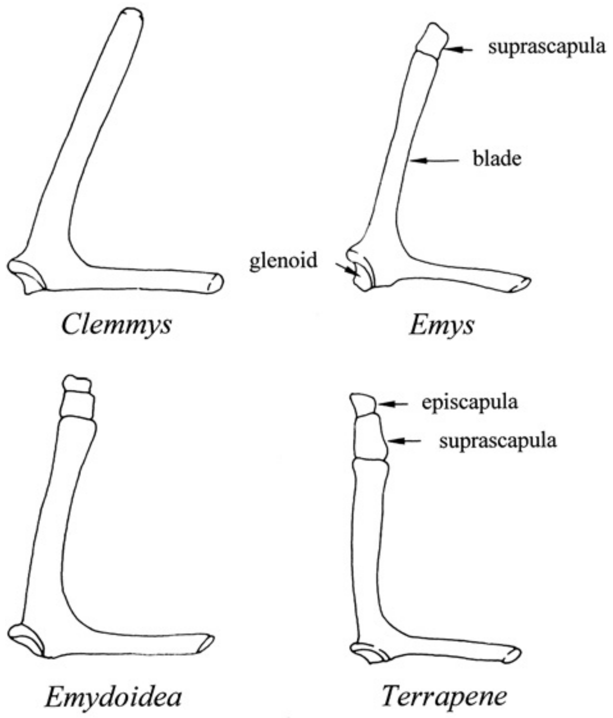


Fig. 19. Anterior views of the right scapulae of genera of emydine turtles. The unsegmented condition seen in *Clemmys* is similar to that of *Deirochelys* and batagurine (geoemydid) Box Turtles. Modified from Bramble (1974, fig. 6).

to close their shell by flexing the scapula differently from Old World batagurine Box Turtles (e.g. *Cuora*) which displace the scapula during shell closure. This shared derived condition (synapomorphy) lead Bramble to conclude that *Emydoidea* belongs to the lineage of semiterrestrial emydids, and not the aquatic line to which *Deirochelys* belongs. He further surmised that the neck and cranial similarities McDowell reported for these two genera are "undoubtedly the result of convergent feeding systems" = homoplasies (Bramble, 1974: 724). Among 20 morphological characters examined by Bramble, *Emydoidea* shares 12 character states with *Emys* and *Terrapene* and only 5 states with *Deirochelys*. In addition, the webbing of the digits on the fore and hindlegs of *Emydoidea* is less extensive (similar to the semiterrestrial emydids) than in *Deirochelys* (S. Gotte and M. Seidel, pers. observ.).

Following Bramble's study, Jackson (1978b) published a re-evaluation of the genus *Deirochelys* based on the morphology of extant and fossil turtles. His description of paleomaterial supports gradual evolution (beginning about 18 m.y.a.) from a general *Chrysemys*-like ancestor to the specialized morphology of Recent *Deirochelys*. The specializations include an elongate skull and neck; and thoracic vertebrae with dorsoventrally compressed centra, laterally compressed neural spines, and rib attachments displaced ventrally. Jackson (1978b), in agreement with Bramble (1974), attributed these character states (all shared with *Emydoidea*) to adaptations for "pharyngeal" or "gape and suck" feeding used to capture fast swimming prey. He theorized that these features are highly adaptive, and therefore it would not be surprising that the suite of characters evolved in parallel (convergence) along different evolutionary lines. Jackson pointed out that the snapping turtle (*Chelydra*) and side-necked turtle (*Chelus*) have also acquired this mode of feeding and specialized morphology, but belong to very divergent families. He concluded his argument on this issue by stating that the Pleistocene and Late Pliocene fossils of *Emydoidea* (no older than 6 million years and referable to extant *Emydoidea*; Taylor, 1943: 250, Preston & McCoy, 1971: 23) show no special resemblance to Late Tertiary *Deirochelys*, other than the convergent characters already noted. While this may be true, it would not exclude the possibility that *Emydoidea* arose as an early offshoot of the *Deirochelys* line, perhaps during the Late Miocene (about 13 m.y.a.). However, this hypotheis would require the assertion that the presence of a specialized scapula (sensu Bramble 1974) in *Emydoidea*, *Emys*, and *Terrapene* is the result of convergence (homoplasy). Maybe this was the assumption of Smith & Smith (1980: 144) who continued to recognize *Emydoidea* and *Deirochelys* as a closely related taxonomic unit. More recently, Hutchison (1981: 1) and Holman (1995b: 548, 2002b: 436) described older fossils, clearly referable to modern *Emydoidea*, which date back to the Miocene. This, combined with Jackson's observations, provide strong paleoevidence that *Deirochelys* and *Emydoidea* evolved in parallel and do not share the ancestral-descendant relationship hypothesized by earlier workers (e.g. Loveridge & Williams, 1957: 188; McDowell, 1964: 275).

Additional evidence for relationships of *Emydoidea* has come from molecular studies. Frair (1982) tested serum protein cross reactions and cellulose acetate electrophoresis in turtles. He found *Emydoidea* and *Emys* more similar to each other (resembling *Clemmys*) than either is to *Deirochelys*. In addition Frair found no distinction between *Deirochelys* and *Pseudemys* (=*Trachemys*). Seidel & Adkins (1989) examined myoglobin variation in emydid turtles and made some phylogenetic inferences using a global outgroup, including examples of Chelydridae, Geoemydidae (batagurines), Kinosternidae, Platysternidae, Testudinidae, and Trionychidae. They found that *Deirochelys* has a derived form of myoglobin (isoelectric point, pI = 6.8; p. 571) which it shares with all of the aquatic emydines. In contrast, *Emydoidea* has a form of myoglobin (pI = 6.9, p. 571) which is uniquely shared with *Emys*, *Clemmys*, and *Terrapene* (Fig. 20). From this point on, essentially all further studies, especially nucleotide sequencing, support the placement of *Deirochelys* and *Emydoidea* in separate lineages of the Emydidae (see Bickham et al., 1996; Feldman & Parham, 2002; Stephens & Wiens, 2003; Wiens et al., 2010; Thomson & Shaffer, 2010; Guillon et al., 2012; Joyce et al., 2012). The fossil record, functional morphology, and biochemical data all indicate that *Deirochelys* belongs to the aquatic group and *Emydoidea* belongs to the semiterrestrial line.

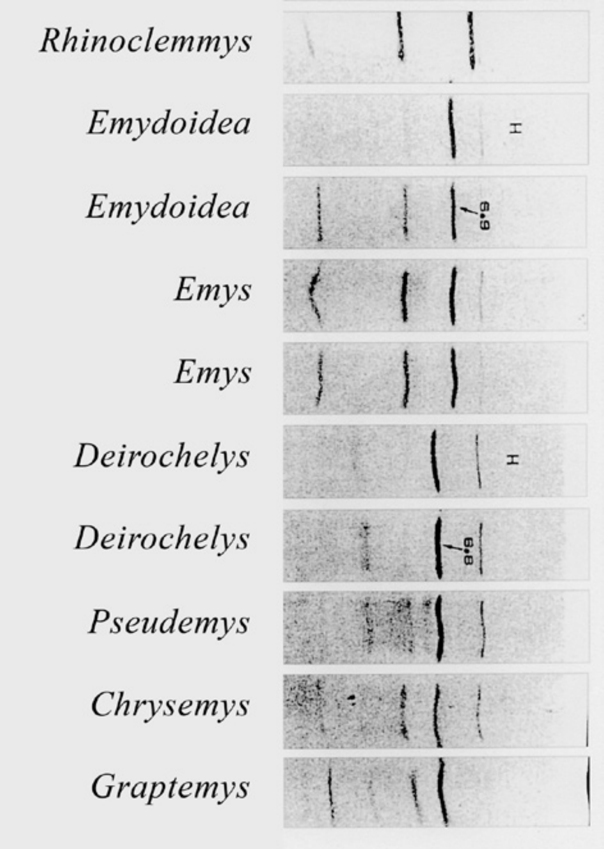


Fig. 20. Electrophoregram of skeletal muscle (unmarked) and heart (H) proteins separated by isoelectric focusing, pH 5-7. Tracks represent samples from different individual turtles. Myoglobin electromorphs are identified by their isoelectric points (pI) 6.8 or 6.9 (Seidel and Adkins 1989, fig. 2).

Two major phyletic lines of Emydids

With the relationship between *Deirochelys* and *Emydoidea* resolved, attention turned toward defining the taxonomic position of all emydid genera. In 1987, Eugene Gaffney and Peter Meylan hosted a symposium and workshop on systematics of turtles at the American Museum of Natural History (AMNH), New York. At that meeting, Seidel (unpublished, Fig. 21) presented a theory on phylogenetic relationships among emydid genera. Using cladistic methodology (PAUP), he analyzed 45 morphological and 5 biochemical characters. Character states were polarized using geoemydids and testudinids as outgroups. The results of this analysis were consistent with previous theories (based mostly on adaptations to habitat, e.g. Pope, 1939) that the family Emydidae (sensu Gaffney 1984) consists of a semiterrestrial lineage, *Clemmys* (including *Actinemys* and *Glyptemys*) *Emydoidea*, *Emys*, *Terrapene*; and an aquatic lineage, *Chrysemys*, *Deirochelys*, *Graptemys*, *Malaclemys*, *Pseudemys*, and *Trachemys*. Gaffney & Meylan (1988: 200) presented a phylogeny for emydids which indicated the same semiterrestrial and aquatic lines (clades) with regard to generic content. Although they used many of the osteological characters of Seidel (Fig. 21), their arrangement of genera in each clade was somewhat different (Fig. 22). Subsequently, molecular studies have substantiated this major bifurcation in emydid evolution (Seidel & Adkins, 1989; Bickham et al., 1996; Stephens & Wiens, 2003; Near et al., 2005; Thomson & Shaffer, 2010; Wiens et al., 2010; Dornburg et al., 2011; Reid et al,. 2011; among others). Gaffney & Meylan (1988) proposed a taxonomic name for each of the two clades: subfamily Emydinae (*nec* McDowell 1964) for the semiterrestrial lineage (p. 200), and subfamily Deirochelyinae for the aquatic lineage (p. 201). Emydinae is defined by the following synapomorphies: palatine bone excluded from the triturating surface of the jaw, posterior palatine foramen much larger than foramen orbito-nasale (Gaffney & Meylan, 1988; McDowell, 1964); and a unique myoglobin electromorph pI = 6.9 (Seidel & Adkins, 1989). Deirochelyinae was defined by the following synapomorphies: humeropectoral sulcus of the plastron excluded from the entoplastron (McDowell, 1964), occurring also in some *Emydoidea* (Gaffney & Meylan, 1988); jugal bone contacts palatine, and foramen caroticopharyngeale reduced or absent (Gaffney & Meylan, 1988); sexual size dimorphism with female larger (Berry & Shine, 1980; Fitch, 1981; Gibbons & Lovich, 1990; Ceballos et al., 2013); plica media of penis spade-shaped (Zug, 1966); no musk glands (pores) present on shell, except infrequently in *Malaclemys* (Waagen, 1972); rostral pores reduced, usually less than two (Winokur & Legler, 1974); plastral scutes sloughed in response to growth (Seidel, unpubl.); a unique myoglobin electromorph pI=6.8 (Seidel & Adkins, 1989: 571); and titillation courtship behavior (Seidel & Fritz, 1997). Note, there may only be rudimentary evidence of this specialized courtship behavior in *Malaclemys* (Sachsse, 1984, but see Seigel, 1980) and *Deirochelys* (see discussion in Seidel, 2010b). As the two lineages of Emydidae sensu stricto gained acceptance, some authors referred to them informally as two complexes, the the *Clemmys* group (p. 203) and the *Chrysemys* group (p. 204) (e.g. Ernst et al., 1994). Now, the formal names Deirochelyinae and Emydinae have received wide acceptance for the two groups (David, 1994; Bonin et al,. 1996; Ernst et al., 2000; Iverson et al., 2001; Bickham et al., 2007). Spinks et al. (2016) estimated "crown" ages of these two subfamilies which extend back to the Oligocene (31 Ma for Deirochelyinae and 29 Ma for Emydinae).

Subfamily Emydinae Rafinesque, 1815.
The Semiterrestrial Emydids

Nomenclatural History. — Similar to the authorship of the family Emydidae, that of the subfamily Emydinae has also been controversial. Several candidates are available, and all are discussed in the family taxonomy presented previously for Emydidae. Both the stem-root and type-genus of Emydidae and subfamily Emydinae are based

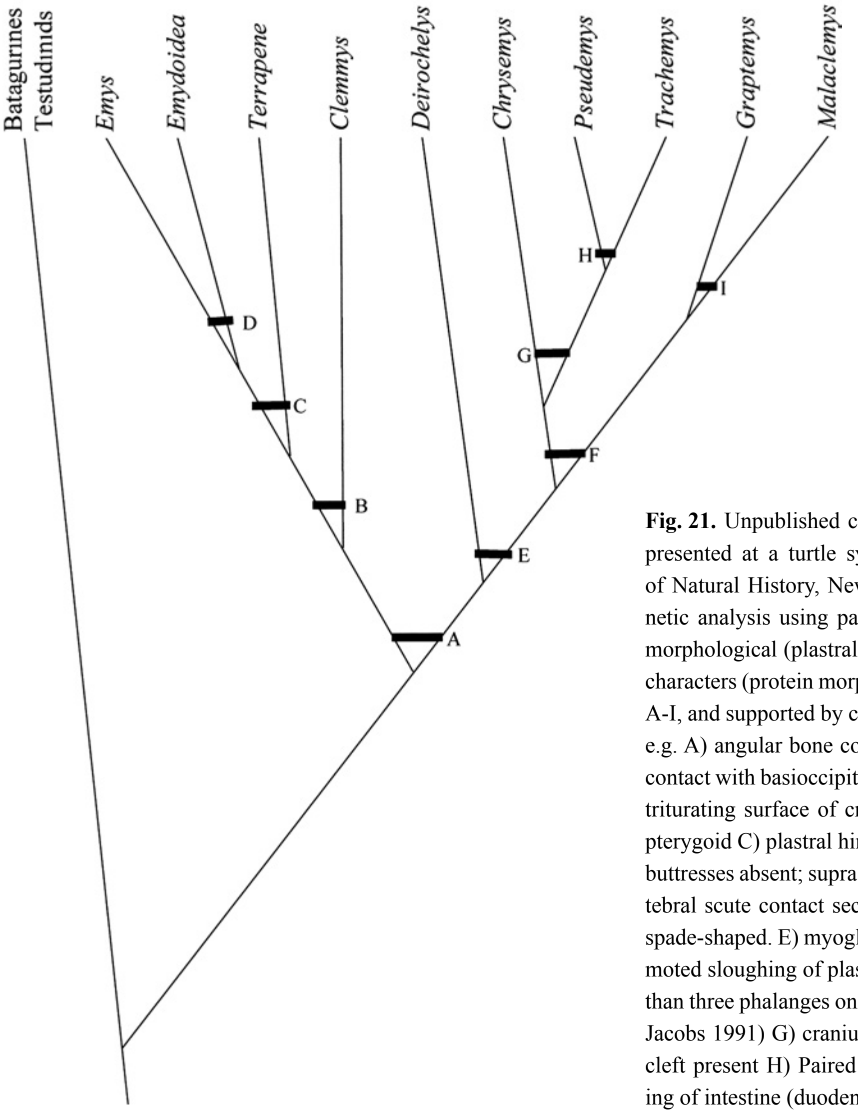


Fig. 21. Unpublished cladogram of emydid turtles (Seidel 1987), presented at a turtle systematic symposium, American Museum of Natural History, New York. Tree was constructed by phylogenetic analysis using parsimony (PAUP) based on 25 skeletal, 19 morphological (plastral scutes and soft anatomy), and 6 molecular characters (protein morphs). Nodes (clades) are identified by letters A-I, and supported by character states (presumed synapomorphies) e.g. A) angular bone contacts Meckel's cartilage; pterygoid not in contact with basioccipital B) myoglobin isoelectric point 6.9; upper triturating surface of cranium without contribution of palatine or pterygoid C) plastral hinge between hypoplastron and hyoplastron, buttresses absent; suprascapula present D) lateral seams of first vertebral scute contact second marginal scutes; plica media of penis spade-shaped. E) myoglobin with isoelectric point 6.8; growth-promoted sloughing of plastral scutes F) reduced mental glands; more than three phalanges on fifth toe of hind leg (refuted by McCoy and Jacobs 1991) G) cranium with median maxillary ridge; internarial cleft present H) Paired tubercles on lingual ridge of dentary; lining of intestine (duodenum) with zig-zag folds and cross bridges I) short cervical scute; premaxilla without median notch.

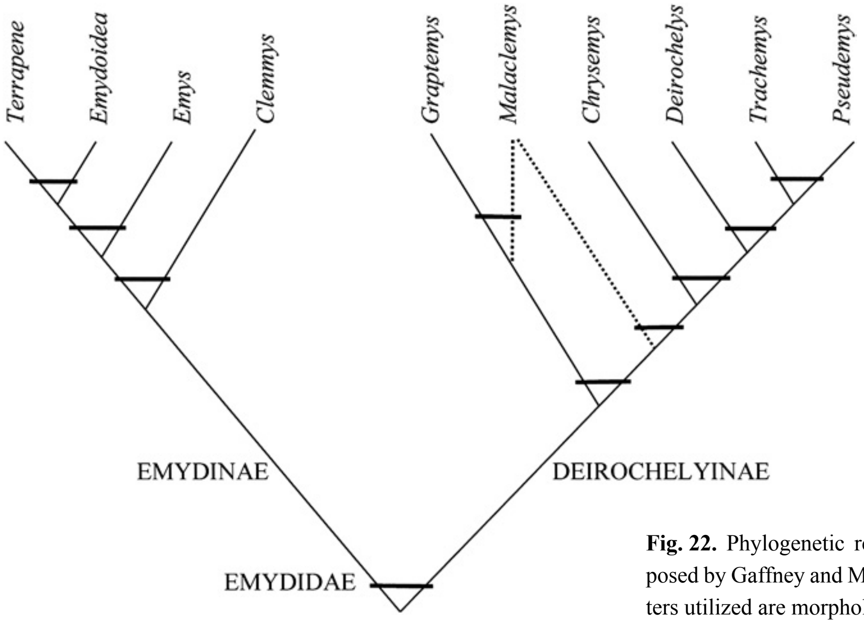


Fig. 22. Phylogenetic relationships in the family Emydidae proposed by Gaffney and Meylan (1988, fig. 5.11). Most of the characters utilized are morphological.

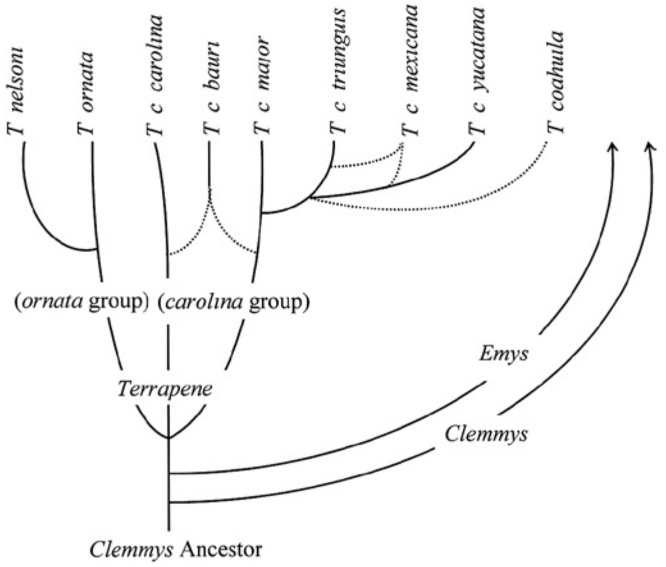


Fig. 23. A theory of relationships of North American Box Turtles (genus *Terrapene*); based on morphology of fossil and extant forms. Modified from Milstead (1969, fig. 3).

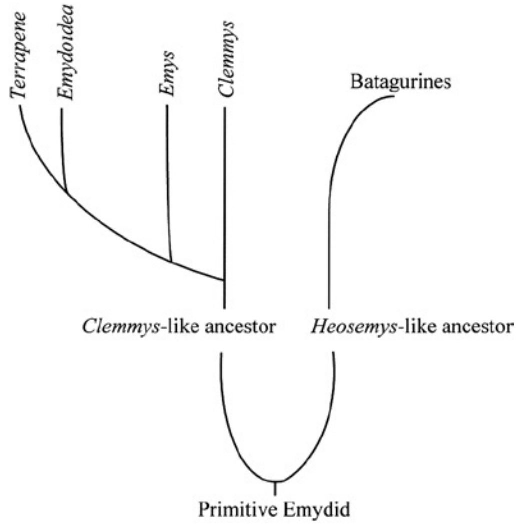


Fig. 24. Schematic representation of phylogenetic relationships among Box Turtles based on anatomy and morphology (modified from Bramble 1974, fig. 12).

on *Emys* Duméril, 1805: 76; which immediately eliminates Brongniart (1805: 27) and Schmid (1819: 11) who used the unavailable genus name *Emydes*, from consideration.

Gray (1825: 210) also introduced the family-subgroup name Emydina for these turtles, based on "Emys, *Brogn.*" (= *Emydes* Brongniart, 1805: 27), copied from an unpublished manuscript of Bell, and not *Emys* Duméril, 1805: 76. Gray's later (1831a: 19) *Emys* was also in error, and mistakenly based on "*Tri*[*onyx*]. (*Emyda*) *Punctatus*, Lacep." = *Testudo punctata* Lacépède, 1788: 171 (= *Lissemys punctata*), an Asian trionychid turtle (Smith 1931: 157); and as such, not available. In addition, Gray (1825) gave erroneous, reversed character descriptions of his two family groups Emydina (p. 210) and Terraphenina (p. 211). Gray (1831a: 7) corrected this by providing an accurate description of the transverse sutured (hinged) plastron subgroup of his all encompassing genus *Emys* (based on Lacépède's 1788 *Emyda*) including the species *Emys orbicularis* and *Terrapene carolina*, but also the modern species *Cuora amboinensis* and *C. trifasciata* of the family Geoemydidae Theobold, 1868: 9.

Rafinesque (1815: 75) introduced and described his family-group "EMIDANIA" (Baur 1892: 41 considered the name a misspelling of Emydania Rafinesque, 1815). Rafinesque's Emidania was clearly based on his newly created genus "*Emyda* R[afinesque]" which was the first genus listed on p. 75 as belonging to his new subfamily; and not based on the use of *Emyda* for a trionychid turtle (Gray 1831a: 49, see above). This makes *Emyda* Rafinesque, 1815, the type-genus of his subfamily Emidania; and also that for all nominal taxa at all ranks in the family-group (Principle of Coordination: Code; Articles 36, 43, and 46). Although it is an unjustified emendation, Rafinesque's *Emyda* is a *nomen novum* correctly derived from *Emys* Duméril, 1805: 76; and therefore Emidania is available as the subfamily name. Smith & Smith (1980) thought, in error, that Rafinesque's Emidania should be rejected as not formed from an explicitly recognized generic name [Code, Article 11.7]). Therefore, Rafinesque (1815: 75) should also be considered the author of the subfamily Emydinae.

Cope (1870: 123) was the first to correct the spelling of the subfamily to Emydinae, and not Lydekker (1889a, 1889b; = Emydin*ae*) as championed by Kuhn (1966), Smith & Smith (1980) and King & Burke (1989).

Relationships in the Subfamily Emydinae. — Following resolution of the phylogenetic position of *Emydoidea* (Jackson, 1978b; Seidel & Adkins, 1989), the generic content of subfamily Emydinae became well established. There remained little doubt that *Terrapene*, *Clemmys*, *Emys*, and *Emydoidea* constitute a monophyletic group. Prior to that, Loveridge & Williams (1957: 185) presented a dendrogram to depict relationships of emydines, although they claimed it was not phylogenetic (Fig. 5). In their arrangement, the genus *Ocadia* (*Mauremys*) (Asian batagurines) appears ancestral to *Clemmys* sensu lato which in turn gives rise to *Emys* along one branch and *Geoemyda* (another Asian batagurine) along another branch. *Geoemyda* is shown to give rise to *Terrapene*. As discussed earlier, these affinities, along with the position of *Emydoidea*, became viewed as unnatural based on the widely accepted designation of the Asian Batagurinae as a separate subfamily (McDowell, 1964: 254). McDowell described a relationship (Fig. 18) which is somewhat the reverse of that presented by Loveridge & Williams. He stated that "Although *Emys* appears to be closely related to *Clemmys* [sensu stricto] as defined here, it cannot be derived from *Clemmys*, for the latter genus is more specialized than *Emys* in the form of the jugal bone and the

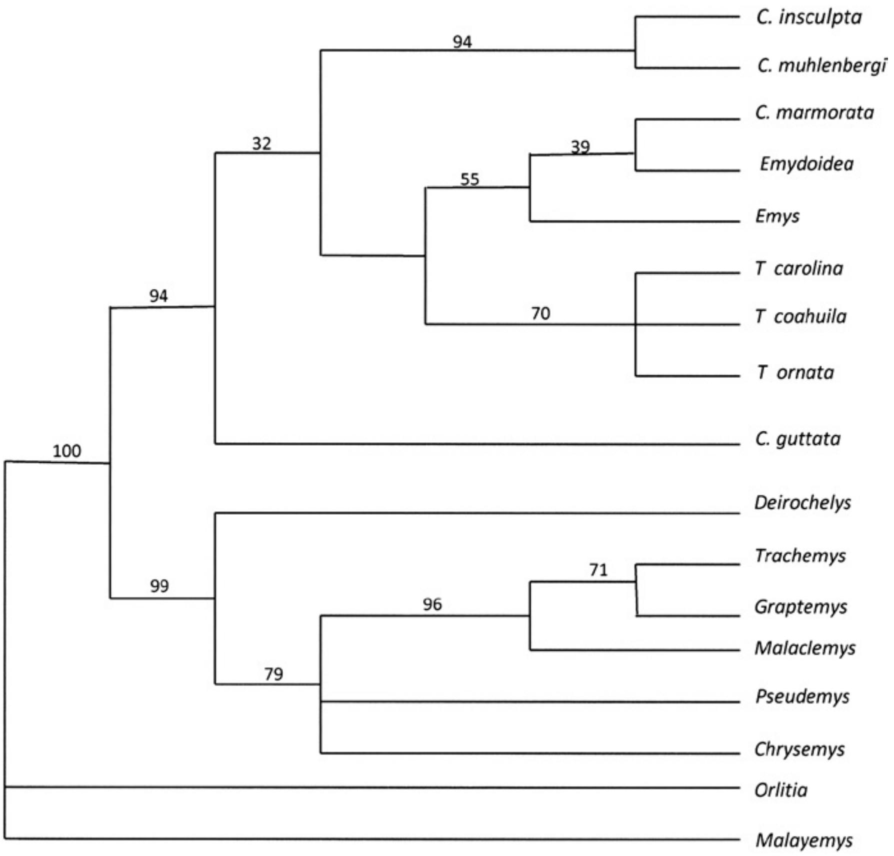


Fig. 25. Emydid relationships illustrated by a strict-consensus tree (based on sequencing of mitochondrial 16S ribosomal RNA gene) constructed from four most-parsimonious trees (Bickham et al 1996, fig. 3). The tree has a consistency index of 0.93. The numbers above certain branches are the percentage of trees generated by bootstrap analysis that support that particular branch.

enlarged caroticopharyngeal foramina." McDowell went on to say that "*Terrapene* is almost certainly an offshoot of *Clemmys*; which it particularly resembles in the large caroticopharyngeal foramina, and in spite of its hinged plastron seems much less closely related to *Emys* than to *Clemmys*." Milstead (1969) found more intergeneric variation in size of the caroticopharyngeal foramina than did McDowell. Similar to Loveridge & Williams (1957), Milstead on p. 19 illustrated *Clemmys* as a basal offshoot, followed by *Emys* and then *Terrapene* (Fig. 23). Bramble's (1974) theory on emydine phylogeny (based heavily on plastral kinesis) generally agrees with Milstead (1969). The main difference is that Bramble included *Emydoidea* in the lineage, and placed it as the sister group to *Terrapene* (Fig. 24).

Although differences exist in the central articulations of their cervical vertebrae (Williams, 1950), other studies which compare species in the genus *Clemmys* (Zug, 1966; Parsons, 1968; Merkle, 1975) have suggested that *C. guttata* and *C. muhlenbergii* are closely related, including a purported case of natural hybridization (Ernst, 1983). Following Agassiz (1857: 252) and Gray (1869: 196, 1870: 28), Ward (1980a: 286) separated *C. insculpta* into a monotypic subgenus *Glyptemys*, placing the other three species (*guttata*, *marmorata*, and *muhlenbergii*) in the subgenus *Clemmys*. He formed that decision from Monks's (1878) description of middle ear bones, Winokur & Legler's (1974) survey of rostral pores, and Merkle's (1975) protein electrophoretic data. Based on plastron scute morphology, Lovich et al. (1991: 428) concluded that *C. guttata*, *C. insculpta*, and *C. marmorata* form a group separate from the presumably more primitive *C. muhlenbergii*. However, subsequent work (especially DNA analysis) does not support these theories, and further indicates that a composite genus *Clemmys* is an unnatural taxon.

Our understanding of intergeneric relationships in the subfamily Emydinae has been greatly enhanced by nucleotide sequence data. Bickham et al.'s (1996) analysis of variation in the mt16S ribosomal RNA gene provides strong evidence that the genus *Clemmys* (comprised of the four North American species, sensu McDowell 1964) is paraphyletic. Their cladistic tests indicated that *C. guttata* is basal and the sister group of all the other emydines (Fig. 25). *Clemmys insculpta* and *C. muhlenbergii* formed a clade which is the sister group to *Terrapene* and a clade consisting of *C. marmorata*, *Emys*, and *Emydoidea*. The placement of *C. marmorata* in that clade was a departure from previous morphological analyses based on plastral kinesis (i.e. Milstead, 1969; Bramble, 1974). Bickham et al. (1996) indicated that the clade of *C. marmorata*, *Emys*, and *Emydoidea* has moderate support, 54% of the bootstrap trees based on sequence data. However, they did not address the significance of synapomorphies as-

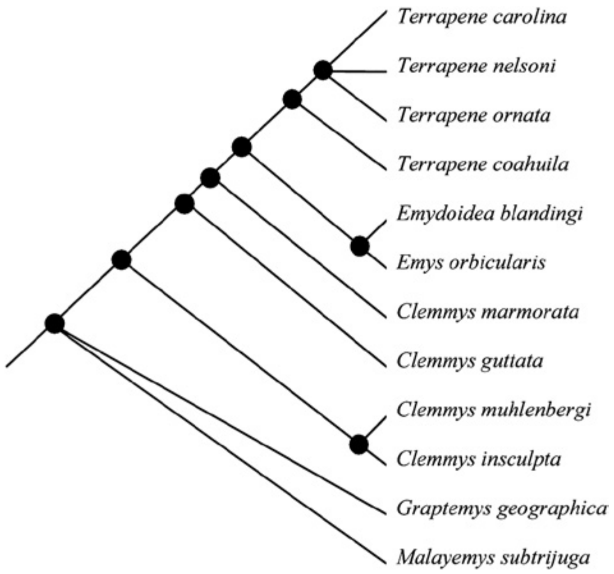


Fig. 26. Hypothesized phylogeny of emydine turtles based on all available evidence (i.e. morphology, behavior, life history, DNA) resulting from strict consensus of two most parsimonious trees (Burke et al. 1996, fig. 3).

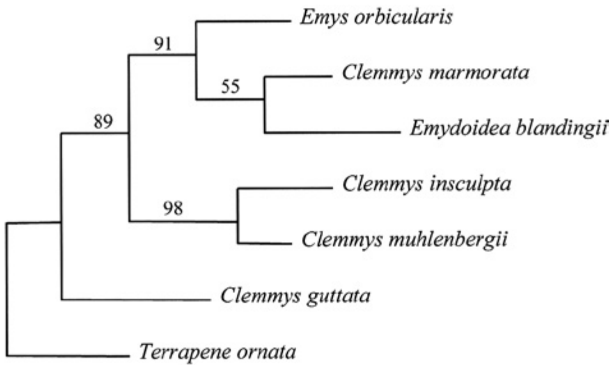


Fig. 27. A 50% majority rule consensus phylogram (based on nucleotide sequences) showing the results of maximum parsimony analysis. Bootstrap values derived from 500 replicates are indicated at nodes of the tree (modified from Lenk et al. 1999, fig. 2). Value not given for *C. guttata* node.

sociated with a hinged plastron. The clade of two sister species, *C. insculpta* and *C. muhlenbergii*, had strong support (93% of the bootstrap trees). Bickham and colleagues concluded that their findings "…could result in taxonomic name changes with *C. marmorata* and *Emydoidea* (Holbrook, 1838) being synonymized with *Emys* (Linnaeus, 1758)" (an arrangement later accepted by Feldman & Parham, 2002; Angielczyk et al., 2010; and Joyce et al., 2012). Nevertheless, Bickham et al. refrained from directly proposing a taxonomic revision. Based on analysis of mitochondrial DNA, Amato et al. (1997) presented further evidence that *C. muhlenbergii* is the sister species to *C. insculpta*. However, their results do not provide a test for monophyly of *Clemmys* because *Emys* and *Emydoidea* were not analyzed.

Burke et al. (1996) also examined phylogenetic relationships in the subfamily Emydinae. They used the ribosomal DNA data of Bickham et al. (1996) in addition to a wide range of behavioral, morphological, and life history data. Their analysis on p. 579 also indicated a clade formed of *C. muhlenbergii* and *C. insculpta*. This was followed on the same page by a branch giving rise to *C. guttata* and then a higher branch containing *C. marmorata* (Fig. 26). Burke and colleagues reported that *C. marmorata* is the sister group to a lineage of *Terrapene* and a clade of *Emydoidea* and *Emys*. This scheme is notable in that *C. marmorata* does not share a lineage (unique common ancestor) with *Emydoidea* and *Emys*. Nevertheless, the four species of *Clemmys*, as observed by Bickham and colleagues, appear to be paraphyletic but these authors also deferred taxonomic revision of the genus. The character states which join the species of *Clemmys* in the phylogeny of Burke et al. (1996) are apparently plesiomorphic. This raises the question whether or not a genus can be defined by primitive characters, especially if they are unique to its extant species. Most systematists would argue no, and reject such a taxon based on paraphyly.The clade of *Terrapene*, *Emys*, and *Emydoidea* reported by Burke et al. is consistent with the specialized (presumably derived) kinetic plastron which they share (Milstead, 1969; Bramble, 1974). Unlike other proposed phylogenies of the decade, it is consistent with the theory that a plastral hinge evolved only once in the Emydinae and has not been lost in any extant species.

Lenk et al. (1999) reported additional DNA sequence data (mt cytochrome b gene) for the Emydinae. Because their primary focus was to examine relationships among various populations of *Emys orbicularis*, they designated all of the other species (Nearctic emydines) as the outgroup. Therefore, the generic phylogeny described by Lenk and colleagues is limited by questionable character polarities. Nevertheless, their phylogenetic results are very similar to Bickham et al. (1996), indicating a paraphyletic *Clemmys* (Fig. 27). They found *C. insculpta* and *C. muhlenbergii* to be sister species (98% bootstrap) and a well-supported monophyletic clade of *C. marmorata*, *Emys*, and *Emydoidea* (91% bootstrap). Feldman and Parham (2001) reported on additional DNA analysis of emydines based on eight mitochondrial gene sequences. Their results were concordant with Bickham et al. (1996), finding that *Clemmys* is a paraphyletic genus and defining a lineage (clade) consisting of *C. marmorata*, *Emydoidea blandingii*, and *Emys orbicularis* (Fig. 28). In this paper, Feldman and Parham deferred proposing a revised monophyletic taxonomy to a paper they cited as "in press" (= Feldman & Parham, 2002). Seidel's (2002b) report on hemoglobin variation among emydids also provided molecular data suggesting that the genus *Clemmys* is not monophyletic. Ernst (2001) reviewed the evidence for intrageneric relationships in *Clemmys* and concluded that the taxonomy is confounded by conflicting data sets.

Holman & Fritz (2001) published a paper describing a new fossil species of *Clemmys* from the Middle

Miocene (Barstovian) of Nebraska (p. 335). They found that the turtle, *valentinensis*, is most closely allied to *C. insculpta* and *C. muhlenbergii*. Recognizing that the genus *Clemmys* is paraphyletic based on data published by Bickham et al. (1996), Burke et al. (1996), and Lenk et al. (1999); Holman and Fritz proposed a revision of the genus. They split off (p. 334) *C. insculpta* and *C. muhlenbergii* into the genus *Glyptemys* which Agassiz (1857: 443) had originally proposed for the species *insculpta*. They further suggested that *G. valentinensis* could be the last common ancestor of these two species, thus indicating a Miocene origin for the clade. This lineage may be unique among the emydids in its absence of temperature-dependent sex determination (TSD). In contrast to all other turtles which have been tested in the family, *G. insculpta* has genetic sex determination (Ewert & Nelson, 1991: 53). *Glyptemys muhlenbergii* is one of the few species which has not been tested, probably due to its endangered status, but it would be phylogenetically informative to determine if it also lacks TSD. Holman & Fritz (2001) resolved the paraphyletic position of *C. marmorata* by assigning (p. 334) it to the genus *Actinemys* (also sensu Agassiz 1857: 252), thus leaving only *C. guttata* in the now monotypic genus *Clemmys*.

Feldman & Parham (2002) examined emydine relationships based on DNA variation of the mt cytochrome b, ND4 genes and adjacent tRNAs. As stated earlier, their results (Fig. 28) are very similar to those of Bickham et al. (1996), indicating that *C. insculpta* and *C. muhlenbergii* are sister species (100% bootstrap) and *C. marmorata* forms a clade with *Emys* and *Emydoidea* (98% bootstrap). Also similar to recent studies, Feldman & Parham (2002: 393) found that the phylogenetic position of *C. guttata* lacks good statistical support and left it in the genus *Clemmys*. They assigned *insculpta* and *muhlenbergii* to the genus *Calemys* (p. 394), proposed originally by Agassiz (1857: 252) for *C. muhlenbergii.* However, it appears that the genus name *Glyptemys* (sensu Agassiz 1857: 252, *G. insculpta*) has legitimacy (ICZN First Revisor Principle; Code, Article 24: 2.1, cited by Holman and Fritz, 2001: 333). Feldman & Parham (p. 394) resolved the paraphyletic position of *C. marmorata* by transferring it, along with *Emydoidea blandingii*, into the formerly monotypic genus *Emys* (i.e. *Emys orbicularis*). Their argument for this nomenclature was that it provides greater phylogenetic information than three separate monotypic genera. They claimed this as a conservative approach because *marmorata* was originally assigned by Baird & Girard (1852: 177) to *Emys*. However, the genus *Emys* at that time was a large composite of many emydid species (see Holbrook, 1838). Perhaps a stronger point Feldman & Parham (2002) could have raised is the more recent recognition of *Emys* as a bitypic genus including *E. orbicularis* and *E. blandingii* (Stejneger & Barbour, 1917–1943; Pope, 1939; Carr, 1952; Schmidt & Inger, 1957; Wermuth & Mertens, 1961).

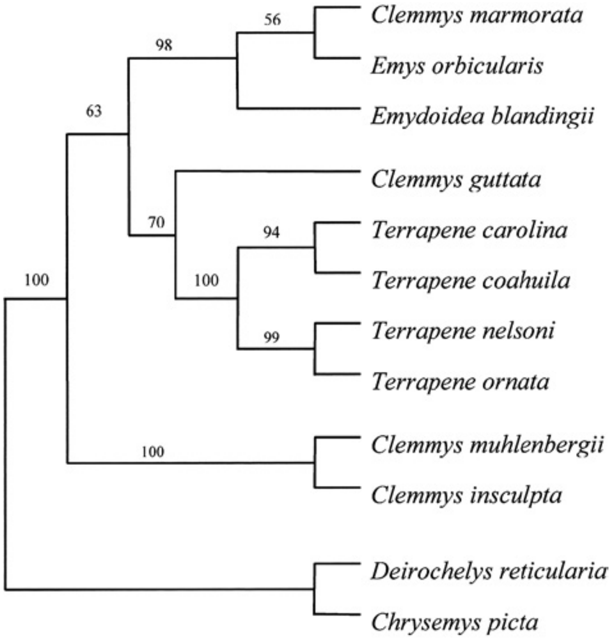


Fig. 28. Single most parsimonious phylogenetic tree for emydine mitochondrial DNA lineages (modified from Feldman and Parham 2001, 2002 fig. 4A). Numbers at nodes indicate bootstrap support.

Concerns with the arrangement of Feldman & Parham (2002) are firstly that it proposes more taxonomic change than is necessary to retain monophyly; and therefore is not consistent with one of the major goals of biological classification "conservation of taxonomic stability" (see discussions by Iverson et al., 2008 and Pauly et al., 2009). Secondly, it assigns two kinetic species with specialized modifications of the scapula bone (*E. blandingii* and *E. orbicularis*), to the same genus as the akinetic less specialized *marmorata*. Thus, it requires the unparsimonious assumption that either *marmorata* has lost the kinetic plastral condition or kinesis has evolved twice in the Emydidae (i.e. independently in *Terrapene*). The former hypothesis is problematic because it would require loss (reversal) of a presumably favorable adaptation, hinging of the plastron in *marmorata*. Unfortunately, the chelonian fossil record does not provide for this. There is apparently no evidence that reversal has occurred in the other two turtle families (i.e. Geoemydidae and Kinosternidae) which contain kinetic species (J. Iverson, pers. comm.). Furthermore, a composite *Emys* (sensu Feldman & Parham 2002: 394) is problematic because it does not account for the highly specialized scapular structure which appears to be "synapomorphic" for all emydines with a hinged plastron (*Emys*, *Emydoidea*, *Terrapene*) and absent in *marmorata* (Bramble, 1974). Parham & Feldman (2002) minimized the significance of this clearly-defined derived character, and referred to shell kinesis as a general, weakly defined condition which may even vary intraspecifically. To the contrary, as pointed out by Bramble (1974), none of the many cases of complete or partial shell kinesis in the order Testudines show evidence of the specialized episcapula or suprascapula bones found exclusively in *Emys orbicularis*, *Emydoidea blandingii*, *and Terrapene*. He concluded (p. 724) that "A multiple origin for the complex closing mechanism held in common by these box turtles appears extremely remote." Angielczyk et al. (2010), in a study based on plastron morphology, concluded that the further phylogenetically removed taxa are, the more distinct their kinetic modifications. The phylogeny presented by Burke et al. (1996: 579) avoids the tenuous assumptions of multiple evolution or reversal of kinesis in *Emys* (sensu Feldman & Parham) by placing *C. marmorata* as the sister group to all of the kinetic emydines, including *Terrapene*. Unlike the other species of *Clemmys*, *C. marmorata* has bony/ horny seams on the bridge which are aligned as they also are in the kinetic emydines (i.e. *Terrapene*, *Emys*, and *Emydoidea*). Joyce et al. (2012: 187) mistakenly reported the bridge seam as ligamentous and kinetic [it is not], and assigned *A. marmorata* to the genus *Emys* (along with *E. orbicularis* and *E. blandingii*). Holman & Fritz (2001) suggested seam alignment along the bridge of *marmorata* as evidence for reversal, i.e. regression of functional plastral hinging. Perhaps a more parsimonious interpretation (consistent with Burke et al., 1996) is that seam alignment served as a pre-adaptation for the evolution of plastral kinesis in *Emys*, *Emydoidea*, and *Terrapen*e, but not in *marmorat*a.

There appears to be molecular support for a clade formed of *Emys orbicularis*, *Emydoidea blandingii* and *Clemmys marmorata*. Nevertheless, lumping all three species under *Emys* (sensu Feldman & Parham 2002; Parham & Feldman, 2002; Spinks & Shaffer, 2005, 2009) is not compatable with alternative phylogenetic theories based on morphology or ancient hybridization. Furthermore, treating them as congeners obscures their pronounced interspecific divergence, especially the extreme osteomorphology of *Emydoidea*. This raises a philosophical question as to whether or not anagenesis (divergent, or upward, evolution) should be reflected in taxonomic nomenclature (see Mayr & Bock, 2002 for discussion). Based on these concerns and in the interest of minimizing nomenclatural change, the Committee on Standard English and Scientific Names for turtles (Crother et al., 2003; Crother, 2008, 2012) followed the revision of *Clemmys* proposed by Holman & Fritz (2001). This arrangement recognized *Emys*, *Emydoidea*, *Actinemys* (*marmorata*), and *Clemmys* (*guttata*) as monotypic extant genera, *Glyptemys* as bitypic (*G. insculpta* and *G. muhlenbergii*) and *Terrapene* as polytypic. Early assumptions that *guttata* and *muhlenbergii* are sister species (based partially on putative hybrididization and their small size) are incorrect. Angielczyk & Feldman (2013) demonstrated that the diminutive size of *muhlenbergii* results from modified duration of ontogeny and consequential shape change, whereas the small size of *guttata* is the product of growth-rate change.

Recent molecular studies, based on both nuclear and mitochondrial DNA, have consistently supported a clade (sister taxon) of *G. insculpta* and *G. muhlenbergii* (Wiens et al., 2010; Thomson & Shaffer, 2010; Guillon et al., 2012). Most of the molecular evidence suggests that it diverged early (basal) from the rest of the subfamily. Stephens & Wiens' (2003) comprehensive phylogenetic analysis of Emydidae included a large data set of published molecular and morphological characters. Their cladistic analysis indicated a paraphyletic *Clemmys* similar to previous studies. It defined a clade consisting of *Emys*, *Emydoidea*, and *Actinemys* which formed the sister group to *G. insculpta* and *G. muhlenbergii* (Fig. 29). Iverson et al. (2007) adopted this phylogeny in their "Tree of Life for Turtles." It clearly assumes that plastral kinesis evolved twice, once in the *Terrapene* line and again in the *Emys*-*Emydoidea* clade. Also as seen in previous phylogenies, support for the position of *Clemmys guttata* is weak, less than 50% bootstrap proportion. The concept that *Clemmys* (i.e. *C. insculpta*, *C. marmorata*, C. *muhlenbergii*, *C. guttata*) is an unnatural taxon has received strong support and broad acceptance since the turn of the century. Nevertheless, several authors (e.g. Buhlmann et al., 2008a; Gosnell et al., 2009) continued to use the traditional concept of *Clemmys* (sensu McDowell 1964: 276) in spite of clear evidence that it is a paraphyletic taxon.

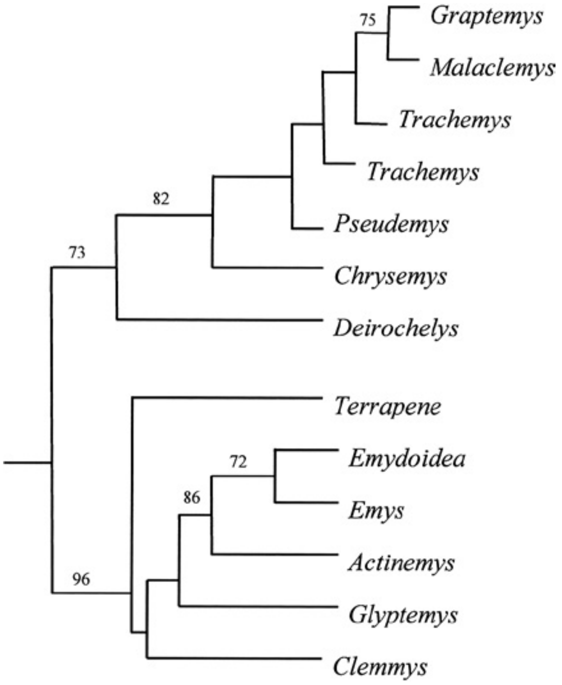


Fig. 29. A tree generated from parsimony analysis of combined morphological and molecular data for genera of emydid turtles. Numbers associated with each branch are bootstrap proportions; values below 50 not shown (modified from Stephens and Wiens, 2003 fig. 7).

Fritz et al. (2011) reviewed the competing taxonomic classifications and hypotheses for the phylogeny of turtles within the Emydinae, and presented a good summary. They concluded that the formerly recognized genus *Clemmys* is clearly paraphyletic, with two of its former species (*Glyptemys insculpta*, *G. muhlenbergii*), making up a well-supported basal clade within the subfamily (sensu Spinks & Shaffer 2009 and Wiens et al., 2010). However, the phylogenetic position of the other two species traditionally assigned to *Clemmys* (*guttata*, *marmorata*) is still controversial as previously discussed. Fritz et al. (2011) suggested that contradictory branching patterns are caused by lineage sorting problems of the selected gene loci, and recommended the continued use of separate genera for *Actinemys*, *Emydoidea*, and *Emys.* They claimed that placing *Actinemys* in the same genus as *Emydoidea* and *Emys* is unacceptable under a phylogenetic classification framework because there is evidence for the non-monophyly of such a clade. Fritz et al. also stated that *Actinemys*, *Emyodidea*, and *Emys* show greater morphological divergence (anagenesis) than seen among species in other emydid genera. Furthermore, these three genera may be considered polytypic based on the fossil species *Emydoidea hutchisoni*, recognition of the cryptic species *Emys trinacris* (Fritz et al., 2005b), and proposed splitting of *Actinemys marmorata* (Spinks et al., 2014).

Debate on species content of *Emys* and recognition of the monotypic genera *Actinemys*, *Clemmys* and *Emydoidea* has not been resolved. An example of that comes from modern checklists which offer alternate generic names (Bonin et al., 2006; Fritz & Havăs, 2007; Turtle Taxonomy Working Group, 2007, 2009). Spinks & Shaffer (2009: 17) stated that phylogenetic relationships in the proposed *Emys* complex (*orbicularis*, *marmorata*, and *blandingii*) and an adequate explanation for its biogeograhic distribution remain obscure. Based mostly on nuclear DNA analysis, these authors concluded that *blandingii* and *orbicularis* form a sister group, which justifies their recognition as congeners in the genus *Emys* (sensu Carr 1952: 132). In contrast, their mitochondrial DNA analysis suggests a sister group relationship between *blandingii* and *marmorata*. Spinks & Shaffer (2009: 13) concluded that this incongruence is real and is the result of an early divergence of *marmorata* in North America about 23 million years ago (Ma) with subsequent divergence of ancestral *blandingii* and *orbicularis* around 17Ma. Presumably this was followed by *blandingii* and *marmorata* coming back into geographic contact ~12 Ma, which allowed for introgression and infusion of *Emys* mitochondrial DNA (*blandingii* mitotypes) into *marmorata* (Fig. 30). Assuming this theory is correct, placement of *blandingii* in the genus *Emys* is justified but inclusion of *marmorata* (sensu Parham & Feldman 2002) would not be prudent. Some of the molecular data (e.g. mitochrondrial DNA, Bickham et al., 1996 and nuclear DNA, Spinks et al., 2009a) is consistent with *Terrapene* evolving along the ancestral line of an *Emys* complex. If *Terrapene* diverged later than *Actinemys*, perhaps 18–20 Ma (note that the oldest recorded Box Turtle fossils are 15 Ma; Dodd, 2001: 26), that could suggest a monophyletic origin of plastral kinesis in the Emydinae. On the other hand, data presented by Spinks et al. (2016) suggest a slightly earlier divergence (origin) for *Terrapene* compared to *Actinemys*, although they acknowledge uncertainty regarding these estimates.

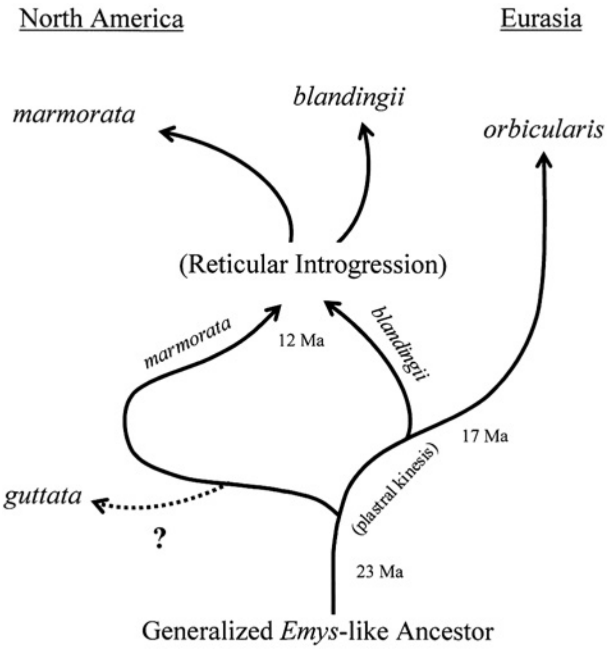


Fig. 30. Representation of an evolutionary theory for species in the *Emys* complex; constructed from concepts (e.g. reticular introgression) described by Spinks and Shaffer 2009. Ma = million years ago.

From analysis of nuclear DNA, Wiens et al. (2010), and subsequently Angielczyk & Feldman (2013), found *marmorata* to be the sister group to *C. guttata* (Fig. 31). Perhaps additional study will substantiate that relationship and justify placement of *marmorata* back into the genus *Clemmys*. A genus *Clemmys* including both *guttata* and *marmorata* had been suggested by Ernst (2001), and it would reduce the number of monotypic genera in the family. Based mostly on mitochondrial DNA, Spinks et al. (2009a; Fig. 32) and Thomson & Shaffer (2010; Fig. 33) indicated *C. guttata* as the sister taxon to *Terrapene*. However, limitations of mitochondrial DNA analysis in sorting out phylogenetic relationships have been revealed by Galtier et al. (2009) and Spinks & Shaffer (2009). Guillon et al. (2012) state that "…the fast evolutionary rate of mtDNA may cause higher levels of homoplasy and thus induce errors in phylogenetic reconstructions." Most recently, Spinks et al. (2016) state that "…we consider phylogenies generated from mtDNA only to be generally unreliable phylogenetic hypotheses for the Emydidae." Mitochondrial DNA data were included in the calculation of three of the four trees presented by these authors. Two of these indicated a sister group of monotypic *Clemmys* (*C. guttata*) and *Terrapene* while the third, a consensus tree, was unresolved (polytomous) for these genera. A fourth tree, constructed exclusively from nuclear DNA, depicted *Clemmys* as the sister taxon to a large clade of *Terrapene*, *Emys*, *Emydoidea*, and *Actinemys.* From this, Spinks et al. (2016) expressed uncertainty regarding *Clemmys* and *Terrapene* as a sister group and referred to the position of the former as "unstable."

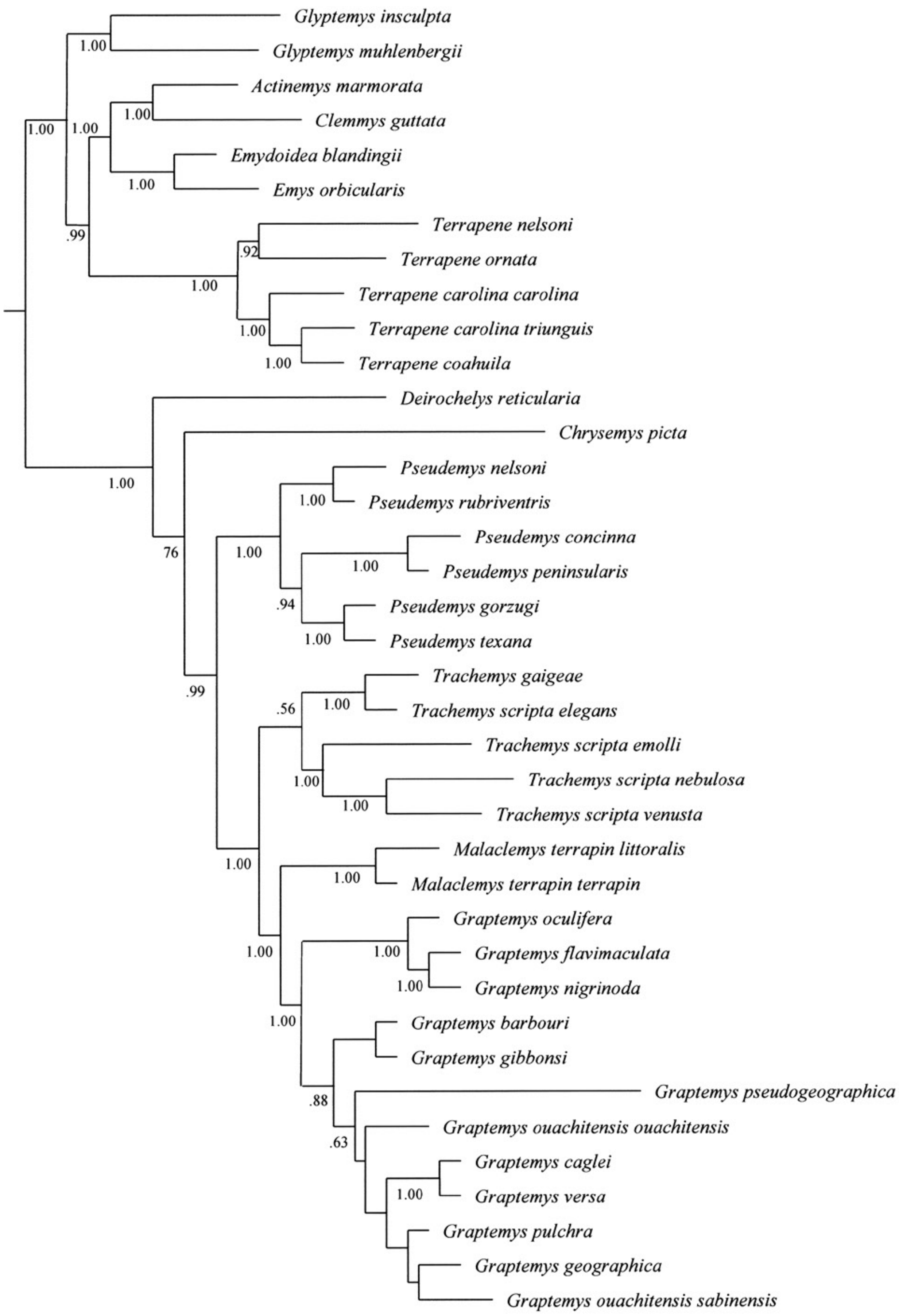


Fig. 31. Phylogeny of emydid turtles based on a combined, partitioned Bayesian analysis of DNA sequences from six nuclear loci. Probabilities adjacent to nodes indicate Bayesian posterior probabilities greater than 0.50 (modified from Wiens et al. 2010, fig. 2).

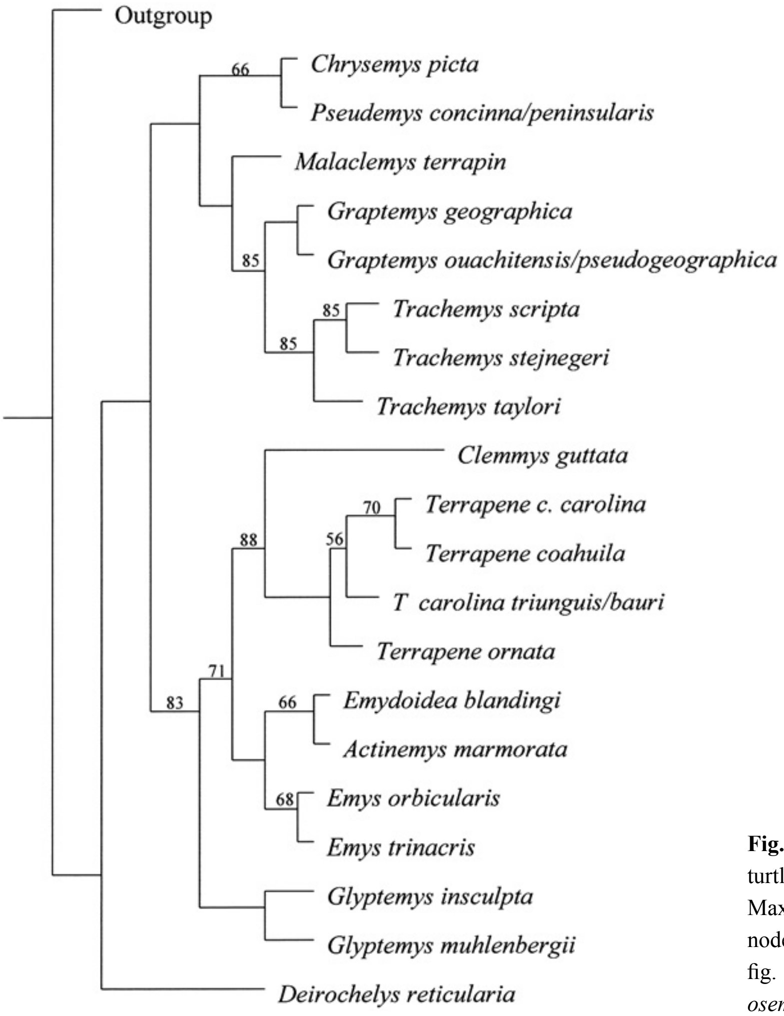


Fig. 32. Maximum likelihood phylogeny for emydid turtles based on mitochondrial cytochrome b data. Maximum parsimony bootstrap values are indicated for nodes less than 90 (modified from Spinks et al. 2009a, fig. 1). Outgroup includes *Chelonia*, *Platysternon*, *Heosemys*, *Mauremys*, and *Psammobates*.

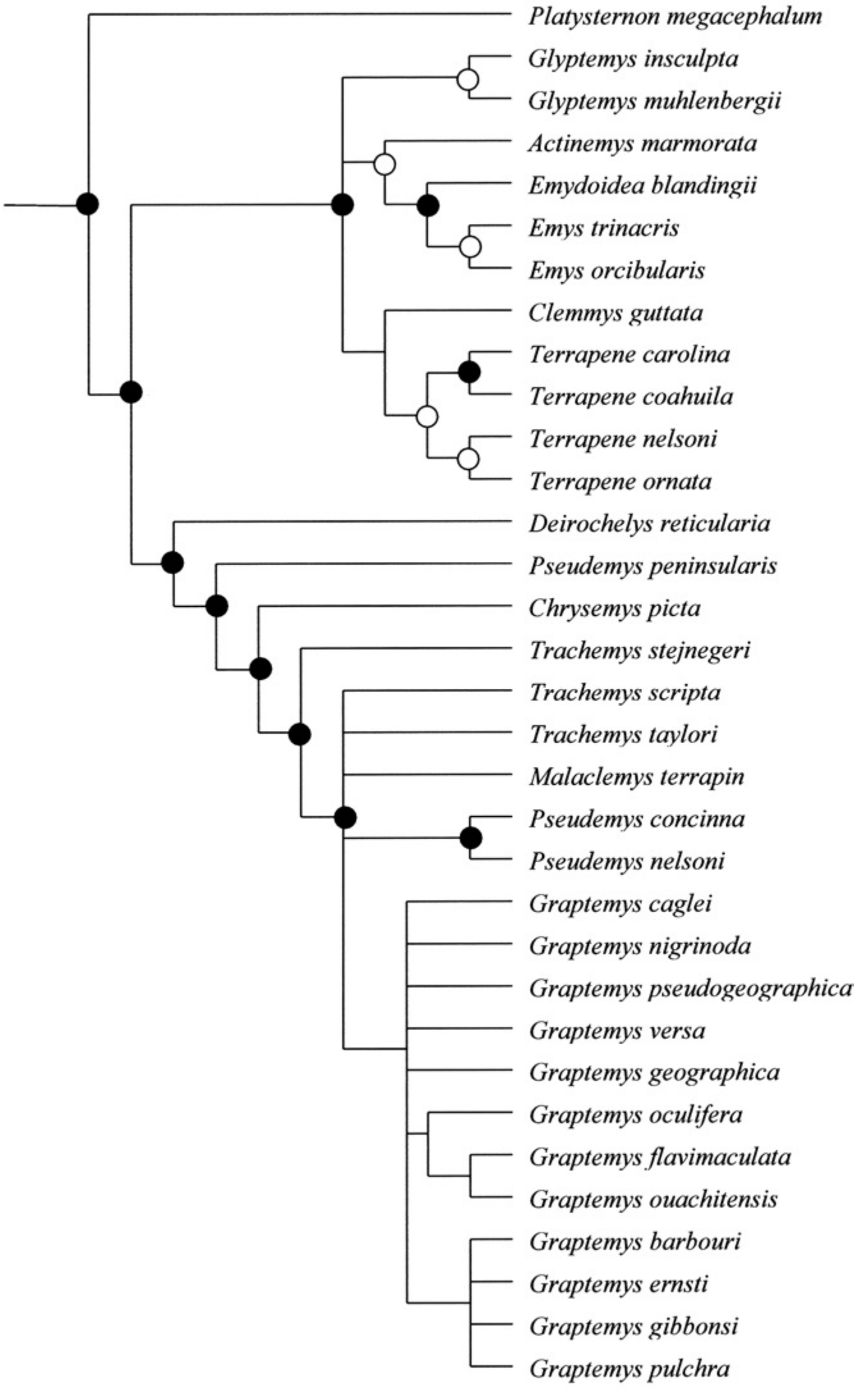


Fig. 33. Phylogenetic relationships among emydid turtles. A majority rule consensus tree derived from a supermatrix data set of nuclear and mitochondrial DNA. Open circles denote nodes with bootstrap proportions greater than 90, closed circles represent proportions greater than 70, and those without circles are less than 70. Modified from Thomson and Shaffer (2010, fig. 5).

Taxonomy Within Emydine Genera.

Emys Duméril, 1805

The genus *Emys* Duméril, 1805: 76 has usually been considered monotypic during recent decades, consisting only of the European Pond Turtle, type species *Emys orbicularis* (Linnaeus, 1758: 198) [but, see Fritz et al., 2005b]. It has an oval, moderately depressed, posteriorly widened, unserrated carapace. According to Fritz (1998), living individuals of *E. orbicularis* may reach a carapace length of 23 cm; however, the majority of subspecies average 12 – 15 cm. Distinct sexual dimorphism is present; males are smaller and flatter than females, and males of most subspecies have reddish irises. Juveniles have a pronounced medial keel that becomes obscured with age. The carapace is usually black, but can be dark brown, olive-brown, chestnut-brown, or yellowish-brown, and is often patterned with yellow to tan dots or radiations. The large plastron varies from almost entirely black to dark brown, brown, or yellow with or without dark markings (particularly along its seams). It has a movable transverse hinge between the pectoral and abdominal scutes (the underlying hyo- and hypoplastral bones), but lacks buttresses in adults. The crushing surface of the upper jaw is narrow and lacks both a ridge and serrations. The head may bear yellowish spots or streaks. The throat is variably colored from black to entirely yellow. Most morphological and color variation occurs in southern European populations. Loveridge & Williams (1957), Fritz (2001b), and Kuzmin (2002) provide more detailed descriptions of the species. Synonyms, particularly those pertaining to subfossils, are listed in Fritz (2001b), Fritz & Havaš (2007), Fritz et al. (2009), and below. The complete mitochondrial DNA genome of *E. orbicularis* has now been sequenced (Lourenço et al., 2012).

Emys orbicularis has an extensive distribution ranging on three continents from the Aral Sea of western Kazakhstan, the Caspian Sea in Russia, Kazakhstan, Turkmenistan, and Iran, and Russia's southern Ural and Caucasus mountains westward through Turkey, the Ukraine and Baltic countries of Latvia and Lithuania, eastern Germany, central France (disjunct); and into southern Europe including Greece, Italy, southern France, Spain, and Portugal. It is also known from Corsica, Sardinia, and Balearic Islands (introduced), and is present on several of the larger and smaller Aegean Islands (Broggi & Grillitsch, 2012). *Emys orbicularis* also occurs in parts of the northwestern African nations of Tunisia, Algeria, and Morocco (Ernst & Barbour, 1989; Arnold & Ovenden, 2002; Fritz, 2001b, 2003). Within this range the Pond Turtle inhabits slow-moving water bodies with soft mud or sand bottoms and abundant aquatic vegetation. It has been found in ponds, lakes, marshes, swamps, brooks, streams, rivers (especially their deltas), and drainage canals. It is relatively tolerant of both brackish and polluted waters.

Formerly *E. orbicularis* was distributed more widely, as postglacial remains have been found in Sweden, Denmark, the Netherlands, Belgium, Estonia, and England (Loveridge & Williams, 1957; Fritz, 1995c). Human agricultural practices possibly extirpated the turtle in much of Central Europe; but it was reintroduced into some parts of this area (Arnold & Ovenden, 2002; Fritz & Havaš, 2004; Fritz et al., 2005a). Sommer et al. (2007, 2009) presented data which indicate that climatic change played an important role in shaping the current distribution of the species. Based on radiocarbon dating and examination of DNA sequences of a large sample of subfossils, they reconstructed Holocene range fluctuations of the species in northern and central Europe. Their data show colonization of those regions from a glacial refuge located in the southeastern Balkans. *Emys orbicularis* was already in northern Central Europe in the Late Preboreal (9100–8600 years ago) and occupied much of Denmark and southern Sweden during the Boreal (8600–7100 years ago). Sommer et al. (2007) hypothesized a minimum dispersal rate of 50 km per 100 years during that period. Maximum range expansion apparently occurred during the Holocene's optimum Atlantic climatic period (7100–3750 years ago) when the turtle reached southern England, central Sweden (58°30'N), and northern Estonia. The species also spread through much of Germany and France during the same favorable period. Once Europe had been colonized, northern populations were probably established by long distance migration along two routes which possibly followed rivers flowing into the Baltic and North seas. Pond turtles apparently reached the Baltic coast at least 9000 years ago. The Swedish subfossil record of *E. orbicularis* ends approximately 5500 years ago as extirpation of the northern populations coincided with climatic cooling and oceanization prior to the Subboreal (Sommer et al., 2009). Recolonization of Sweden may have been prevented by Holocene submergence of the land connection across the Danish Straits. This left the species occupying a more southern distribution generally comparable to its present natural range.

Emys (feminine gender) was first used as a vernacular name, "*EMYDES* (*emys*)," by Duméril (1805: 76). In a taxonomic key on the next page, Duméril used *Emyde* as the genus of *E. orbicularis*, but did not designate a type species. The taxon *Testudo lutaria* Linnaeus, 1758: 198 (a junior subjective synonym of *Testudo orbicularis* Linnaeus, 1758: 198) was subsequently used for the genus *Emys* Duméril, 1805, by Lindholm (1929: 281–282), and was accepted as the type species of the genus by the first revisor action of Mertens & Wermuth (1960: 12; ICZN 1995, Opinion 1800: 111) who also included *E. blandingii* in the genus. *Emys* has been used since the early nineteenth century as the genus for *Emys orbicularis* and synonyms (Schweigger, 1812; Merrem, 1820; Gray, 1831a; and others).

Our interpretation of the taxonomy recognizes only two living species in the genus *Emys* (*E. orbicularis* Linnaeus, 1758: 198 and *E. trinacris* Fritz et al., 2005: 364; Fritz & Havaš, 2007), but see other interpretations discussed under *Actinemys* and *Emydoidea*. Fossils belonging to *Emys* have been found in European stratigraphic deposits dating from the Upper Miocene to present (Mlynarski, 1976; Fritz, 1995c, 1998, 2001a, 2001b; Holman, 1998; de Broin, 2001, Chesi et al., 2008). Because *E. orbicularis* and *E. trinacris* are the only "Old World" emydids, their evolutionary history is of particular interest. Paleo-species assigned to *Emys*, with the possible exception of the Pliocene *E. wermuthi* Mlynarski, 1956: 154, are chronospecies leading to the extant *E. orbicularis* (Fritz 1995c). The first two are from the Middle to Upper Miocene (8.5–14 Ma) of the Ukraine: *Emys tarashchuke* (Chkhikvadze 1980: 722) and *Emys sukhanovi* (Chkhikvadze, 1983: 56). *Emys tarashchuke* was originally *Emidoidea tarashchuki* (both genus and trivial names are *lapsus calami* for *Emydoidea tarashuke*, of which *Emydoidea tasbaka* Chkhikvadze 1989: 24 is a junior synonym). The latest apparent link in the development of *E. orbicularis* is the middle Pliocene

(2.8–4.0 Ma) *E. o. antiqua* Khosatzky, 1956: 325. Its description is preceded by a photograph on p. 323 bearing the name "*Emys orbicularis antiqua*" and has synonyms *Clemmys mehelyi* Kormos, 1911: 508 [from Hungarian fossils, now assigned to the fossil genus *Clemmydopsis* Boda, 1927 by Fritz & Farkas, 1996: 104]; and *Emys semjonovi* Chkhikvadze, 1983: 57–58 (from eastern and central Europe, and possibly also Georgia and Italy; Fritz, 1995c). These three taxa are represented by various carapace and plastron bone fragments which show developmental changes leading to the shell structure of modern *E. orbicularis*; but unfortunately no remains of the skull, neck, or thoracic rib cage (which could be more diagnostic) have been found.

The exact position of *Emys wermuthi* Mlynarski, 1956: 154, from the Polish Pliocene (2.5–4.5 Ma) is uncertain. It appears to be a more terrestrial turtle than *E. orbicularis*. While some of its shell measurements fall within the ranges of extant subspecies of *E. orbicularis*, others do not (Fritz, 1995c). Some shell ratios of *E. wermuthi* are comparable to those of turtles from intergradation zones between *E. o. orbicularis* (Linnaeus, 1758: 198) and *E. o. galloitalica* (Fritz 1995c: 217). At present, data are insufficient to determine if *E. wermuthi* was a component of the general evolutionary path to *E. orbicularis*.

Fritz (1998) hypothesized that the precursors of the genus *Emys* most likely crossed the Bering Land Bridge from North America to the Palaearctic during the Middle or Upper Tertiary, implying a subsequent Old World radiation of the genus from East Asia westward into Europe and northern Africa. His conclusion was based on Miocene and Pleistocene fossils that are distributed from east to west (Khosatsky, 1956; Mlynarski, 1956, 1976; Chkhikvadze, 1980, 1983, 1989; Caloi et al., 1981; Fritz, 1995c, 1998, 2001a, 2001b; Holman, 1998; Hervet & Salotti, 2000; de Broin, 2001; Chesi et al,. 2008; and others) and modern genetic studies (Lenk et al., 1999; Fritz, 2003; Fritz et al, 2005a, 2006, 2007, 2009; Velo-Antón et al., 2007, 2008, 2011a, 2011b; Sommer et al., 2007, 2009; Pedall et al., 2009, 2011). The oldest (Middle Miocene) fossil *Emys* are from the area of the former Turgai Strait in Central Asia which separated Europe and East Asia until the Oligocene. Along the Mediterranean, the fossil record is incomplete with the oldest finds dating from the Villafranca at the border of the Pliocene and Pleistocene.

Emys orbicularis, with its broad geographic distribution, is one of the most diverse chelonian species. By the beginning of the 21st Century, 14 subspecies were recognized (Fritz & Havaš, 2007) on the basis of morphological variation (i.e. carapace length; shell and head/shell proportions; color of the shell, head, eyes, and limbs; and the light patterns of the shell, head, and limbs): *E. o. orbicularis* (Linnaeus, 1758: 198); *E. o. capolongoi* Fritz, 1995b: 204; *E. o. colchica* Fritz, 1994: 57; *E. o. eiselti*, Fritz et al. 1998: 113; *E. o. fritzjuergenobsti* Fritz, 1993: 131; *E. o. galloitalica* Fritz, 1995b: 217; *E. o. hellenica* (Valenciennes, 1832: 61); *E. o. hispanica* Fritz et al. 1996: 129; *E. o. iberica* Eichwald, 1831: 196; *E. o. ingauna* Jesu et al., 2004: 176; *E. o. lanzai* Fritz, 1995b: 211; *E. o. luteofusca* Fritz, 1989b: 143; *E. o. occidentalis* Fritz, 1993: 131; and *E. o. persica* Eichwald, 1831: 196. Several of these subspecies were synonymized later (Velon-Antón, et al. 2008; Fritz et al., 2009; Stuckas et al., 2014). In addition, two unnamed subspecies are known to occur in southern Turkey and eastern Algeria and northern Tunisia.

Fritz (1995b, 1996) first reported that populations of *E. orbicularis* could be separated by morphology and coloration into five subspecies groups; and (1996) combined these groups into three more inclusive lineages. These included an eastern lineage group of *E. o. orbicularis*, *E. o. colchica*, *E. o. eiselti*, *E. o. hellenica*, *E. o. iberica*, and *E. o. persica*; and a western subspecies group which consisted of *E. o. capolongoi*, *E. o. fritzjuergenobsti*, *E. o. galloitalica*, *E. o. hispanica*, *E. o. ingauna*, *E. o. lanzai*, and *E. o. occidentalis*. *Emys orbicularis luteofusca* was thought to represent the third group. Molecular studies (Lenk et al., 1999; Fritz et al., 2005a, 2006, 2007, 2009; Velo-Antón et al., 2007, 2008; Sommer et al., 2009) did not provide strong support for some recognized subspecies of *E. orbicularis*. Subsequent phylogeographic studies based on hundreds of specimens and using mitochondrial DNA sequences and microsatellite loci (Velo-Antón et al., 2011a, 2011b; Sommer et al., 2009; Pedall et al., 2009, 2011; Stuckas et al., 2014; Vamberger et al., 2015) confirmed that some of the formerly recognized subspecies are not valid. However, these studies found that within *E. orbicularis*, there are nine distinct mitochondrial DNA lineages that correspond to the following subspecies (Fig. 34): 1) *Emys orbicularis orbicularis* (characterized by mitochondrial DNA lineages I and II, which are less differentiated from one another than the other mitochondrial DNA lineages are), 2) *Emys orbicularis hellenica* (characterized by mitochondrial DNA lineage IV), 3) *Emys orbicularis galloitalica* (mitochondrial DNA lineage V), 4) *Emys orbicularis occidentalis* (mitochondrial DNA lineage VI), 5) *Emys orbicularis persica* (mitochondrial DNA lineage VII), and 6) *Emys orbicularis eiselti* (mitochondrial DNA lineage X). Also, there are two further mitochondrial DNA lineages from southern Turkey (lineage VIII; Fritz et al., 2009) and eastern Algeria and Tunisia (lineage IX; Stuckas et al., 2014) that are thought to represent distinct subspecies, which have not yet been named.

In addition to the above mentioned six subspecies, another one has been described from Liguria, Italy, *Emys orbicularis ingauna* Jesu et al., 2004. Specimens of this subspecies had been included in the type series of *Emys orbicularis galloitalica* and the morphological characters of *E. o. ingauna* suggest that it falls into the morphological variation range of *E. o. galloitalica.* Thus its recognition as a distinct subspecies is questionable. We tentatively recognize this form and await further analysis which may place it in the synonymy of *E. o. galloitalica.* Also, its distribution range is located completely within

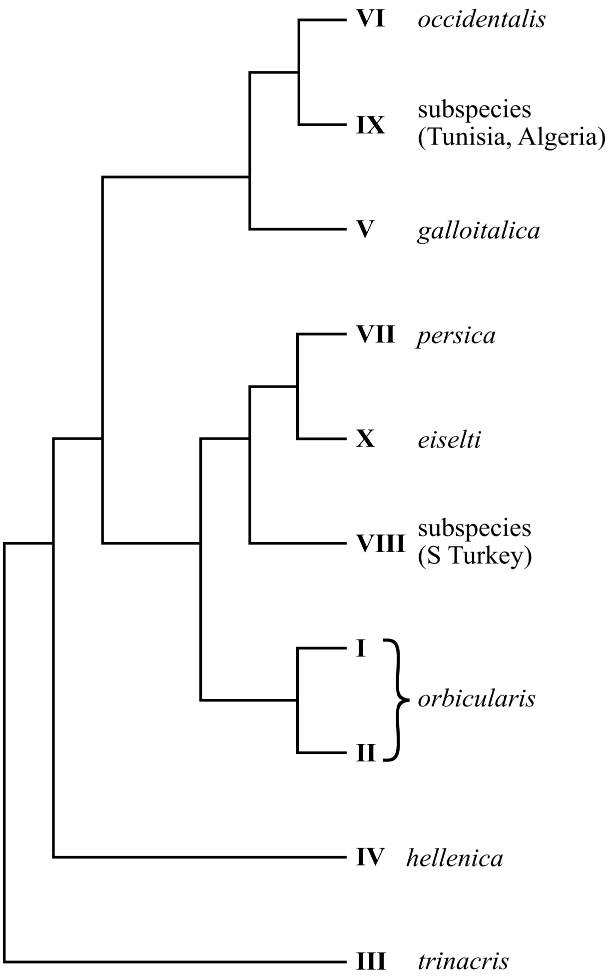


Fig. 34. Phylogenetic relationships of subspecies (mitochondrial lineages) of *Emys orbicularis* and *E. trinacris*. Nomenclature for lineages follows Lenk et al. (1999), Fritz et al. (2007) and Stuckas et al. (2014) in that Roman numerals designate mitochondrial lineages (clades of haplotypes) as revealed by phylogenetic analyses of 3475 bp of mitochondrial DNA. Modified from Stuckas et al. (2014, fig. 3).

the range of *E. o. galloitalica*, so that a distinct subspecies makes no biogeographical sense.

The currently recognized subspecies of *E. orbicularis* (Fig. 35) are as follows: *Emys orbicularis orbicularis* (Linnaeus, 1758: 198) is quite variable in its color pattern, morphology, and haplotypes (mitochondrial DNA lineages I, II; Fritz et al., 2005b, 2007), and essentially as physically described for the species. Its carapace reaches 23 cm, and the plastron of its hatchlings is almost entirely dark pigmented. This is the northernmost race of *E. orbicularis*, ranging from the Aral Sea in Kazakhstan to Central Europe. It may have survived the Pleistocene glaciation in a refuge north of the Caucasus (Fritz, 1992), and in the Balkan Peninsula (Fritz et al., 2007). Most of the species' populations in the principal Russian range are of *E. o. orbicularis.* Bannikov (1954) thought that two varieties of *E. o. orbicularis* occur in Daghestan. The first, resembling *E. o. orbicularis*, has a very dark brown or black carapace with numerous small oval yellow spots, distinct carapace growth rings, straight borders on the first vertebral scute, and no dark pattern on its plastron. The second has a lighter, olive-brown carapace with round or crescent-shaped yellowish spots often coalesced to form numerous light patches, a relatively smooth carapace surface with poorly developed growth rings, concave borders on the first vertebral scute, and a plastron with large dark spots. These second turtles correspond to Nikolsky's (1915: 19) *E. o. aralensis*, which has been synonomized with *E. o. orbicularis*; as have also the questionable (Fritz et al., 1998; Kuzmin, 2002) subspecies *E. o. colchica* Fritz (1994), and the Anatolian populations formerly referred to as *E. o. hellenica*, and *E. o. luteofusca* have now been assigned to *E. o. orbicularis* (Fritz et al., 2009).

Emys orbicularis eiselti Fritz, Baran, Budak & Amthauer, 1998: 113, has a dark black, 11 – 13 cm, carapace with a few small yellowish spots in males and narrow streaks in females; an almost entirely black plastron; and a very dark throat. Its very small gular scutes and short intergular seam differentiate *eiselti* from all other subspecies of *E. orbicularis*. It corresponds to the mitochondrial lineage X (Fritz et al., 2009), and is only found in the upper section of the Amik-Maraş rift valley of southeastern Turkey.

Emys orbicularis galloitalica Fritz, 1995b: 217, is a small to medium-sized, 10 – 15 cm, turtle (both normal-sized and dwarfed individuals occur in southeastern France), whose carapace varies from dark brown with yellow markings to almost completely yellowish; the carapace may or not become melanistic with age. The plastron is yellow, and may or may not have dark seam borders. This taxon ranges eastward from northeastern Spain and the Balearic Islands (introduced) along the Mediterranean coast of southern France to the Gulf of Policastro in southern Italy; it also occurs on the islands of Corsica and Sardinia. Different habitats are occupied in various parts if its range: either standing or slow moving waters with or without aquatic vegetation; or fast running, clear brooks with sand to gravel bottoms; brackish waters are seldom inhabited (Fritz et al., 1995). Differentiation in microsatellite loci suggests that *E. o. galloitalica* survived the Pleistocene in refuges on the Apennine peninsula and along the Mediterranean Coast of Spain (Pedall et al., 2011). Populations of *E. orbicularis* on Sardinia and Corsica were formerly recognized as *E. o. capolongoi* and *E. o. lanzai* respectively (Fritz, 1995b). Compared to mainland *E. o. galloitalica*, turtles from Corsica are darker with broader heads in females; and turtles from Sardinia have shorter heads, which are also more slender in males (Fritz, 1995b, 2001b; Fritz et al., 1995). Dark colored turtles predominate on Corsica, but Sardinian individuals are mostly light-colored. In the continental populations of *galloitalica*, both color forms occur at approximately equal frequency, causing Fritz (1995b) to propose that the populations on Corsica and Sardinia might have undergone a genetic bottleneck that resulted in selection of different genotypes on each island. Subsequently, variation in Tyrrhenian populations of *E.*

Fig. 35. Genus *Emys.* Row 1: Carapace of *Emys orbicularis orbicularis,* and plastron of *Emys o. orbicularis*. Photos by Carl H. Ernst and Melita Vamberger. Row 2: Carapace of *Emys o. hellenica*, and plastron of *Emys o. hellenica.* Photos by Melita Vamberger. Row 3: Carapace of dark phase *Emys trinacris,* and plastron of *Emys trinacris.* Photos by Stefana D'Angelo and Uwe Fritz.

orbicularis was examined by Schulze & Fritz (2003) using a greater sample of males from southern France, Corsica, and Sardinia, and females from France and both islands. They applied a discriminant analysis of morphological characters to classify individuals. Based on their results, Schulze & Fritz (2003) concluded that turtles in southern France represent the subspecies *galloitalica*, and that *lanzai* in Corsica and *capolongoi* in Sardinia are distinct taxa (sensu Fritz 1995b). Results from a more conclusive genetic study by Pedall et al. (2011) gave a different interpretation. These authors found that *capolongoi* and *lanzai* are not differentiated from continental populations of *E. o. galloitalica*; neither in their mitochondrial nor quickly evolving microsatellite markers. Curiously, the fossil record shows a continuous presence of *E. orbicularis* since the Middle Pleistocene on both Islands (Caloi et al., 1981; Hervet & Salotti, 2000; Chesi et al., 2008). This suggests that native populations of Pond Turtles became extinct and that the present populations were later introduced by prehistoric settlers. Lack of genetic differentiation of the pond turtles from Sardinia and Corsica indicates that neither *capalongoi* nor *lanzai* are valid taxa, but merely synonyms of *E. o. galloitalica*. *Emys o. galloitalica* intergrades with *E. o. orbicularis* in the westcentral portions and in the Rhone River watershed of France, and with other subspecies in northern Spain and *E. o. hellenica* in southern Italy (Vamberger et al,. 2015), but not Sicily (Mascort et al., 1999; Fritz, 2003; Fritz et al., 2005a). *Emys orbicularis galloitalica* is characterized by the mitochondrial DNA lineage V and intergrades in eastern Spain and southern Italy with other subspecies.

Emys orbicularis hellenica (Valenciennes, 1832: 61) has a 10–19 cm carapace length, normally 12–15 cm, with a trapezoid-shaped nuchal bone; a yellow plastron with variable amounts of dark pigment; a slightly broadened head (particularly in older individuals), with light reticulations in males but spots in females; and a yellow throat. This subspecies harbors the mitochondrial DNA lineage IV and has a circum-Adriatic distribution from southeastern Italy northwards to the Padan Plain, and from there southwards along the Adriatic and Ionic Coasts to the Peloponnese and Evvia in Greece. There are some dwarfed populations known with males not exceeding 10 cm shell length. Genetic studies by Pedall et al. (2011) and Vamberger et al. (2015) suggest the *E. o. hellenica* survived the Pleistocene in refugia located in Greece and southern Italy. Intergradation between *E. o. hellenica* and *E. o. orbicularis* occurs on the Balkan Peninsula (Pedall et al., 2011). *E. o. hellenica* also intergrades with other subspecies in the southeastern Balkans and southern Italy (Fritz & Obst, 1995; Fritz, 2003; Fritz et al., 2005b). Fritz (1994) thought Asian populations of *hellenica*, *iberica* and *persica* form a natural group which originated in the eastern Mediterranean region. Synonyms of *E. o. hellenica* include *Emys antiquorum* Valenciennes (1833: plate 9, Fig. 1), *E. hoffmanni* Fitzinger (1835: 123; a *nomen nudum*), *E. orbicularis hoffmanni* Schreiber (1875: 537), *E. o.* var. *atra* Werner (1897: 15), *E. o.* var. *maculosa* Dürigen (1897: 15), and *E. o.* var. *hellenica* Kovatscheff (1903: 171).

Emys orbicularis ingauna Jesu et al., 2004: 176 is the most recently described subspecies. This small < 15 cm turtle has a smooth, straight lateral-edged, flat carapace; and a broad posterior plastron lobe. The carapace is chestnut-brown, with, in some individuals, black posterior scute borders, and small whitish spots in males. The forelimbs normally have a yellow stripe extending from the elbow to between the first two toes. The subspecies exhibits a unique sexual dichromatism, particularly during the mating season, with females having yellowish heads and jaws bearing lemon to gold lateral spots on a gray background. Males have dark gray or brown heads (which darken during mating season) and jaws that lack a bright pattern, but yellow spots are present on the throat. The small carapace and other characters indicate *E. o. ingauna* is closely related to the *E. o. galloitalica* group; and may actually be a population of that subspecies. It differs in shell color, a yellowish or light brown head color, brighter ground color of the limbs, along with its sexual dichromatism. *Emys o. inguana* inhabits the lower reaches of streams, irrigation canals, ditches and coastal ponds at low elevations (< 100 m) in the Liguria region of Savona Province, northwestern Italy; an area close to the ranges of several other subspecies. Jesu et al. (2004: 190) hypothesized that *E. o. ingauna* became differentiated after being isolated (presumably by habitat destruction and the Würmian glaciations) from northwestern Italian populations of *E. orbicularis*. Its haplotype has not been reported, but other close localities of *E. orbicularis* from northwestern coastal Italy have haplotype V.

Emys orbicularis occidentalis Fritz, 1993: 131 has a dark brown to black 12–17 cm carapace with small yellow marks; a yellow plastron that has dark pigment only along its seams or one that is almost entirely dark; and a long intergular seam and short interhumeral seam. Fritz (1996) and Fritz et al. (1996) thought that *E. o. occidentalis*, *E. o. fritzjuergenobsti* (now contained in *E. o. occidentalis*), and the former subspecies of *E. o. hispanica* formed a natural group in North Africa and on the Iberian Peninsula. *Emys o. occidentalis* is characterized by the mitochondrial DNA lineage VI (Velo-Antón et al., 2008; Fritz et al., 2007), and is found in Morocco and the Iberian Peninsula (if the taxonomic revision of Stuckas et al., 2014 is accepted). North African populations of *E. orbicularis* in Algeria and Tunisia (north of the Atlas Mountains) may represent a new subspecies based on the mitochondrial DNA analysis of Stuckas et al. (2014) and are characterized by the distinct mitochondrial DNA lineage IX. However, these authors abstained from a formal description pending future morphological comparisons to other populations of *E. o. occidentalis*.

Emys orbicularis persica Eichwald 1831: 196 (haplotype VII) has a mostly dark, sometimes yellow-spotted, 15–18 cm carapace, which fades greatly with age in some populations; a yellowish, darkly marked, plastron, which may be entirely black; and very small gular scutes compared to other subspecies in the eastern part of the range. It is found in the Kura River watershed of the central Caucasus Mountains, the southern coast of the Caspian Sea in northern Iran, and the adjacent Uzboi Region of Turkmenistan. *E. o. persica* harbors the mitochondrial DNA lineage VII. *Emys o. iberica* Eichwald (1831: 196), *E. o. kurae* Fritz (1994: 57), and *E. o. orientalis* Fritz (1994: 57) are considered synonyms of *E. o. persica* Eichwald 1831: 196 (Fritz et al., 2009). The name *E. o. iberica* appeared before that of *E. o. persica* on p. 196 of Eichwald (1831), where both were described as varieties of *Emys europaea* "Brongn." [Brongniart]; Fritz et al. (2009), as first revisers (Code, Article 24A), chose the name *persica* instead of *iberica* for the subspecies.

A second extant species of *Emys* (*Emys trinacris*) described by Fritz et al. (2005b: 364) occurs only on Sicily and possibly Calabria in adjacent southern Italy. It was originally distinguished from *E. orbicularis* on the basis of mitochondrial DNA variation and nuclear genomic fingerprinting. Fritz et al. (2005b) found that *E. trinacris* possesses a distinct mitochondrial DNA lineage (III). Nevertheless, populations of *E. o. galloitalica* from southern Italy, adjacent to Sicily, are genetically divergent from *trinacris.* Consequently, Fritz et al. (2005b, 2007, 2009) considered *E. trinacris* a sister species to a variable, weakly supported, clade of *E. orbicularis* subspecies (2007: Fig. 1). Morphologically, *E. trinacris* is poorly defined. Adults have a carapace which is relatively small (length 10.0–15.5 cm) and originally described as dark and almost patternless. However, more recent analysis of Sicilian populations by Fritz et al. (2006) indicates considerably more color and pattern variation may have occurred in the past. The turtle's yellowish plastron varies in intensity and may be patterned with scattered dark pigment, or be predominately black. The male iris is whitish, yellowish, or red; and the pupil of some individuals lies in the center of a darker five-pointed star. Nevertheless, adult *E. trinacris* cannot be clearly distinguished by either color or morphological characters from neighboring Italian populations of *E. o. galloitalica* (Fritz et al., 2006). Hatchlings, however, appear smaller, lighter, and have different shell patterns than those of *E. orbicularis* (Fritz et al., 2006). The color and morphology shared by *E. o. galloitalica* and *E. trinacris* may be due to ancestral polymorphism (Fritz et al., 2006), but modern allochthonous (differential) exchange must also be considered (Fritz et al., 2005b). More recently, Pedall et al. (2009, 2011) and Vamberger (2015) used mitochondrial DNA gene sequences (cytochrome *b*) and up to 15 polymorphic microsatellite loci to describe genetic differentiation and gene flow within and between the ranges of *E. orbicularis* and *E. trinacris.* Vamberger et al. (2015) found negligible gene exchange between *E. orbicularis* and *E. trinacris.*These results support the species status of *E. trinacris* are valid phylogenetic species.

The genus *Emys* is reviewed in Ernst & Barbour (1989), Ernst et al. (2000), Hödl & Rössler (2000), Fritz (2001a, 2001b, 2003), Kuzmin (2002), and Fritz & Havaš (2004, 2007).

Actinemys Agassiz, 1857

Until recently (Spinks et al., 2014), the Western Pond Turtle, *Actinemys marmorata* (Baird & Girard, 1852), was considered the sole species currently assigned to the genus *Actinemys* Agassiz, 1857: 252 (Fig. 36). It has a maximum carapace length of 24 cm. The low, keelless carapace is grayish-brown with a pattern of light mottled spots or lines. The hingeless plastron is yellowish. The skin is gray with some pale yellow on the chin, neck, forelegs, and tail. The crushing surface of the upper unnotched jaw is narrow and ridgeless. Males have a concave plastron. It occupies a wide variety of habitats ranging from rivers and streams (both permanent and intermittent), lakes, ponds, impoundments, human-made canals, shallow ephemeral wetlands, and sewage treatment lagoons; although streams are the typical habitat. It is a generalist carnivore, feeding on small invertebrates (e.g. neuston, mollusks, crustaceans, insects) and, rarely, small vertebrates. The species formerly occurred in British Columbia, but is likely extirpated there. Its modern range extends southward west of the Cascade-Sierra crest from the Puget Sound and Columbia River Gorge of Washington through the Pacific Coastal states of Oregon and California to Baja California Norte, Mexico. Inland, small isolated populations occur in the Truckee and Carson Rivers, and possibly the Humboldt River in Nevada; and in the interior-draining Mojave River of southern California. Its fossil range is more extensive and fills in some of the present distributional gaps (see summary in Ernst & Lovich, 2009). The species was described and named *Emys marmorata* by Baird & Girard (1852: 177) based on specimens taken in the area about Puget Sound during the United States Exploring Expedition of 1841. These specimens still exist in the collection of the United States National Museum (Reynolds et al., 2007).

Fig. 36. Genus *Actinemys*. Carapace of *Actinemys marmorata,* and plastron of *Actinemys marmorata*. Photos by Carl H. Ernst.

In the past *A. marmorata* has been included in several genera other than *Emys* (Baird & Girard, 1852: 177) or *Actinemys* (Agassiz, 1857: 252): *Clemmys* (Strauch, 1862: 114), *Geoclemmys* (Gray, 1870: 27). *Chelopus* (Cope, 1879[1875]: 53), and *Melanemys* (Shufeldt, 1919: 155). Holman & Fritz (2001: 334) reassigned the species to *Actinemys.* Feldman & Parham (2002) and Buskirk (2002) listed it under its original genus *Emys*. Their designation was rejected by Crother et al. (2003), Iverson et al. (2007), and Fritz et al. (2011) who returned it to the genus *Actinemys* (see previous discussion of the taxonomy of the subfamily Emydinae Rafinesque, 1815 for contemporary alternate usages of *Emys* or *Actinemys*). Several early authors assigned different names to the species *marmorata* that are now considered synonyms: *Emys nigra* (Hallowell, 1854: 91), *Clemmys wosnessenskyi* (Strauch, 1862: 114), and the fossil *Clemmys hesperia* (Hay, 1903: 238). The fossil species *Clemmys saxea* Hay, 1903: 241, and *C. owyheensis* Brattstrom & Sturn, 1959: 65 may also prove to be remains of *A. marmorata* after further comparisons with osteological material from modern *A. marmorata* (Carlsen, 2003). Over most of its history, the Western Pond Turtle has been included as a fourth North American species of the genus *Clemmys* Ritgen, 1828: 270; along with *C. guttata* (Schneider, 1792: 264), *C. muhlenbergii* (Schoepff, 1801: 132), and *C. insculpta* (Le Conte, 1830: 112). The latter two species are now assigned to the genus *Glyptemys* Agassiz, 1857: 252).

Seeliger (1945: 158) was first to recognize geographic variation, and named the subspecies *C. marmorata pallida* based on morphological and color differences in preserved specimens from Orange County, California. This divided the species into a northern race, *marmorata* (with a modern range extending from at least the Puget Sound region of Washington south to San Francisco Bay and western Nevada); and a southern race, *pallida* (ranging south from the San Francisco Bay into Baja California Norte, Mexico). Buskirk (1990), after examining live turtles throughout the species range using the morphological characters and color patterns identified by Seeliger, concluded that designation of the southern populations as a separate subspecies was probably invalid. He attributed this to Seeliger having only examined preserved specimens, particularly in which the color patterns could have changed over time. Buskirk (1990) consequently suggested that "microbiochemical taxonomy" be used to clarify possible subspecific differences within the species. Since then, several molecular studies have been conducted. Holland (1992, 1994) examined variation in a 300–400 base pair sequence of the cytochrome *b* gene sampled from 76 *A. marmorata* across its geographic range. Although variation in the gene was relatively low, he identified several possible haplotypes. Gray (1995) used DNA fingerprinting to analyze the genetic composition of nine populations in Washington, Oregon, and California. Her analysis of population substructure indicated significant genetic divergence between northern and southern populations; and that a lack of gene flow between the north and south has occurred for a long time. Gray concluded that her analysis upholds separation of *A. marmorata* into the two subspecies; northern *A. m. marmorata* and southern *A. m. pallida*.

In 1997, Janzen et al. published preliminary results of their evaluation of molecular genetic differentiation among populations of *A. marmorata*. They first conducted an overview of variation (cytochrome *b* base pair segment 307) across the entire species range, and then analyzed possible microgeographic differences within a restricted geographic range in Oregon. Their tests showed that, based on single-strand conformation polymorphism (SSCP), most individual *A. marmorata* exhibit the same genotype for cytochrome *b*. However, several unique genetic variants were evident, chiefly in populations from southern coastal California and Baja California Norte (possibly sufficient to warrant specific status). The findings of Janzen et al. (1997) generally agreed with the DNA fingerprinting results of Gray (1995). They proposed that the results from their study and Gray (1995) may reflect the inherently low rate of molecular evolution in turtles (Avise et al., 1992), or recent migration events within the range (Hewitt, 1996), or both. Janzen et al. concluded that further study is needed using more sophisticated molecular techniques to determine the validity of subspecific designations.

Spinks & Shaffer (2005) conducted a range-wide molecular analysis of *A. marmorata*, with emphasis on cryptic variation and distance isolation, using both mitochondrial and nuclear DNA sequences. Their nuclear data revealed low levels of genetic variation. However, phylogenetic analyses based on mitochondrial DNA indicated four distinct and geographically coherent lineages: 1) a large northern clade of populations ranging west of the Coast Ranges from Washington south to San Luis Obispo County, California; 2) a San Joaquin Valley clade in the southern Central Valley of California; 3) a restricted clade in Santa Barbara and Ventura counties, California; and 4) a southern clade occurring in California south of the Tehachapi Mountains and west of the Transverse Range which extends into Baja California Norte, Mexico. An analysis of molecular variance (AMOVA) based on regional drainages indicated that populations south from Washington to the Sacramento Valley, California, had virtually the same genetic composition, with no substantial population variance among northern river watersheds. Elsewhere, there is evidence of extensive variation throughout California and Mexico. The northern clade reported by Spinks & Shaffer matches the range of what is currently recognized as *A. m. marmorata* Baird & Girard, 1852: 179, but their analysis showed no clade matching the distribution of *A. m. pallida* (Seeliger, 1945: 158) in the south. From these results, Spinks & Shaffer concluded that the current subspecific split was unwarranted, and that there is sufficient evidence of cryptic genetic variation in southern California (but see below).

Angielczyk & Parham (2005) studied the geometric morphometry of plastron shape in *A. marmorata*, focusing predominately on shape variation ontogeny, sexual dimorphism and phylogeography. Size and plastron shape are correlated and sexual dimorphism is present but subtle. Their study suggests that each of the four geographic clades proposed by Spinks & Shaeffer (2005) differs significantly in plastron shape, giving more credence to Spinks and Shaeffer's conclusions.

Similar to deirochelyine turtles, phenotypic variation in Western Pond Turtles has been influenced by environmental pressures. Three studies of *A. marmorata* have indicated environmentally-influenced character displacement. Germano & Bury (2001), during a study of populations in California's Central Valley, showed that individual turtles at a Fresno County water treatment plant grew at a faster rate and achieved a larger adult size than those from Dry Creek, Fresno County which had cooler water. Their finding parallels that reported for the eastern deirochelyine turtles, *Chrysemys picta* (Ernst & McDonald, 1989), and *Trachemys scripta* (Avery et al., 1993; Christy et al., 1974; Etchberger et al., 1993; Gibbons et al., 1981). Warmer water at sites such as treatment plants enhances the growth of algae and invertebrate populations, providing a richer protein diet than that at most natural freshwater habitats. This results in accelerated metabolism, faster growth and earlier attainment of sexual maturity at such sites, thus skewing the population structure. Ashton et al. (2006) noted similar results in a comparative study of populations of *A. marmorata* from impounded and natural flow sections of the Trinity River, California. The river's mainstream had a water temperature more than 10°C colder than natural-flow tributary sites. Body size (carapace length, mass) per given age was significantly greater for both sexes inhabiting the warmer tributaries compared to those in the impounded mainstream. Gravid females from the natural tributaries were also significantly larger and appeared to mature at a later age, while females from the dammed mainstream of the river were significantly smaller and apparently matured at an earlier age. Lubcke & Wilson (2007) conducted a study of shell morphology in *A. marmorata* from various habitats in northern California including foothill creeks (FC), valley sloughs (SR), and human-made canals (HC). Maximum carapace length (MCL) differed among the three habitats. Combined data for the sites indicated that males were significantly larger in mean MCL than females, but also that mean MCL differed significantly with habitat type: HC > SR > FC. Within the sites, males were larger than females at SR and HC, but not different at FC. Turtles from FC were flatter and narrower than those from the other two sites. Lubcke & Wilson speculated these differences may be the result of variation in prey availability, water temperature, or microhabitat differences; and suggested that phenotypic plasticity is responsible for determining maturization size in the species. It also seems possible that stream flow-rate may have an influence on morphological development. Examples of phenotypic character expressions which are strongly or entirely influenced by immediate environmental conditions should be identified and avoided when describing taxonomic variation.

Spinks et al. (2009b) published an updated DNA analysis of variation in *A. marmorata*. Their data set consisted of one mitochondrial DNA and five nuclear DNA loci, and a combination of phylogenetic and network-based approaches were used. They elucidated zoogeographic variation in California populations; and revealed a relatively ancient (about 2–8 Ma) north/south split, as well as an area of intergradation chiefly in the Central Coast Ranges of California. Also indicated was gene flow from northern populations and from populations in the San Joaquin Valley into California's Central Coast Ranges. This apparently occurred after the Pliocene-Pleistocene marine encroachment of the Great Central Valley subsided. Spinks et al. (2009b) concluded that California's Central Coast Ranges have played a major role in shaping the current geographic genetic composition of *A. marmorata*. They stated (p. 553) "We recovered a deep north/south split within the Western Pond Turtle, suggesting that an alternative to the current subspecies descriptions could be to elevate the *marmorata* and *pallida* groups to full species status… (Seeliger 1945)." Recently, Spinks et al. (2014, 2016) analyzed a greatly expanded DNA data set (including 104 nuclear markers; 30 nuclear genes) for *Actinemys.* From these results, they confidently recommended recognition of two species (*A. marmorata* and *A. pallida*), an arrangement which we follow. *Actinemys marmorata* was reviewed in the Catalogue of American Amphibians and Reptiles (CAAR) by Bury (1970); Bury & Germano (2008) reviewed the species in Conservation Biology of Freshwater Turtles and Tortoises; and Bury et al. (2012) published a monograph on the general biology.

Clemmys Ritgen, 1828

At present, the genus *Clemmys* Ritgen, 1828: 270 is commonly recognized as monotypic (Turtle Taxonomy Working Group, 2011; Crother, 2012) comprised of only the Spotted Turtle, *Clemmys guttata* (Schneider, 1792: 264) (Fig. 37). It has a black keelless carapace marked with yellow to red dots. Its posterior rim lacks a notch. The hingeless plastron is yellowish with a large dark blotch on each scute. The upper jaw lacks a notch and its crushing surface is narrow and ridgeless. A large yellow tympanic blotch is present. Females have yellow jaws, a broader carapace, flat plastron, and short tail; males have brown jaws, a narrower carapace, slightly concave plastron, and a longer tail. Fossil species have been assigned to this genus but most have been re-classified into other genera. *Clemmys wosnessenskyi* from the Sacramento River (Strauch, 1862: 114) and *C. hesperia* from Rattlesnake Creek, Oregon (Hay, 1903: 238) have been placed in the synonymy of *Actinemys marmorata* (Brattstrom & Sturn 1959). The fossils *C. saxea* Hay, 1903: 241 (Upper Miocene of Oregon) and *C. owyheensis* Brattstrom & Sturn, 1959: 65 (Pliocene of Oregon) are probably also fossils of this species. A fossil, described as *Clemmys morrisiae* Hay, 1908b, was provisionally reassigned to the geoemydid species "*Rhinoclemys terrestris*" (Cope, 1873: 464) by West & Hutchison (1981); and another fossil, *C. backmani* Russell, 1934: 107, is now considered to belong to the fossil family Macrobaenidae (Parham & Hutchison 2003: 784).

Clemmys guttata ranges from southern Quebec and Maine southward along the Coastal Plain and Piedmont to northcentral Florida; and westward through Ontario, New York, Pennsylvania, central Ohio, northern Indiana, Michigan, and northeastern Illinois. It is a denizen of a wide variety of shallow, soft-bottomed waterbodies including wet pastures and sedge meadows, fens, bogs, cattail marshes, cyprus and sphagnum swamps, ponds, ephemeral pools, woodland brooks, drainage ditches, and Carolina bays.

Clemmys guttata was one of the four earliest emydine turtles to be named; following the Old World *Emys orbicularis* (Linnaeus, 1758: 198), and North American *Terrapene carolina* (Linnaeus, 1758: 198) and *Chrys-*

Fig. 37. Genus *Clemmys*. Carapace of *Clemmys guttata,* and plastron of juvenile *Clemmys guttata.* Photos by Roger W. Barbour and Carl H. Ernst.

emys picta (Schneider, 1783: 348). All four species were originally placed in the then all-inclusive genus *Testudo* Linnaeus, 1758: 197. The Spotted Turtle was first assigned to *Clemmys* by Ritgen (1828: 270), who created the new genus for *Testudo punctata* Schoepff, 1792: 25 (= *Testudo guttata* Schneider, 1792: 264) and several other diverse species belonging to the families Chelidae, Emydidae, Geoemydidae, Kinosternidae, and Pelomedusidae. *Testudo guttata* (= *C. guttata*) was subsequently designated the type species of *Clemmys* by Baur (1892: 43). The genus *Clemmys* has had an interesting history. At various times the European emydine *Emys orbicularis* (Fitzinger, 1835); several species of the American deirochelyine genera *Deirochelys*, *Graptemys*, *Malaclemys*, *Pseudemys*, and *Trachemys* (Fitzinger, 1835; Strauch, 1862, 1890; Gray, 1863, 1870; Boulenger, 1889); and the modern geoemydinae genera *Heosemys*, *Kachuga*, *Mauremys*, *Melanochelys*, *Morenia*, *Orlitia*, *Pangshura*, *Rhinoclemmys*, *Sacalia*, and *Siebenrockiella* (Loveridge & Williams, 1957; Fritz & Havaš, 2007) have been assigned to it.

As previously discussed, the genus was restricted to the living North American turtles of the subfamily Emydinae that lack moveable plastrons (McDowell, 1964). Two species (now recognized as belonging to a separate genus *Glyptemys* Agassiz, 1857: 252), *G. muhlenbergii* (Schoepff, 1801: 132) and *G. insculpta* (Le Conte, 1830: 112), were placed in *Clemmys* by Fitzinger (1835: 124); and Strauch (1862: 108) assigned a fourth turtle from the North American Pacific Coast, *Actinemys marmorata* (Baird & Girard, 1852: 177), to the genus. Agassiz (1857: 252) later created generic names for *guttata* (*Nanemys*), *insculpta* (*Glyptemys*), *muhlenbergii* (*Calemys*), and *marmorata* (*Actinemys*), and placed them in a new subfamily Clemmydoidae (p. 442). However, with few exceptions, by the end of the 19th century, the four species were considered to belong to the single genus *Clemmys* Ritgen, 1828: 270 (Boulenger, 1889; Lindholm, 1929; Pope, 1939; Carr, 1952; Schmidt, 1953; Ernst & Barbour, 1972; Iverson, 1992; Ernst et al,. 1994; Stephens & Wiens, 2003). The most notable exceptions were the use of the generic names *Melanemys* for *guttata* (p. 155), *marmorata* (p. 155), and *muhlenbergii* (p. 157) by Shufeldt (1919), and *Chelopus* for all four species by Cope (1877: 53); but neither designation became widely accepted. Since it was originally described, *Clemmys guttata* has had several synonymous names: *Testudo anonyma* Schneider (Schoepff, 1792: 25, a *nomen nudum*); *Emys guttata* (Schweigger, 1812: 295); *E. punctata* (Merrem, 1820: 24); *Terrapene punctata* (Bonaparte, 1831: 159); *Chelopus guttata* (Rafinesque, 1832: 64); *Geoclemys guttata* (Gray, 1856b: 19); *G. sebae* (Gray, 1869: 188); *Chelopus guttatus* (Cope, 1877: 53); *Geoclemmys guttata* (Gray, 1890: 29); and *Melanemys guttatus* (Shufeldt, 1919: 155).

No subspecies of *C. guttata* have been named, and there appears to be little geographic variation across the range. Nevertheless, sexual dimorphism and ontogenetic differences are evident. Laemmerzahl (1990) studied several morphometric and color pattern parameters on the shells of 270 *C. guttata* from throughout the species range. Analysis of within species variation showed that the number of carapace spots increases with size, and that sexual differences occur in shell shape. However, a combination of hierarchical cluster analysis and discriminant analysis did not reveal any meaningful differences between populations. Laemmerzahl suggested that the apparent lack of geographic variation in *C. guttata* might be explained by early paleogeographic events. Perhaps *C. guttata* was derived from a single relict population along the Atlantic Coastal Plain, possibly in southern Georgia and northern Florida, at the end of the Pleistocene Wisconsinian (Rancholabrean) glaciation. The oldest record of a fossil Spotted Turtle is from South Carolina, which lends credence to this theory of a southern origin (Bentley & Knight, 1993, 1998). With the climate becoming warmer and the retreat of the Wisconsinian glaciers, *C. guttata* may have extended its range northward along the Atlantic Coastal Plain and then westward (Smith, 1957). The apparent lack of morphological (biogeographic) variation may have been maintained by the turtle's choice of similar microhabitat conditions throughout the range and a general lack of genetic isolation. Spotted Turtles exhibit terrestrial activity and their distribution is not restricted to drainage systems. Unlike many of the emydid turtles, species status of *C. guttata* has not been questioned.

Clinal size variation is well documented in *C. guttata*. Ontario females are larger than those from more southern populations and the smallest adult turtles have been reported from populations near the center of the species distribution (Haxton, 1998; Litzgus et al., 2004). Latitudinal variation suggestive of Bergman's rule was supported by analysis of 818 turtles across the range. However, when a population of large *C. guttata* at the northern extreme of the range was removed from the analysis, latitudinal variation was not apparent (Litzgus et al., 2004). Several studies have suggested that latitudinal clines (e.g. body size) may be related to physiological responses. These may occur from the effects of temperature on cell division resulting in larger cells, and thus larger individuals, from cooler higher latitudes (Partridge et al., 1994; Van der Have & de Jong, 1996; Van Voorhies, 1996; French et al., 1998). To test this hypothesis, Litzgus et al. (2004) measured the diameter of skin cells. Their results indicated that cell size does not increase with higher latitude and accompanying lower environmental temperature. Thus, Litzgus et al. (2004) concluded that neither Bergmann's rule (latitudinal variation) nor cell size variation sufficiently explain clines in Spotted Turtles. Alternatively, they proposed that patterns in body size are likely related to variation in female body size at maturity and reproductive cycles. This may represent a direct phenotypic response to environmental conditions (i.e. ambient temperatures and food availability) rather than genetic variation. Color variation of the light skin markings may also occur among populations. Most *C. guttata* have yellow to orange light skin pigmentation, but others have skin with pinkish pigmentation (Ernst, pers. observ.). These differences are lost with preservation of museum specimens, and thus a thorough interpopulational examination of living individuals would be informative. Again, this variation may be environmentally induced.

The genus *Clemmys* and species *C. guttata* were reviewed, respectively, in the CAAR by Bury & Ernst (1977), and Ernst (1972a). Meylan (2006b) reviewed the species in Chelonian Research Monograph 3.

Emydoidea Gray, 1870

The genus *Emydoidea* Gray, 1870: 19 contains only one living species, the Blanding's Turtle, *Emydoidea blandingii* (Holbrook, 1838: 35) (Fig. 38). It achieves a carapace length of 28 cm. The carapace is smooth; neither keeled nor serrated, and is black with tan to yellow irregular-shaped spots of slight radiating lines on each scute. The plastron is hinged and yellow with a large dark blotch at the outer edge of each scute. The neck is very long and the throat yellow. The crushing surfaces of the notched upper jaw are narrow and ridgeless. Males have darkly pigmented jaws, slightly concave plastrons, and longer tails than females. The turtle ranges from southwestern Quebec and southern Ontario, Canada, south through the Great Lakes region and west into Iowa, northeastern Missouri, southeastern South Dakota, and west central Nebraska. Isolated small populations also occur in southeastern New York, eastern Massachusetts, southern New Hampshire and adjacent Maine, and Nova Scotia. Throughout this range, *E. blandingii* is found in lakes, ponds, bogs, swamps, marshes, fens and wet prairies, creeks, and sloughs with clean shallow water, a soft but firm organic bottom, and abundant aquatic vegetation. The fossil record for the genus dates from the Late Miocene (see below, and review in Ernst & Lovich, 2009).

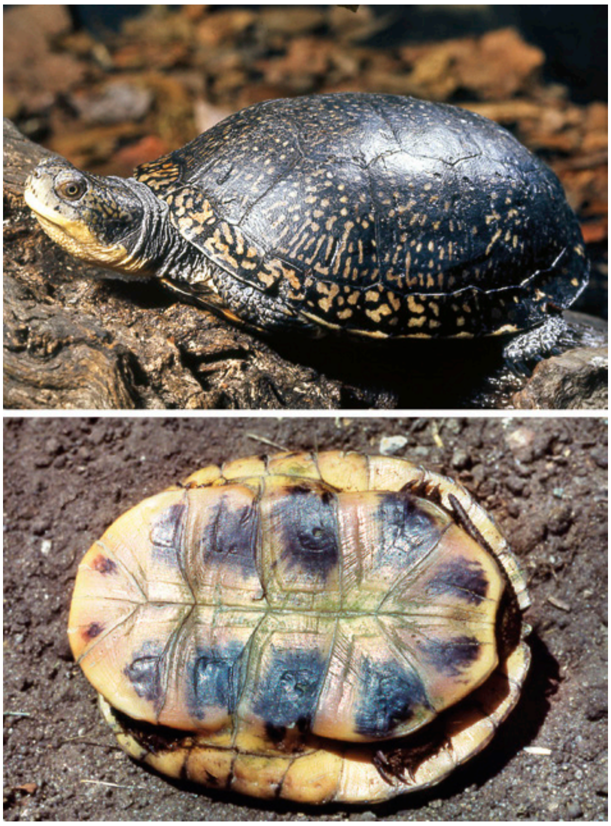


Fig. 38. Genus *Emydoidea*. Carapace of *Emydoidea blandingii*, and plastron of juvenile *Emydoidea blandingii.* Photos by Roger W. Barbour and Carl H. Ernst.

The turtle *Emydoidea blandingii* was first named *Testudo flava* by Lacépède (1788: 135) and soon after as *Testudo meleagris* by Shaw (*in* Shaw & Nodder, 1793: 144) [see explanation on p. 5]. Holbrook (1838: 35), on the basis of its hinged plastron, placed it in the genus *Cistuda* Fleming, 1822: 270 along with the Box Turtle (*C. carolina*), and described it as the full species *Cistuda blandingii*. Both *T. flava* Lacépède, 1788: 135 and *T. meleagris* Shaw, 1793: 144 are erroneous and based on *Emys orbicularis* (Linnaeus, 1758: 198). Mertens & Wermuth (1961) petitioned the ICZN to suppress these names because they are senior subjective synonyms of *Cistuda blandingii* Holbrook, 1838: 35; and to place the species name *blandingii* Holbrook, 1838, on the *Official List of Specific Names in Zoology*. In 1963 (Opinion 660; Bulletin of Zoological Nomenclature 20: 187–190), the ICZN suppressed both *T. flava* Lacépède, 1788 and *T. meleagris* Shaw (*in* Shaw & Nodder, 1793) under the

Law of Priority (Code, Article 23), but not for the Law of Homonymy (Code, Article 52), and declared *blandingii* Holbrook, 1838: 35, an official species name. Some confusion occurred regarding the use of the name *meleagris.* Holbrook (1838) used the name *Lutremys meleagris* for the species. Later, Le Conte (1854: 189) used both *C. blandingii* and *L. meleagris* for the turtle, while Agassiz (1857: 252), Cope (1877) and Yarrow (1882: 37) dropped *blandingii* in preference of *meleagris*. Strauch (1862: 28) resurrected Holbrook's specific name *blandingii*, and Gray (1870: 19) proposed that the North American species *blandingii* be placed in its own genus, *Emydoidea*. Boulenger (1887: 163) concurred with Gray's (1870) designation, and relegated the name *meleagris* to the synonymy of *Testudo europaea* Schneider, 1783: 323, = *Emys orbicularis orbicularis* (Linnaeus, 1758: 198), making it unavailable for *Cistuda blandingii* Holbrook. However, Boulenger retained *blandingii* in the genus *Emys.* Lindholm (1929: 282) substituted the genus name *Neomys* for *Emydoidea*, but this arrangement was not followed because of homonymy with the family-rank nominal taxon Emydoidea based on *Emys*. Loveridge & Williams (1957: p. 202) referred both *flava* Lacépède, 1788: 135 and *meleagris* Shaw, 1793: plate 144 to the synonymy of *Emys orbicularis.* Further, the name *meleagris* should not be available because it follows (is secondary to) the name *blandingii* on the same page in Holbrook (1838: 35), giving page position priority to *blandingii* (Code, Article 24.2.2).

Morphological and molecular similarity between North American *Emydoidea blandingii* and Old World *Emys orbicularis* has added to the taxonomic confusion during the last decade, especially with the application of DNA techniques (Bickham et al., 1996; Burke et al., 1996; Mockford et al., 1999, 2007; Feldman & Parham, 2001, 2002; Holman & Fritz, 2001; Rubin et al., 2001; Parham & Feldman, 2002; Iverson et al., 2003; Libants et al., 2004; Spinks & Shaffer, 2009; Angielczyk et al., 2010; Fritz et al., 2011; Joyce et al., 2012). This has been previously discussed in detail under the section 'Birth of a modern restricted family Emydidae Rafinesque, 1815'.

Two fossils have been assigned to the genus *Emydoidea*. The first, *Emys twentei* Taylor, 1943: 250, from the Pleistocene (Illinoian) of Kansas, is now considered a synonym of *Emydoidea blandingii* (Preston & McCoy, 1971: 23). The second, more recently described, *Emydoidea hutchisoni* Holman, 1995b: 549, from the Middle Miocene (Barstovian) of Nebraska, is apparently distinct from *E. blandingii* and possibly ancestral to it (Holman, 2002a, 2002b). Unfortunately, it is based only on a single elongated nuchal bone and a cervical scute impression which resemble that of *E. blandingii*, but differing from it in having a somewhat shorter and broader nuchal and a cervical impression which is not raised and broader dorsally rather than ventrally. The only other known Miocene specimens of *Emydoidea* (*E. hutchisoni*) consist of three hyoplastra also from the Barstovian of Nebraska (Hutchison, 1981). While *E. hutchisoni* is currently a recognized species, its status is questionable and more Miocene material is needed to determine its status. A number of Pliocene and Pleistocene specimens of *Emydoidea* [all *blandingii*] have been reported (see Ernst & Lovich, 2009 for a review of the genus fossil record).

The genus *Emydoidea* and species *E. blandingii* were reviewed in the Catalogue of American Amphibians and Reptiles by McCoy (1973), and Congdon et al. (2008) reviewed the species in Conservation Biology of Freshwater Turtles and Tortoises.

Glyptemys Agassiz, 1857

Agassiz (1857: 252, 443) created a new genus *Glyptemys* for the North American Wood Turtle, *Emys insculpta* (= *Testudo insculpta*, Le Conte, 1830: 112). Turtles of the genus *Glyptemys* (which now also includes the North American Bog Turtle, *G. muhlenbergii* [Schoepff, 1801]) have a carapace with some indication of a keel. The brown carapace surface may be either rough or smooth and only slightly notched posteriorly. The plastron is hingeless and contains a large dark blotch on each scute. The neck is yellow to orange in one species (*G. insculpta*) or a large yellow, orange, or red blotch is present on the other species (*G. muhlenbergii*). The upper jaw is slightly notched, and its crushing surface is narrow and lacks a ridge or tuberculations. Males are larger than females, and have longer tails.

Glyptemys muhlenbergii (Schoepff, 1801: 132) and *G. insculpta* have in the past been assigned to several other genera: *Testudo* (Schoepff, 1801: 132), *Emys* (Schweigger, 1812: 310), *Chersine* (Merrem, 1820: 30), *Terrapene* (Bonaparte, 1831: 160), *Clemmys* (Fitzinger, 1835: 124), *Geoclemys* (Gray, 1856b: 19), *Calemys* (Agassiz, 1857: 252, 443), *Geoclemmys* (Gray, 1869: 188), *Chelopus* (Cope, 1875: 53), and *Melanemys* (Shufeldt, 1919: 157). Agassiz (1857: 442) also proposed a separate subfamily of emydine turtles, Clemmydoidae, which included new generic names for the four species most frequently associated with the genus *Clemmys* Ritgen, 1828. On p. 443 he introduced the separate generic names *Calemys* for *muhlenbergii* and *Glyptemys* for *insculpta* (he had previously listed them on p. 252 as *nomina nuda*). Later use of the name *Kalemys* by Ennis (1861: 124) is a misspelling of *Calemys* Agassiz, 1857: 252 (Code, Article 33.3). Agassiz's four generic names were not widely accepted, and by the late 1800s both *insculpta* and *muhlenbergii* were regarded as members of the genus *Clemmys*, along with *C. guttata* and *C. marmorata* (Fitzinger, 1835: 124; Strauch, 1862: 107).

As discussed earlier (*Relationships in the Subfamily Emydinae*) Holman & Fritz (2001) published a morphological study that revised the modern genus *Clemmys*. In it they reassigned both *muhlenbergii* and *insculpta* to *Glyptemys* Agassiz, 1857, for which *Testudo insculpta* Le Conte, 1830 (= *Glyptemys insculpta*) is the type species. A year later, Feldman & Parham (2002) published a molecular (mitochondrial DNA) phylogenetic study that indicated paraphyly of the four species assigned to the genus *Clemmys*, and included robust data for grouping *muhlenbergii* and *insculpta* together as a monophyletic clade. Unfortunately, apparently unaware of Holman & Fritz's (2001) revision of *Clemmys*, Feldman & Parham resurrected the genus *Calemys* Agassiz, 1857, for *muhlenbergii* (its type species) and *insculpta*. Apparently their decision was based on Agassiz (1857: 443) having described *Calemys* immediately before the description of *Glyptemys*, which gives *Calemys* page priority over *Glyptemys* (Code, Article 23.1). However, the name *Glyptemys* must be applied to the two species since it was the first revised name proposed by Holman & Fritz (Code, Article 24.2.1). This arrangement is now generally accepted (King & Julian, 2004; Tessier et al., 2005; Bonin et al., 2006; Saumure et al., 2007; Turtle Taxonomy Working Group, 2007; Iverson et al., 2008; Ernst & Lovich, 2009; Spinks & Shaffer, 2009; Angielczyk et al., 2010; Spradling, et al. 2010; Wiens et al., 2010; Fritz et al., 2011; Joyce et al., 2012). The species identity of *G. insculpta* and *G. muhlenbergii* has not been questioned over the last century.

The Wood Turtle, *Glyptemys insculpta*, is a moderate sized emydine, growing to 230 mm carapace length (Fig. 39). It currently occupies a range extending from Nova Scotia, New Brunswick, and Maine south through New England, eastern and central New York, northern New Jersey, Pennsylvania, and into northern Virginia and West Virginia. The range continues west through southern Quebec, southwest Ontario, northern Michigan, Wisconsin, eastern Minnesota, and northeastern Iowa. The Wood Turtle may have historically occurred in northeastern Ohio (Thompson, 1953). Miocene (Barstovian) and Pleistocene (Rancholabrean) fossils show that *G. insculpta* previously had a much larger range reaching south to northern Georgia and Tennessee and farther west to Nebraska (Ernst & Lovich, 2009). The Rancholabrean specimens from northwestern Georgia (Holman, 1967) and Tennessee (Parmalee & Klippel, 1981) may represent Pleistocene refugial populations from which the species extended its range northward with the retreat of the Wisconsinian glaciers. Within this range, the semiaquatic *G. insculpta* is always found in habitats near water, especially the shorelines of rivers, streams in woods and cultivated lands that have hard sand, loam, or gravel bottoms. From mid-Fall to early Spring, streams are used almost daily for movements and reproductive activities, and serve as hibernacula during the cold months. During Summer, *G. insculpta* tends to become more terrestrial (Niederberger & Seidel, 1999). Present agricultural practices appear to be having a widespread negative effect on populations (Saumure et al., 2007).

The Wood Turtle was given two other names by John Edward Gray: *Emys speciosa* (1831a: 10), and *Emys speciosa* var. *levigata* (1831b: 26). Both are considered invalid junior synonyms of *Testudo insculpta* Le Conte, 1829 (Code, Article 10.6). Gray's (1831b: 26) *Emys inscripta* is an invalid spelling of *insculpta* (Code, Article 33.3).

No subspecies of *G. insculpta* have been described, but geographic variation occurs in the light skin pigmentation of the neck and forelimbs of adult males. Those from east of the Appalachian Mountains in New York, Pennsylvania, and West Virginia are brighter, with orange or reddish pigment on the neck and forelimbs, while males from the Midwest have a lighter yellow or yellow-orange skin. Interpopulational genetic variation has been reported by Tessier & Lapointe (2001) and Tessier et al. (2005). They studied five microsatellite loci at six Canadian sites from the northernmost extent of the species range in Quebec. Tessier and coauthors reported a high degree of polymorphism in each population. There appears to be a dichotomy between the two northernmost populations and the four southern ones sampled. In another study, Spradling et al. (2010) used microsatellite DNA (11 loci) to compare genetic variation in Wood Turtles from Iowa and Minnesota to a population in West Virginia. Substantial variation was detected across the range, with turtles in Iowa showing genetic divergence from those in West Virginia. Although often considered an isolated population, *G. insculpta* in Iowa have probably experienced limited gene exchange with a nearby population in southern Minnesota. Therefore, no recent populational bottleneck was indicated.

The Bog Turtle, *Glyptemys muhlenbergii* (Schoepff, 1801: 132), is a small emydine, less than 120 mm in carapace length (Fig. 39). It has a discontinuous range in the eastern United States, occurring from western Massachusetts, Connecticut, and eastern New York, southward through eastern Pennsylvania and New Jersey, to northern Delaware and northern Maryland. Some isolated populations exist (or existed) in northwestern New York, northwestern Pennsylvania, southern Virginia, the Piedmont of North Carolina and eastern Tennessee, northwestern South Carolina, and northern Georgia. *Glyptemys muhlenbergii* has adapted to some of the most ephemeral aquatic environments, i.e. shallow water bodies subject to both natural drying through succession and draining for agriculture. It prefers clear, slow-moving water with soft, highly organic substrates: cattail and sphagnum bogs, swales, marshy meadows, tamarack and black spruce swamps, and brooks or rivulets in both wooded and pasture lands.

Lee & Herman (2004) surmised that the current scattered distribution (absence from some watersheds within the general range of *G. muhlenbergii*) cannot be explained by availability of its preferred microhabitat. According to these authors, there are suitable sites that are not inhabited, and there are disjunct colonies that are not easily explained. Lee & Herman agreed with Smith's (1957) hypothesis that the Bog Turtle expanded its range eastward during the Pleistocene from ancestral habitats in Midwestern prairies. They proposed that the species main eastward dispersal routes were along glacial outlets and through the Pleistocene Laurentian and Teays Basins. Accordingly, the original prairie populations were eliminated during glacial expansions and consequential drying of southern habitats. Lee & Herman (2004) pro-

Fig. 39. Genus *Glyptemys.* Row 1: Carapace of *Glyptemys insculpta,* and plastron of *Glyptemys insculpta.* Photos by Roger W. Barbour and Carl H. Ernst. Row 2: Carapace of *Glyptemys muhlenbergii,* and plastron of hatchling *Glyptemys muhlenbergii.* Photos by Roger W. Barbour and Carl H. Ernst.

posed a Pleistocene refugium for the Bog Turtle in the Susquehanna watershed from which the turtle expanded northward into taiga-like communities with the retreat of the Wisconsinian glaciers. In the southern Appalachians the species may have dispersed between river basins through stream capture or by way of portals (in the areas of capture); and were thus able to negotiate barriers formed by mountain chains and cross ridges.

While Lee & Herman's (2004) theory seems plausible, it is not supported by fossil evidence. There is no record of a fossil *G. muhlenbergii* from the Midwest. The only fossils are Pleistocene; reported from Alleghany County, Maryland (Holman, 1995a) in the Potomac River drainage, and Dorchester County, South Carolina (Bentley & Knight, 1998). No fossils are known from the Susquehanna watershed. It seems more likely that clearing of the eastern forests for agriculture destroyed many colonies. Bog Turtles frequently occur in wooded streams and adjacent ephemeral pools (Ernst, pers. observ.). Populations were probably always scattered and with this practice the range probably became severely fragmented, leaving many isolated colonies. The distributional hiatus from southcentral Pennsylvania to southern Virginia was probably caused by extensive agricultural activities which destroyed its shallow water habitats in the Shenandoah Valley of Virginia. We agree that the Susquehanna drainage may have served as the glacial refugium of the species; but believe that *G. muhlenbergii* was always an eastern turtle, not a species of the Midwest.

Glyptemys muhlenbergii has been assigned several other names. Say (1824 [1825]: 212) gave a vague description of a small dark turtle which he named *Emys biguttata*. Although his description mentions neither the enlarged temporal spot of *G. muhlenbergii* nor the numerous light carapace spots of *Clemmys guttata*, it better fits the former species. Gray (1831a: 7) mistakenly referred to the Bog Turtle as a variety of the Box Turtle, *Testudo carolina* Linnaeus, 1758: 198 (= *Terrapene carolina*), *Emys* (*Cistuda*) *carolinae* var. *fusca.* Later in the same publication (p. 10) he erroneously referred to the turtle as *Emys bipunctata*, a lapsus for *Emys biguttata* Say, 1824: 212. Gray (1831b) upgraded his var. *fusca* to a full species, *Emys fusca*, although as a *nomem nudum*. All of these names are clearly invalid junior synonyms of *Testudo muhlenbergii* Schoepff, 1801: 132 (Code, Article 10.6).

Considering the threatened conservation status and fragmented range of *G. muhlenbergii*, the occurrence of possible subspeciation has not been adequately studied. Dunn (1917: 624) described a second southern species of Bog Turtle, *Clemmys nuchalis*, from a site at 4,200 feet elevation in Avery County, North Carolina. His comparative sample was small; including only three females and one male *nuchalus*, and 13 male and six female *muhlenbergii* from scattered localities in Rhode

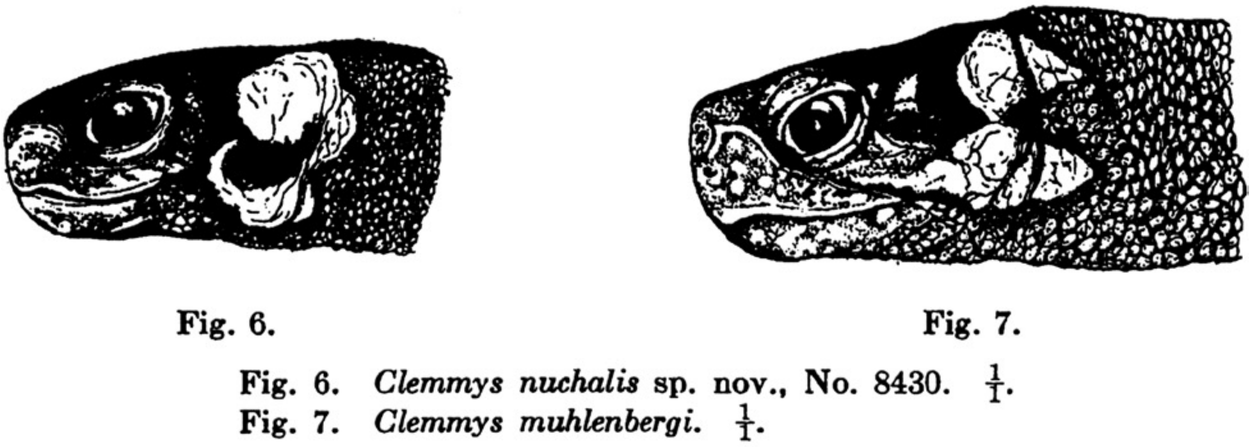


Fig. 40. Illustration of the shape of the temporal blotch which Dunn (1917) used to partition *C. muhlenbergii* into two species.

Island, New York, New Jersey, and Pennsylvania. Only the turtles from Chester County Pennsylvania were from higher than "100 feet" elevation. Dunn reported that the Southern Bog Turtle, *nuchalis*, has a longer nuchal scute. The length of the nuchal scute (NL) was reported as 6.0–7.1 mm (NL/CL, 12.7–13.2%) in female *nuchalis*, and 4–6 mm (13.6–16.4%) in female *muhlenbergii*. Male *nuchalis* had a carapace length (CL) of 98 mm, and the three females were 79–94 mm. *Glyptemys muhlenbergii* appeared to be smaller, males 84–98 mm and females 60–90 mm (CL not defined as a straight-line measurement or over the carapace curvature). Dunn noted that female *nuchalis* had a lower (CH) and broader (CW) carapace, and that with age female *muhlenbergii* showed a gradual decrease in CW/CL but were always proportionally higher than female *nuchalis*. Wright (1918) examined 10 New York specimens (five males, four females, one young) collected at 400–600 feet elevations, and concluded that the shell ratios and temporal blotch differences presented by Dunn for North Carolina turtles were not sufficiently different from New York *muhlenbergii*; but again the sample size was small. The reported ratios are subject to ontogenetic variation (Lovich et al., 1998; Angielczyk & Fox, 2006), and considering both Dunn's and Wright's relatively small sample sizes, the reported differences are suspect.

In Dunn's (1917) description of *nuchalis*, his most discrete character was the posterior border of the large, light, temporal blotch. As illustrated in his figures 6 and 7 (Fig. 40), the posterior border of *nuchalis* is more rounded, forked ventrally, and nearly fragmented by a narrow cleft in the ground color originating from the ventral side. Northern *C. muhlenbergii* have the light blotch indented posteriorly to produce two distinct backward (often spike-like) extensions. These variants of the temporal markings appear to have potential as a character which distinguishes northern and southern populations of *C. muhlenbergii*. Based on examination of turtles from two southeastern Pennsylvania populations, it appears that geographic variation in temporal blotch pattern may be valid (Ernst, unpubl.). A comprehensive analysis using larger samples (adequate for statistical analysis) is needed to determine if significant geographic differences exist among populations of *G. muhlenbergii.* Such a study should examine condition of the temporal blotch and shell morphology, including ontogenetic variation. In examining condition of the temporal blotch, the "75%" rule could be applied (Amadon, 1949; Patten & Unitt, 2002; Haig et al., 2006); i.e., 75% of the individuals of a particular population must be distinguishable from the most proximate populations. In this case, Bog Turtles from Maryland northward (*muhlenbergii*) would be compared to those from the southern Appalachians (potentially, the separate taxon *nuchalis*).

Molecular genetic studies of *G. muhlenbergii* to this date have not supported taxonomic differentiation of the southern and northern populations. Amato et al. (1997) sampled sequenced portions of the 16S ribosome mitochondrial gene in 20 Bog Turtles from disjunct populations in Georgia, North Carolina, Maryland, Delaware, Pennsylvania, and New York; and recovered only two haplotypes. Nineteen turtles had an identical haplotype, but the 20th from New York had one that varied by a single base change. Their finding of limited geographic differentiation in *G. muhlenbergii* is consistent with that of other eastern North American turtles, and suggests there may be little genetic divergence between northern and southern populations. In a more recent study, Rosenbaum et al. (2007) examined 2,793 base pairs of mitochondrial DNA spanning three genes (cytb, nd4, and d-loop). They sampled 41 Bog Turtles from 21 populations throughout the range and, similar to Amato et al. (1997), found only low levels of genetic divergence. This was especially noteworthy regarding southern populations which they presumed were disjoined during the Pleistocene refugia. Rosenbaum et al. proposed that *G. muhlenbergii* experienced a genetic bottleneck, followed by a rapid postglacial expansion into the species present northern range. Ernst & Lovich (2009) hypothesized that the southern populations were most likely still exchanging genetic material (through the Shenandoah Valley) with northern populations at least until colonial times. Subsequently, agricultural practices and habitat destruction by traversing armies during the American Civil War presumably interrupted gene flow between the two regions. Geographic separation this recent probably represents too little time for substantial divergence to develop.

The genus *Glyptemys* (under the genus name *Clemmys*) and its species *insculpta* and *muhlenbergii* were reviewed in the CAAR by Bury & Ernst (1977), Ernst (1972b), and Ernst & Bury (1977), respectively.

Terrapene Merrem, 1820

New World Box Turtles (genus *Terrapene* Merrem, 1820: 27) inhabit the eastern and central United States, extending south into several regions of northern and western Mexico, and the Yucatan Peninsula. The genus has an extensive fossil record extending from the Miocene (Ernst & McBreen, 1991a, 1991b). They are moderate in size (up to 22 cm carapace length) and exhibit omnivorous feeding habits (Fig. 41). All of the turtles in this genus have a vaulted carapace and a well-developed hinged plastron which allows them to close the shell completely. Box Turtles are the most terrestrial species in the family Emydidae. They utilize a wide variety of habitats including woodlands, meadows, xeric scrublands, prairies, and desert grasslands. At times they may frequent aquatic microhabitats, including ponds, marshes, and temporary pools. One species, *T. coahuila* Schmidt & Owens, 1944: 101, is mostly aquatic, utilizing shallow waters with soft bottoms, abundant vegetation, and slow current.

American Box Turtles have been classified in the world-wide composite genera *Testudo* (Linnaeus, 1758: 198), *Emys* (Schweigger, 1812: 317), *Terrapene* (Merrem, 1820: 27), and *Cistuda* (Fleming, 1822: 270). The generic names *Didicla* 1815: 75 and *Monoclida* 1822: 5 were introduced by Rafinesque and apparently applied to Box Turtles of the genus *Terrapene*; however, both names were unaccompanied by suitable descriptions, and are *nomen nudums* and not available names. Rafinesque (1822: 5) used the name *Monoclida kentuckensis* for *Terrapene carolina carolina* (Linnaeus, 1758) in an article in the local Lexington newspaper "Kentucky Gazette." All names published in this article were suppressed by the ICZN (1984: 221; Opinion 1280) as "no name acquired the status of availability by reason of having been published therein." The newspaper was also suppressed and placed on "The Official Index of Rejected Invalid Works in Zoology." Rafinesque later (1832: 64) used the synonym *Didicla clausa* (= *Testuda clausa* Gmelin, 1789: 1042) for *Terrapene carolina*. In 1888 Baur revised the content of *Terrapene*, restricting it to North America. The Eastern Box Turtle, *T. carolina* (Linnaeus, 1758: 198), was the first described species; followed by descriptions of the Mexican Box Turtle, *T. mexicana* (Gray, 1849: 17); Ornate Box Turtle, *T. ornata* (Agassiz, 1857: 392); Three-toed Box Turtle, *T. triunguis* (Agassiz, 1857: 279); Gulf Coast Box Turtle, *T. major* (Agassiz, 1857: 445); Yucatan Box Turtle, *T. yucatana* (Boulenger, 1895: 330); Florida Box Turtle, *T. bauri* (Taylor, 1895: 576); Nelson's Box Turtle, *T. nelsoni* (Stejneger, 1925: 463); and Aquatic Box Turtle, *T. coahuila* (Schmidt & Owens, 1944: 101).

Polytypic variation in American (Eastern) Box Turtles was recognized taxonomically by Strecker (1910: 121) who relegated *T. triunguis* to a subspecies of *T. carolina*. This left *T. c. carolina* (Stejneger and Barbour, 1917: 115) as a nominate subspecies. Carr (1952) stated that *T. c. triunguis* "… intergrades with the common box turtle [*T. c. carolina*] where their ranges meet in the eastern part of the Mississippi valley." Nevertheless, *triunguis* is a distinct morphological form with a well-defined fossil history (Gillette, 1974). Two subspecies of *T. nelsoni* were recognized by Stejneger (1925: 463) in his original description: *T. n. nelsoni* from northern Nayarit and *T. n. klauberi* from southern Sonora and northern Sinaloa, Mexico. Subsequently, Müller (1936) placed *T. nelsoni* (along with *T. goldmani* Stejneger, 1933: 119) in the synonymy of *T. mexicana*. However, that decision regarding *nelsoni* was later refuted by Smith & Smith (1980). *Terrapene yucatana* was relegated to a subspecies of *T. mexicana* by Smith (1939: 17), and Carr (1940) reduced *T. bauri* (p. 100) and *T. major* (p. 101) to subspecies of *T. carolina* based on color pattern and morphology. In 1998: 101, Ernst et al. synonomyzed the fossil species *Terrapene innoxia* Hay, 1916: 61, under *T. c. bauri. Terrapene ornata* was partitioned by Smith & Ramsey (1952: 45) into *T. o. ornata*, native to grasslands of the central United States, and *T. o. luteola* which inhabits semi-arid and desert regions of southern Arizona, New Mexico, and adjacent Mexico. Milstead (1967: 168) assigned *T. m. mexicana* and *T. m. yucatana* to subspecies of *T. carolina*. These subspecific designations were adopted by Wermuth & Mertens (1977) and Pritchard (1979). In an unpublished abstract, Ward (1980b) returned several subspecies of *T. carolina* to species status (i.e. *T. major*, *T. bauri*, *T. yucatana*). Subsequent authors continued to recognize these turtles as subspecies (e.g. Obst, 1986; Ernst & Barbour, 1989; David, 1994), except Smith et al. (1996) who treated both *mexicana* and *yucatana* as full species.

William M. Milstead, biology professor at the University of Missouri (Kansas City), pioneered our understanding of *Terrapene* evolution. He was first to comprehensively analyze relationships among the species and subspecies (Milstead, 1960, 1965, 1967; Auffenberg & Milstead, 1965; Milstead & Tinkle, 1967). Based on fossil and morphological evidence, Milstead (1969: 19) defined two major groups within *Terrapene*. Although not a cladistic analysis (Fig. 23), he showed a "sister pair" relationship between *T. ornata* and *T. nelsoni* (his *ornata* group) which forms a "sister group" to *T. carolina* plus *T. coahuila* (his *carolina* group). The evolutionary position and origin of the Aquatic Box Turtle, *T. coahuila*, has been the subject of considerable speculation. Milstead (1969) stated that this species evolved from a

Fig. 41. Genus *Terrapene* Row 1: Carapace of *Terrapene carolina* (four North American subspecies, left to right: *T. c. bauri, T. c. triunguis, T. c. major, T. c. carolina*), and plastron of *Terrapene carolina triunguis.* Photos by Roger W. Barbour. Row 2: Carapace of *Terrapene coahuila,* and plastron of *Terrapene coahuila.* Photos by Roger W. Barbour. Row 3: Carapace of *Terrapene nelsoni klauberi,* and plastron of *Terrapene n. klauberi.* Photos by Roger W. Barbour. Row 4: Carapace of *Terrapene ornata ornata,* and plastron of *Terrapene o. ornata.* Photos by Roger W. Barbour and Carl H. Ernst.

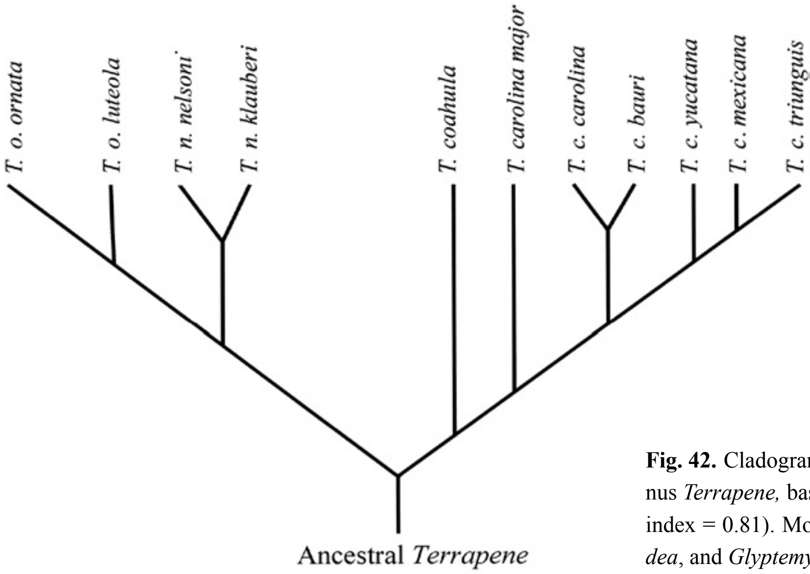


Fig. 42. Cladogram showing phylogenetic relationships in the genus *Terrapene,* based on 32 morphological characters (consistency index = 0.81). Modified from Minx (1996, fig. 1). *Emys*, *Emydoidea*, and *Glyptemys* were used as a composite outgroup.

forest-dwelling (presumably terrestrial) *carolina*-group ancestor. His evolutionary tree placed it as a relatively late (higher level) divergence in the *carolina* lineage. Similarly, Brown (1971) hypothesized that *T. coahuila* is a derived form of Box Turtle which became specialized for aquatic life. This would seem logical because all other extant Box Turtles are terrestrial, and their ability to close the shell (a primary *Terrapene* trait) could be explained as an adaptation to resist desiccation on land (see comparative water loss results in Ernst, 1968). An alternate theory presented by Bramble (1974), based on analysis of functional morphology, suggests that *Terrapene* was originally aquatic. Bramble proposed that the hinged plastron evolved as a pre-adaptation (for predator defense) prior to terrestrial radiation. Dodd (2001: 33) pointed out that it is more parsimonious to consider *T. coahuila* a relict Pleistocene form of *Terrapene* which retained its ancestral aquatic habits. Curiously, on this same page, he mentions this is consistent with Milstead (1960, 1965), seemingly overlooking Milstead's later opinion (1969: 83–84) that *T. coahuila* evolved more recently from a terrestrial ancestor.

Minx (1996) provided a cladistic analysis of *Terrapene* taxa based on morphology. He examined 32 characters, including external and skeletal features. The phylogeny proposed by Minx (Fig. 42) supported Milstead's theory of two major lineages, but placed *T. coahuila* as an early (basal) divergence from the *carolina* line. Burke et al. (1996) also reported *T. coahuila* as a basal offshoot (Fig. 26). This is consistent with Bramble's theory that early *Terrapene* were aquatic. Stephens & Wiens (2003) included all forms of *Terrapene* in their morphological analysis of emydid phylogeny. They found the position of *T. coahuila* unclear but stated (p. 586) that "The seemingly specialized Mexican Aquatic Box Turtle [*T. coahuila*] is descended from an ancestor that was either a terrestrial specialist…or semi-terrestrial generalist." Thus, the evolutionary position of *T. coahuila* remained speculative. Another finding from the phylogenetic analysis by Stephens & Wiens (2003) was support for Smith et al.'s (1996) recognition of *yucatana* and *mexicana* as full species. This interpretation was followed by Iverson et al. (2007) in their "tree of life for turtles." Nevertheless, the Turtle Taxonomy Working Group (2007), in a checklist appearing in that same volume and co-authored by Iverson, treated these Box Turtles as subspecies of *T. carolina*. It is noteworthy that Iverson reportedly was out-voted by co-authors in that decision (pers. comm.). Although recent checklists recognize them as subspecies (Fritz & Havaš, 2007; Turtle Taxonomy Working Group, 2011), the taxonomic status of *mexicana* and *yucatana* remains unresolved.

Joyce et al. (2012: 179) described a new fossil species of *Terrapene* from the Miocene/Pliocene boundary (Hemphilian) of Oklahoma. Based on skeletal characteristics of the shell, they found this turtle (*T. parornata*) allied to *T. ornata*; and forming a sister group defined in part by the presence of a unique pair of anterior mental glands exclusively shared with extant *T. ornata* (Waagen, 1972). Joyce et al. placed the fossil species *T. longinsulae* Hay, 1908a: 166 (upper Miocene – lower Pliocene, Phillips Co. Kansas) in the synonymy of *T. ornata*; and questioned the identity of the fossil species *T. corneri* Holman & Fritz, 2005: 83 (middle Miocene, Webster Co. Nebraska) due to fragmentary evidence. They presented a morphology based phylogenetic analysis of relationships in *Terrapene* which supported the two major lineages (*ornata* and *carolina* clades) proposed by Minx (1996). Joyce et al. (2012) did not include subspecies of *T. carolina* in their study. Thus, the phylogenetic position of *T. coahuila* and other Mexican *Terrapene* was not tested.

Recently, phylogenetic relationships in *Terrapene* have been tested by DNA analysis. The bulk of evidence supports the two major clades defined by morphological studies: *T. carolina* + *T. coahuila* and *T. ornata* + *T. nelsoni* (Stephens & Wiens, 2009; Thomson & Shaffer, 2010, Fig. 33; and Wiens et al., 2010, Fig. 31). However, the concept of all of the subspecies of *T. carolina* forming a sister group to *T. coahuila* is not supported by Stephens & Wiens (2008) and Spinks et al. (2009a, Fig. 32). Stephens & Wiens (2009) later suggested that their 2008 analysis may have been misleading because it excluded *T. nelsoni*. Spinks et al. (2009a) also implied that their resolution of *Terrapene* was incomplete based on nuclear and mitochondrial DNA.

Butler et al. (2011) used morphological and molecular data to study variation among Gulf Coast subspecies of *T. carolina*, including *bauri*, *major*, and *triunguis*. Their primary objective was to test the validity of *T. c. major* Agassiz, 1857: 445. The Pleistocene fossil, *T. putnami* Hay, 1907: 30 (relegated to subspecies *T. c. putnami* by Auffenberg, 1958: 53) has been reported to be very similar morphologically to *T. c. major* (Milstead, 1969). Milstead suggested that *major* is an admixture of subspecies which intergrade in the Gulf coastal area. This was also supported by Butler et al.'s (2011) mitochondrial DNA analysis of haplotype lineages. The latter authors suggested the possibility that populations in this region (including *major*) could represent genetic variation passed down from *putnami.* Butler et al. (2011) concluded that Box Turtles phenotypically identified as *T. c. major* occur within the range of other subspecies and that this form is not a valid (diagnosable) taxon. Based on both morphological and molecular data, these authors further proposed elevation of *T. c. bauri* to full species. That taxonomic decision was adopted by Iverson et al. (2012) and Dodd et al. (2012), although the strength of evidence for *T. bauri* has been questioned. Species recognition by Butler et al. (2011) was based on differentiation of a single mitochondrial DNA gene in a not particularly robust phylogenetic tree (P. P. Van Dijk, pers. comm.). Furthermore, if recognition of *T. bauri* is accepted, it creates a paraphyletic relationship among the remaining subspecies of *T. carolina* (Turtle Taxonomy Working Group, 2011). Therefore we tentatively retain *bauri* as a subspecies of *T. carolina*, and conservatively recognize *T. c. major* as well.

More recently, Martin et al. (2013) examined phylogenetic relationships in the genus *Terrapene* based on mitochondrial and nuclear DNA sequencing. Their analysis was comprehensive, including all extant taxa except *T. nelsoni klauberi.* Similar to previous studies, they concluded that *T. ornata* and *T. nelsoni* form a clade which is the basal sister group to a clade of *T. coahuila* and subspecies of *T. carolina.* They too could not clearly resolve the phylogenetic position, and thus the appropriate taxonomic level, for *T. carolina bauri.* Consistent with the results of Butler et al. (2011), Martin et al. were also unable to resolve *T. c. major* as a valid subspecies (Fig. 43), nor did they find *T. ornata luteola* divergent enough from *T. o. ornata* to be considered a separate subspecies. While the taxonomic validity of *T. c. major* appears uncertain, the status of *T. o. luteola* should not be questioned until tested by a broad morphological analysis. Perhaps the most striking result of Martin et al. (2013) was resolution (based on mitochondrial DNA sequencing) of a clade consisting of *T. c. mexicana*, *T. c. yucatana*, and *T. c. triunguis*; collectively representing a sister group to the other subspecies of *T. carolina* plus *T. coahuila* (Fig. 43). Monophyly of *mexicana*, *yucatana*, and *triunguis* agrees with the morphological results of Minx (1996) and Milstead (1969) in part (see Figs. 23 and 42); but in those two studies the three forms appear paraphyletic with respect to other subspecies of *carolina.* Although not supported by their nuclear DNA sequencing, Martin et al. concluded that *triunguis*, *mexicana*, and *yucatana* should be recognized as subspecies of *T. mexicana* (elevated as the older of the three names, Gray, 1849: 17). In their book on Mexican turtles, Legler & Vogt (2013) considered both *mexicana* and *yucatana* full species, although the basis for that decision was not clear. Fritz & Havaš (2014), along with Spinks et al. (2016), pointed out the weaknesses in data interpretation by Martin et al. (2013), and concluded that *mexicana*, *yucatana*, and *triunguis* should remain as subspecies of *T. carolina.* A response by Martin et al. (2014) did not address the specific flaws raised by Fritz & Havaš, and thus was not convincing. While future study may confirm the relationships proposed by Martin et al., we conservatively continue to recognize the three forms as subspecies of *T. carolina.* The appropriate taxonomic level for recognizing the different forms of American Box Turtles remains problematic. Discrete separation of species may be obscured by a long and well-documented history of natural hybridization (Clark, 1935; Shannon & Smith, 1949; Smith, 1955; Blaney, 1968; Ward, 1968; Lutterschmidt et al., 2007; Cureton et al., 2011) and frequent geographic translocation of turtles by hu-

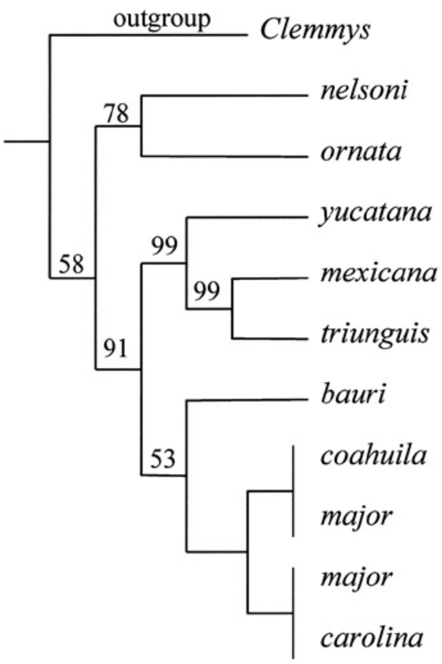


Fig. 43. Phylogenetic relationships in the genus *Terrapene* derived from DNA sequencing of the mitochondrial cytochrome b gene. Bootstrap values are indicated at nodes. Modified from Martin et al. (2013, fig. 2).

mans (Adler, 1970). Moreover, taxonomic recognition may balance on which "species concept" is favored (i.e. phylogenetic, biological, or evolutionary). Future studies of systematic relationships in *Terrapene* should be geographically comprehensive and include DNA analysis of all forms, especially *mexicana* and *yucatana*.

Ernst & McBreen (1991a) reviewed the genus *Terrapene* in The Catalogue of American Amphibians and Reptiles (CAAR) and presented a dichotomous key for the species. Keys for Mexican subspecies are in Smith & Smith (1980). The following species were reviewed in CAAR: *T. carolina* (Ernst & McBreen, 1991b), *T. coahuila* (Iverson, 1982a), *T. nelsoni* (Iverson, 1982b), *T. ornata* (Ward, 1978). Farrell et al. (2006) and Kiester & Willey (2015) also reviewed *T. carolina* in Chelonian Research Monographs. Other species accounts published in Chelonian Research Monographs are of *T. coahuila* (Howeth & Brown, 2011) and *T. nelsoni* (Buskirk & Ponce-Campos, 2011). Various reviews of fossil *Terrapene* have been presented by Hay (1908b), Auffenberg (1958), Milstead (1965, 1967, 1969), Ernst & McBreen (1991a, 1991b), and Dodd (2001). A comprehensive review of the identification and natural history of *Terrapene* species is presented by Dodd (2001).

Subfamily Deirochelyinae *Agassiz*, 1857. The Aquatic Emydids

Nomenclatural History. —Agassiz (1857) first proposed the now recognized subfamily-group of deirochelyid emydines. Unfortunately, he caused confusion by spelling it "Deirochelyoidae," using the family ending "idae;" first as a *nomen nudum* on introductory page *xlix*, but later properly described on pp. 355–356 of his text. It is clear that he meant the name Deirochelyoidae to represent a subfamily, not a family; for on p. 355 he stated that "The minor differences of form observed among the Emydoidae [= Emydidae], suggest the following subdivisions, which appear to bear the character of subfamilies…" Gaffney & Meylan (1988: 201) corrected Agassiz's spelling of the subfamily to Deirochelyinae. Initially, Agassiz (1857) reserved the subfamily only for his new genus *Deirochelys*, its sole species *D. reticulata* (= *Testudo reticularia* Latreille, 1802: 124). Presently, in addition to *Deirochelys*, the subfamily includes the genera *Chrysemys*, *Graptemys*, *Malaclemys*, *Pseudemys*, and *Trachemys* (Gaffney & Meylan, 1988; Seidel & Adkins, 1989).

Relationships in the Subfamily Deirochelyinae. — Over the years there has been considerable debate regarding generic assignment in the aquatic lineage of emydids, making their taxonomy unstable. For example, Painted Turtles have historically been placed in the monotypic genus *Chrysemys* Gray, 1844: 27, i.e. *C. picta*; and Cooters and Sliders have been assigned to the polytypic genus *Pseudemys* Gray, 1856a: 197, e.g. *P. concinna* and *P. scripta*, respectively (Cope, 1875; Baur, 1893a; Hay, 1908b; Stejneger & Barbour, 1917, 1943; Mertens, 1933; Carr, 1952; Schmidt, 1953; but not Boulenger, 1889). Based on skull characters, number of phalanges, and scute morphology; McDowell (1964: 273) redefined a subgroup of aquatic species, resurrecting *Chrysemys* sensu lato (Boulenger, 1889: 69) and partitioning at the subgenus level. McDowell's composite genus *Chrysemys* included Cooters (subgenus *Pseudemys*), Painted Turtles (subgenus *Chrysemys*), and Sliders (subgenus *Trachemys* Agassiz, 1857: 252). Boulenger's (1889: 69, 75) composite genus *Chrysemys* was similar, but included Chicken Turtles (*Deirochelys* Agassiz, 1857: 441) as well. McDowell's recognition of three subgenera was a reversion back to the arrangement of Agassiz (1857), although Agassiz used the name *Ptychemys* (p. 431) instead of *Pseudemys* (sensu Gray, 1863). Preceding McDowell, Archie F. Carr (1952, p. 234), a recognized authority on turtles at the University of Florida, had commented that recognition of three distinct groups "… (which would revive the old generic name *Trachemys* for the *scripta* section) seems fairly reasonable." Five years later, Zweig & Crenshaw (1957), comparing the electrophoretic patterns of serum proteins in *Pseudemys scripta*, *P. floridana* (= *P. peninsularis*), *P. nelsoni*, and *P. suwanniensis*, found extreme differences in the pattern of *P. scripta* versus those of the other three species; reinforcing the use of *Trachemys* for the Sliders.

McDowell's (1964) decision to consolidate (i.e. *Chrysemys* sensu lato) was based on greater variation he observed between Cooters and Sliders within *Pseudemys*, compared to variation between Painted Turtles and Sliders. His criticism was clearly directed at the concept of *Pseudemys* sensu lato and not necessarily at *Chrysemys* sensu stricto. A distinct advantage of recognizing three full genera is that it would have avoided a cladistic problem. McDowell (1964) theorized that Sliders, subgenus *Trachemys*, are ancestral to *Malaclemys* Gray, 1844: 28 (including *Graptemys* Agassiz, 1857: 252) and *Deirochelys* Agassiz, 1857: 252. Thus, his genus *Chrysemys* sensu lato became a paraphyletic taxon. Subsequent workers who followed McDowell's generic revision of *Chrysemys* seemed to have overlooked this pitfall.

In 1967, Peter C. H. Pritchard, a doctoral student of Archie F. Carr, published a popular book on "Living Turtles of the World." It was not surprising that he did not follow McDowell's (1964) proposed taxonomy for *Chrysemys*. Neither did Robert Stebbins in either his "Amphibians and Reptiles of Western North America" (1954), or his acclaimed "Field Guide to Western Reptiles and Amphibians" (1966). However, Rose & Weaver (1966) and Weaver & Rose (1967) examined fossil and extant species of emydids and found support for McDowell's arrangement. They based it on the conclusion that Painted Turtles (*Chrysemys picta*) and Sliders (*Pseudemys scripta*) have essentially the same skull morphology. Therefore, they believed that Cooters (e.g. *Pseudemys concinna*) are more divergent, and the best taxonomic solution was to follow McDowell (1964) by lumping them all into *Chrysemys*. Nevertheless, they disagreed with McDowell's contention that Sliders (*Trachemys*) represent a natural group. This was based on their description of a fossil species (*C. carri* = *P. caelata* Hay, 1908b: 356) which reportedly had a Cooter-like (*P. nelsoni*) shell and a Slider-like (*P. scripta*) mandible. Subsequently, Jackson (1976: 655) refuted their interpretation by observing that the fossil mandible was actually similar to that of Cooters (e.g. *P. concinna*).

Although evidence was accumulating for a shift to *Chrysemys* sensu lato, many authors were reluctant to abandon the familiar genus *Pseudemys* (i.e. Milstead & Tinkle, 1967; Gibbons, 1968a, 1968b; Holman, 1968; Parsons, 1968; Rand, 1968; Thorson, 1968; Bellairs, 1969; Folkerts & Mount, 1969; Freiberg, 1969; Mahmoud & Lavenda, 1969; Zangerl, 1969; Jackson, 1970; Legler & Webb, 1970; Moll & Legler, 1971; Mrosovsky & Pritchard, 1971; Weathers & Morgareidge, 1971; Frair, 1972; Gatten, 1974; Seidel, 1975; Wermuth & Mertens, 1977; and Legler, 1990). Nevertheless, the concept of *Chrysemys* sensu lato began to gain momentum in the 1970s (Ernst, 1970; Blaney, 1971; Graham, 1971; Bayless, 1972; C. Jackson & Davis, 1972a, 1972b; Mittermeier, 1972; Bickham & Baker, 1976; D. Jackson, 1976; Seidel, 1977; and Gaffney, 1979). Although none of these authors specifically tested generic status, their taxonomic assignments could have been influenced by two prominent texts (Ernst & Barbour, 1972 and Conant, 1975) which adopted *Chrysemys* sensu lato. Holman (1977: 274) expressed doubt about the concept of *Chrysemys* sensu lato based on ecological observations. He noted that four species of the genus are microsympatric in northwestern Tennessee, yet no evidence of hybridization has been reported. Furthermore, it seems that niche competition would be intense enough to exclude one or more of the four purported congeners. In 1980, Vogt & McCoy addressed the issue using protein electrophoresis, as well as skull and shell morphology. Their analysis was phenetic and did not distinguish characters which were primitive or derived. Nevertheless, their biochemical (LDH and general protein) results identified divergent character states among all three subgroups of *Chrysemys* sensu lato (Painted Turtles, Sliders, and Cooters). Ward (1980a, 1984) also found divergence among these groups and recognized three genera: *Chrysemys* (Painted Turtles), *Pseudemys* (Cooters) and *Trachemys* (Sliders). His analysis was based mostly on cranial morphology, but again did not utilize an outgroup or distinguish between primitive and advanced states. Another phenetic analysis (Ernst & Ernst, 1980) utilized a similarity index of endoparasites in these turtles. Ernst & Ernst stated that Painted Turtles (*Chrysemys* sensu stricto) and Cooters and Sliders collectively (*Pseudemys* sensu lato) are "sufficiently different to warrant recognition at the generic level."

During the early 1980s generic status of *Chrysemys* and *Pseudemys* remained very unstable. As an example, collectively in 1983 volumes of the Journal of Herpetology, Copeia, and Herpetologica, seven authors applied *Chrysemys* sensu lato and 18 authors used *Chrysemys* sensu stricto (plus genus *Pseudemys*). In an effort to bring some stability to the situation, Seidel & Smith (1986) re-evaluated the systematic status of the subgenera proposed by McDowell (1964): *Chrysemys*, *Pseudemys*, and *Trachemys*. They evaluated all characters analyzed in previous studies and their approach was, in part, cladistic. It utilized Map Turtles (genus *Graptemys*) as the primary outgroup and Chicken Turtles (genus *Deirochelys*) as a secondary outgroup. Seidel & Smith (1986) determined that *Pseudemys*, *Trachemys*, and *Graptemys* are equally divergent from each other, sharing seven synapomorphies. In contrast, *Chrysemys* appeared to be the most divergent, sharing no more than three synapomorphies with the other genera. Because no clear sister-group relationship could be determined, the authors concluded that the most conservative approach was to recognize McDowell's (1964) subgenera (sensu Agassiz, 1857) as full genera, *Chrysemys*, *Pseudemys*, and *Trachemys*. Although it could be argued that this limited the information content of genus nomenclature, it avoided questionable suppositions on phylogenetic affinities. From another perspective, Gaffney (1979) noted that recognition of an overly "split classification will more readily allow the development of phylogenetic hypotheses than a lumped one." Seidel & Smith (1986) also pointed out (as did Holman, 1977) that there are no known cases of natural hybridization among the three genera, in spite of numerous hybrid reports within *Pseudemys* sensu stricto (Crenshaw, 1955, 1965; Smith, 1961; Mount, 1975) and *Trachemys* (Seidel & Adkins, 1987; Fritz, 1995a; Seidel et al., 1999; Tuberville et al., 2005). Seidel later presented evidence (Seidel & Fritz, 1997; see also Fritz, 1991) that *Pseudemys* sensu stricto is monophyletic based on its unique form of courtship behavior. Unlike other genera of Deirochelyines in which the male faces the female during titillation, a *Pseudemys* male positions himself above the female facing the same direction. Seidel & Smith (1986) were successful in achieving taxonomic stability for the group and most authors have accepted their arrangement of genera. Notable exceptions were Legler's (1990) application of *Pseudemys* sensu lato and Savage's (2002) use of *Chrysemys* sensu lato, but no specific refutation of the three genera arrangement was forthcoming. More recently, phylogenies based on DNA sequence data have offered stong evidence that *Chrysemys* and *Pseudemys* are monophyletic genera (Wiens et al., 2010). However, the monophyletic status of *Trachemys* and its relationship to *Graptemys* has been questioned (e.g. Stephens & Wiens, 2003).

Similar to his treatment of *Chrysemys* in 1964, McDowell (following Carr's inference, 1952 p.162), resurrected *Malaclemys* Gray, 1844: 28 sensu lato (Hay, 1892 = *Malacoclemmys* Cope, 1875 [1877], Boulenger, 1889). This composite genus of aquatic emydids included the monotypic genus of Diamondback Terrapins, *Malaclemys terrapin*, and all of the recognized species of Map/ Sawback Turtles, *Graptemys* sensu Agassiz (1857: 252), Carr (1952), and Loveridge & Williams (1957). Again, McDowell's justification (based on skull characters) was that the differences between the two genera are no greater than intrageneric differences (i.e. among species of *Graptemys*). *Malaclemys* sensu lato did not receive the attention of McDowell's (1964) *Chrysemys* sensu lato revision. Perhaps part of the reluctance of many authors was based on the very different behavior and physiology of Terrapins compared to Map Turtles. *Malaclemys terrapin* inhabits coastal salt marshes (Hartsell & Ernst, 2004) and are able to tolerate (osmoregulate in) hypertonic saline water due to their unique lachrymal salt glands (Cowan, 1969, 1971, 1974; Dunson, 1969, 1976) and ability to concentrate plasma urea (Gilles-Baillien, 1970). All Map Turtles utilize strictly freshwater riverine habitats, possess no salt glands, and have no specialized ability to osmoregulate in brackish water (Ernst & Lovich, 2009). Nevertheless, Zug (1966, 1971) and Cochran & Goin (1970) apparently found McDowell's morphological evidence convincing and adopted *Malaclemys* sensu lato.

In 1977, Roger Wood authored an essay which addressed the relationship between *Malaclemys* and *Graptemys*. He acknowledged that the fossil record of these turtles was insufficient to provide any insight, and based his theory on qualitative characters such as pigmentation and shell shape of extant forms. Without any substantive evaluation of data, he concluded that *M. terrapin* was ancestral to all of the modern species of *Graptemys*, thus supporting McDowell's (1964) *Malaclemys* sensu lato. The idea of a primitive *Malaclemys* evolving into modern *Graptemys* was not novel, but rather a reversion to Hay's (1908b) theory. Wood (1977) hypothesized that *M. terrapin* extended its range from coastal estuaries up river systems, and then became isolated from the parent population inhabiting coastal marshes during various ice ages. This isolation in different river systems presumably allowed for the eventual speciation of different Map Turtles (*Graptemys* sp.) recognized today. Because this speculative relationship would represent paraphyly between the two genera, Wood (1977) recommended placing *Graptemys* in the synonymy of *Malaclemys*, thus following McDowell (1964).

There are several problems with Wood's hypothesis. First, there is no strong evidence for the assertion that *Malaclemys* moves from brackish water, up rivers into freshwater. To the contrary, a multitude of reports indicate that they do not utilize freshwater habitats (Carr, 1952; Ernst et al., 1994; Ernst & Lovich, 2009). Furthermore, species of *Graptemys* are not able to tolerate brackish water (hypertonicity) for extended periods due to their lack of salt glands. This would require an unparsimonious evolutionary model for the independent regression (loss) of the salt gland in the various species of Map Turtles. An additional problem with the assumption that *Malaclemys* is the ancestor of all modern *Graptemys* comes from variation in pigment pattern. The 12 species of *Graptemys* have neck, limb, and tail striping which is typical of all aquatic emydids except *Malaclemys*. Diamondback Terrapins have soft parts which are spotted, a presumably derived condition. Therefore it would have to be assumed they had a primitive striped pattern which more recently evolved into a spotted pattern throughout their extensive range. This hypothesis seems unlikely and also unparsimonious.

Wood's (1977) effort to popularize the concept of *Malaclemys* sensu lato was not successful and most authors continued to recognize *Graptemys* as a distinct genus. Subsequently Dobie & Jackson (1979) reported the first fossil record for *Malaclemys* (Pleistocene) and described several characters which separate the genus from *Graptemys* (e.g. width of nuchal bone, notching of anterior costal bone, anterior width of vertebral scute). That was followed by a more extensive comparison of external and skeletal morphology (Dobie, 1981). Dobie's analysis, which distinguished between primitive and derived states, found strong evidence of divergence between the two genera. Lamb & Osentoski (1997) conducted a molecular assessment of five subspecies of *Malaclemys terrapin* and twelve species of *Graptemys* using *Trachemys* as an outgroup. They sequenced portions of the mitochondrial cytochrome *b* gene and control region. Their phylogenetic analysis of those data produced 32 equally parsimonious trees, all of which showed *Malaclemys* and *Graptemys* as distinct monophyletic clades. Thus the conclusions of Lamb & Osentoski (1997) also refute Wood's (1977) hypothesis that *Malaclemys* is paraphyletic with respect to *Graptemys*. More recent nucleotide studies (especially Spinks et al., 2009b; Fritz et al., 2012; Reid et al., 2011) further substantiate the validity of a monophyletic *Malaclemys*. Presently, recognition of a separate genus *Graptemys* is unilaterally accepted.

While the generic composition of the subfamily Deirochelyinae has become taxonomically stable, relationships among the six genera have remained uncertain. Loveridge & Williams (1957) were among the first to theorize on evolutionary origins of these turtles. They presented a dendrogram (p. 185) that suggested that *Pseudemys* sensu lato is basal, giving rise to *Deirochelys* along one branch, *Chrysemys* sensu stricto along a second branch, and *Graptemys* / *Malaclemys* along a third (Fig. 5). McDowell's (1964) theory on relationships was similar, except he described *Trachemys* as the common ancestor of *Malaclemys* (including *Graptemys*) and *Deirochelys*. McKown (1972) proposed that *Graptemys* and *Malaclemys* evolved from a *Trachemys*-type ancestor during early Tertiary times. Ward (1980a, p. 310) proposed an unusual phylogeny for emydids which is not consistent with recognition of the two subfamilies Emydinae and Deirochelyinae. He placed *Malaclemys* and *Graptemys* in the semi-terrestrial lineage Emydinae, rather than in the aquatic group Deirochelyinae. In 1988 Gaffney & Meylan presented a cladogram (Fig. 22) which is almost the inverse of trees proposed by Loveridge & Williams (1957) and McDowell (1964). Gaffney & Meylan (1988) showed *Graptemys* and *Malaclemys* as

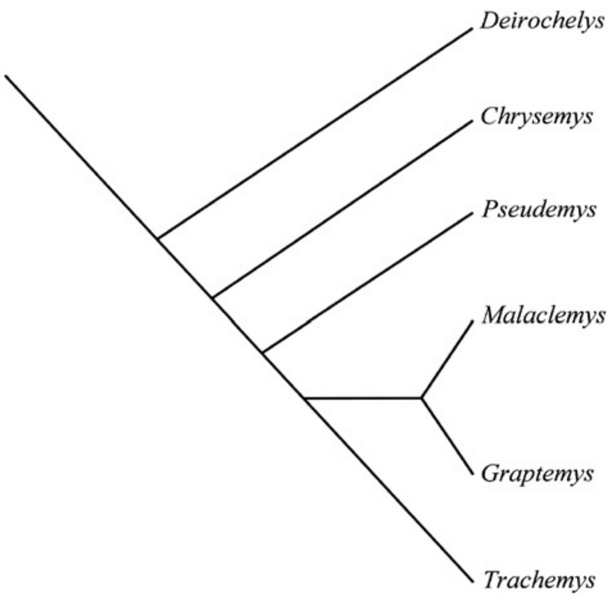


Fig. 44. A theory on the phylogenetic position of *Trachemys* (Seidel and D. R. Jackson 1990, fig. 5.1) derived from synapomorphies listed in their table 5.1 of 28 characters. Tree is rooted at upper left margin.

basal (early offshoots) and *Deirochelys* as the sister group to *Pseudemys* and *Trachemys*. Seidel's 1987 unpublished cladogram (Fig. 21, based on biochemical and morphological characters) showed *Deirochelys* as basal while *Graptemys* and *Malaclemys* formed the sister group to a clade of *Chrysemys*, *Pseudemys*, and *Trachemys*. Seidel & Jackson (1990) present a similar arrangement (Fig. 44), except that *Chrysemys* appeared as the sister group to a trichotomy of *Pseudemys*, *Trachemys*, and *Graptemys* / *Malaclemys*. A basal position for *Deirochelys* is consistent with Jackson's conclusion that the genus diverged by at least the early Miocene. Also, there is some indication that the pattern of courtship behavior in Chicken Turtles may be a primitive form (prototype) of titillation seen in the other, presumably more advanced deirochelyines (Seidel, 2010b).

Bickham et al. (1996) were the first to examine relationships of the Deirochelyinae based on nucleotide sequence data. By studying variation in the 16S ribosomal RNA gene, they found *Deirochelys* to be a basal offshoot (sister taxon to all other members of the subfamily), similar to the results of Seidel (1987 unpubl.). Consensus trees presented by Bickham et al. (1996) indicate strong evidence for a clade consisting of *Trachemys*, *Graptemys* and *Malaclemys* (corroborating earlier hypotheses by McDowell 1964, and McKown 1972). This clade either forms an unresolved trichotomy with *Chrysemys* and *Pseudemys* (Fig. 25) or appears as the sister group to a terminal clade of *Chrysemys* and *Pseudemys*. Starkey (1997) also tested relationships in the Deirochlyinae by sequencing fragments of mitochondrial DNA from the ND4 gene. His results were very similar to Bickham et al. (1996). Starkey reported *Deirochelys* as a basal sister group to all of the other Deirochelyines and defined a clade of *Chrysemys* and *Pseudemys* that formed the sister group to *Graptemys*, *Malaclemys*, and *Trachemys* (Fig. 45). Most noteworthy was that Starkey (1997) examined a large number of *Trachemys* species and found they form a highly resolved monophyletic lineage (clade) which is the sister group to *Graptemys* and *Malaclemys*. In 2003, Stephens & Wiens published results from a comprehensive phylogenetic analysis of the family Emydidae. It was based on a large data set of previously published morphological and molecular (except Starkey, 1997) characters, and included nearly all of the emydid species. As in earlier studies, they found that *Deirochelys* is basal and the sister group to all other turtles in the subfamily (Fig. 29). More recent molecular studies based on DNA sequencing have further substantiated the basal position of Chicken Turtles (Thomson & Shaffer, 2010; Wiens et al., 2010), except for the surprising results of Spinks et al. (2009b, Fig. 32) which indicated *Deirochelys* as basal to all emydids.

Similar to Seidel & Jackson (1990), Stephens & Wiens (2003) found that *Chrysemys* appeared as the next most basal genus in the subfamily, subsequent to the divergence of *Deirochelys*. The nuclear DNA data of Wiens et al. (2010) supported this position of *Chrysemys* (Fig. 31) but their mitochondrial data did not. A large supermatrices database phylogeny presented by Thomson & Shaffer (2010) shows *Chrysemys* as an early divergent lineage if the peculiar position of *Pseudemys peninsularis* is disregarded (Fig. 33). The terminal clade including *Graptemys*, *Malaclemys*, *Pseudemys*, and *Trachemys*, is also supported by a presumptive synapomorphic form of hemoglobin, pI 8.3, reported by Seidel (2002b). Within that lineage, essentially all molecular and morphological studies indicate monophyly and a sister group relationship for *Graptemys* and *Malaclemys*. A single exception is the mitochondrial DNA based phylogeny of Spinks et al. (2009b) which suggested a sister group relationship of *Malaclemys* to a clade formed of *Graptemys* and *Trachemys* (Fig. 32). Stephens & Wiens (2003) found that *Trachemys* appeared to be paraphyletic with respect to *Graptemys* (Fig. 29). It could be inferred from their results that all Slider species (*Trachemys*) share a set of defining primitive character states but not synapomorphies. Stephens & Wiens (2003) did not list the characters which supported the branches, nor did they separately analyze the subfamily Deirochelyinae. If they had used the subfamily Emydinae as an outgroup, perhaps the polarity of several characters would have reversed to synapomorphies supporting a monophyletic *Trachemys*? Furthermore, it appears that Stephens & Wiens (2003) did not include (and perhaps were unaware of) Starkey's (1997) DNA data which characterized a monophyletic *Trachemys*. Iverson et al. (2007), in their tree of life for turtles, mostly adopted the emydid phylogeny of Stephens & Wiens (2003), including the paraphyletic position of *Trachemys*. Recognizing the shortcomings of their 2003 phylogeny, Stephens & Wiens (2008) stated "… in that study, many species lacked molecular data, many parts of the tree were weakly supported (by parsimony bootstrap-

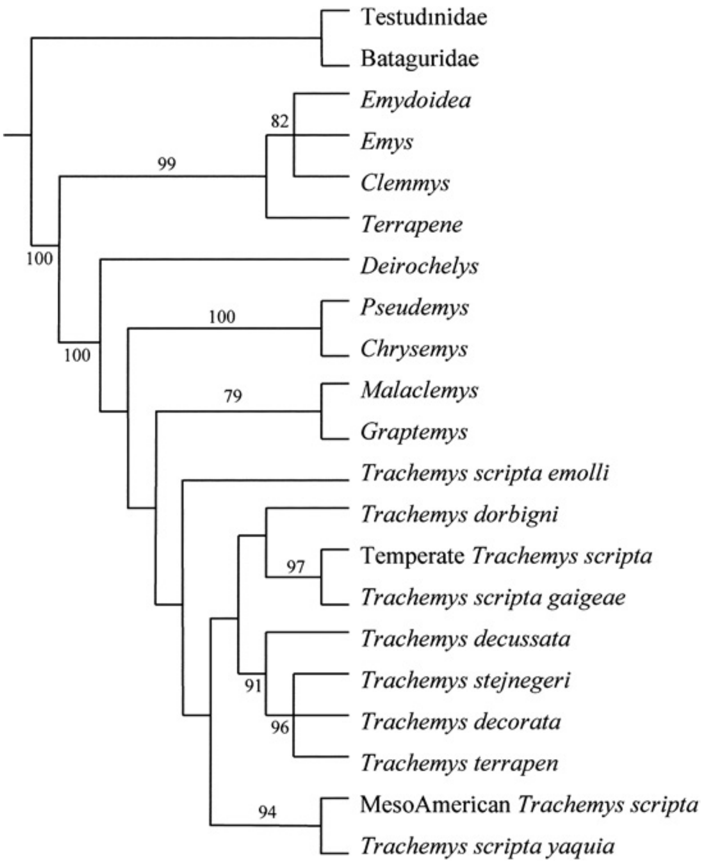


Fig. 45. Cladogram resulting from Maximum Parsimony analysis of emydid turtles based on mitochondrial DNA data (Starkey 1997, fig. 15). The numbers at nodes indicate bootstrap support, some values not provided. Taxa were specifically selected to test relationships of the genus *Trachemys*.

ping), and the combined data were not analysed using model-based methods." Stephens & Wiens (2009) presented an updated phylogenetic theory of relationships in the Emydidae depicting a single lineage for *Trachemys*. Using a larger molecular data set in 2010, Wiens et al. found their nuclear DNA based phylogeny did indicate that Sliders, *Trachemys*, are monophyletic and form the sister group to *Malaclemys* and *Graptemys* (Fig. 31). However, again this relationship was not supported by their mitochondrial DNA data. As stated earlier, Galtier et al. (2009) criticized the value of mitochondrial DNA for resolving these types of species relationships. The phylogeny based on mitochondrial DNA cytochrome *b* data of Spinks et al. (2009b) did produce a monophyletic *Trachemys* but only three species, *T. scripta*, *T. stejnegeri*, and *T. taylori*, were included in their analysis. Reid et al. (2011) and Fritz et al. (2012) presented strong evidence for the taxonomic integrity of Slider Turtles. Fritz et al. stated that "… our mtDNA data suggests [sic] with high support the monophyly of *Trachemys*." They speculated that previous mitochondrial DNA studies were biased by reliance on universal turtle primers. From their analysis of mitochondrial cytochrome *b* and ND4 genes, McCranie et al. (2013) stated that "All [of their] phylogenies consistently revealed *Trachemys* as a monophyletic group with respect to the emydid outgroup [i.e. *Malaclemys*, *Graptemys*, *Chrysemys*, *Pseudemys*] with high bootstrap support." Seidel (2002a) had identified six, purportedly derived, morphological character states which define all Sliders: ventral surface of mandible rounded, upper mandible surface narrow, cutting surface of upper jaw medially forms an angle, zygomatic arch narrow, narial opening of cranium narrow, and entoplastron not elongate. The bulk of recent DNA evidence, especially analysis of nuclear DNA, indicates the genus *Trachemys* is a natural monophyletic taxon. Monophyly of *Trachemys* has recently been corroborated by the expanded data set of nuclear DNA employed by Spinks et al. (2016). Whether Sliders can be described by a set of shared-derived or shared-primitive morphological characters raises a taxonomic question regarding how we define a genus.

Most studies, with the possible exception of Thomson & Shaffer (2010), have presented strong evidence that species in *Pseudemys* form a monophyletic group. Based on morphological characters, Gaffney & Meylan (1988) reported *Pseudemys* as the sister group to *Trachemys* (Fig. 22). The large combined molecular and morphological data set of Stephens & Wiens (2003) depicted *Pseudemys* as the next most basal genus; subsequent to the divergence of *Chrysemys* and *Deirochelys*, placing it as the sister group to a clade of *Graptemys* and *Malaclemys*, and *Trachemys.* This position has been supported by the nuclear DNA based phylogeny (Fig. 31) of Wiens et al. (2010) and most recently that of Spinks et al. (2016). In conclusion, relationships among genera in Deirochelyinae are becoming better resolved by results from molecular studies. Nevertheless, species boundaries within several of the genera (i.e. *Graptemys*, *Pseudemys*, *Trachemys*) remain largely problematic.

Taxonomy Within Deirochelyine Genera.

Deirochelys Agassiz, 1857

Agassiz (1857: 252) first proposed *Deirochelys* as a new monotypic genus for the species *Emys reticulata* (= *Testudo reticularia* Latreille, *in* Sonnini & Latreille, 1802: 124), with a more complete description of the genus on p. 441.

Chicken Turtles, *Deirochelys reticularia* (Latreille, 1801), are of moderate to large size (up to 25 cm carapace length) with a long neck, reticulate carapace pattern, longitudinal rough ridges on the carapace, broad vertebral scutes, vertical light stripes on the rump, and a very wide foreleg stripe. The head is elongated with a prominent mouth. The upper jaw lacks a notch. The crushing surface of the upper jaw is narrow and ridgeless. They are semi-terrestrial turtles which range throughout much of the southern United States (Fig. 46). They occur along the Atlantic Coastal Plain from southern Virginia, through Florida and the Gulf Coast states to eastern Texas, and up the Mississippi Valley to southern Missouri. *Deirochelys* inhabits shallow, still, or slowly moving waters including ponds, lakes, ditches, wet prairies, grassy marshes, Carolina Bays, and cypress swamps. Males exhibit terrestrial activity in Spring and Summer while females are more terrestrial in Fall and Winter, corresponding to their atypical nesting season. Chicken turtles are mostly carnivorous, but Seidel (unpubl.) observed a captive juvenile avidly feeding on vegetation.

Early on Chicken Turtles were classified in the composite genera *Testudo* (Latreille, 1802: 124), *Emys* (Schweigger, 1812: 281), *Terrapene* (Bonaparte, 1831: 155), and *Clemmys* (Fitzinger, 1835: 124). Agassiz (1857: 252) recognized their extreme level of distinction by placing them in the monotypic genus *Deirochelys* (*D. reticularia*). Nevertheless, subsequent authors retained Chicken Turtles in the composite genera *Clemmys* (Strauch, 1862: 32) or *Chrysemys* (Cope, 1877: 53; Boulenger, 1889: 75). For more than a century now, following Baur (1890: 1099) and Stejneger & Barbour (1917: 121), most authors have recognized living *Deirochelys reticularia* (sensu Agassiz, 1857: 252, 441) as a well-defined taxon. Based on morphological variation across its geographic range, Schwartz (1956) described three subspecies: *D. r. reticularia* (Latreille, 1802: 124) (Virginia, North Carolina, South Carolina, Georgia, Florida, Alabama, Mississippi, Louisiana), *D. r. chrysea* Schwartz, 1956: 467 (Florida), and *D. r. miaria* Schwartz, 1956: 467 (Louisiana, Arkansas, Oklahoma, Texas). The former two reportedly share a zone of intergradation in northern Florida. The three subspecies are distinguished by carapace shape, plastral pattern, and markings on the ventral surface of marginal scutes. The value of recognizing subspecies as a useful taxonomic unit has been debated vigorously over the last 30 years (e.g. Frost & Hills, 1990; Ernst & Lovich, 2009).

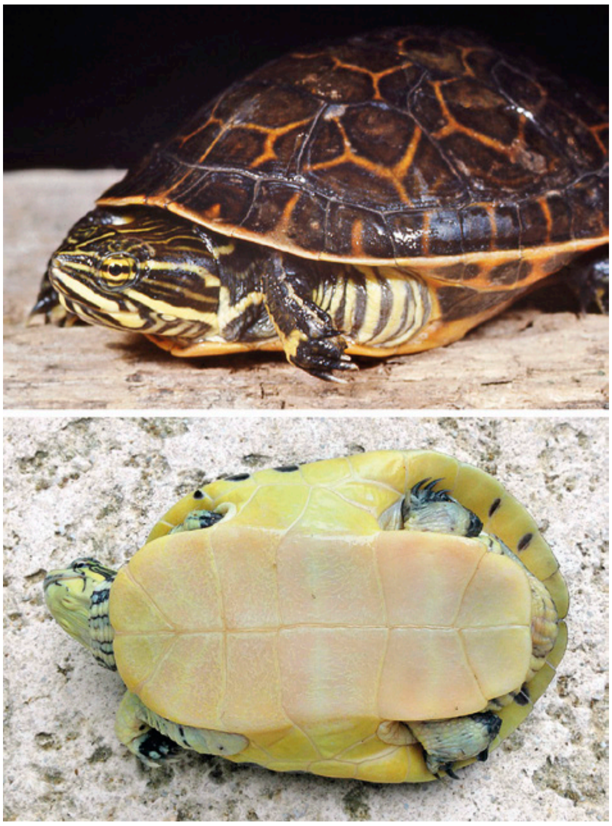


Fig. 46. Genus *Deirochelys*. Carapace of juvenile *Deirochelys reticularia reticularia*, and plastron of *Deirochelys r. reticularia*. Photos by Roger W. Barbour and Michael E. Seidel.

Zug & Schwartz (1971) reviewed the genus *Deirochelys* and species *D. reticularia* in the Catalogue of American Amphibians and Reptiles, Ewert et al. (2006a) reviewed the species in a Chelonian Research Monograph, and Buhlmann et al. (2008b) reviewed the species in Conservation Biology of Freshwater Turtles and Tortoises. Jackson (1978b: 43) reported divergence of the species from other deirochelyines by analyzing skeletal characters and fossils. He described a new fossil species, *D. carri*, from the Pliocene and earlier fragments from the Florida Miocene which he did not assign to species. Other later Pleistocene Rancholabrean and sub-Recent fossils are listed in Ernst & Lovich (2009). Divergence of *D. reticularia* has been further substantiated by nucleotide sequence data reported in Bickham et al. (1996), Starkey (1997), Walker & Avise (1998), Thomson & Shaffer (2010), and Wiens et al. (2010).

Chrysemys Gray, 1844

Painted Turtles, genus *Chrysemys* Gray, 1844: 27, are small or moderate sized (usually less than 20 cm carapace length) aquatic turtles. The extant species, *Chrysemys picta* (Schneider, 1783: 348), ranges from Nova Scotia and New Brunswick westward to British Columbia and south to northern Georgia, Alabama, central Mississippi, Louisiana, northeastern Texas, Oklahoma, eastern Colorado, Wyoming, Idaho and Oregon. It also occurs in scattered populations in western Texas, New Mexico, Colorado, Arizona (Lovich et al., 2014c), Utah, and Chihuahua, Mexico; and the genus has a fossil record in North America extending from the Late Miocene to the late Pleistocene (Ernst & Lovich, 2009) (Fig. 47). The smooth, dark, keelless carapace has yellow or reddish seam borders, red markings on the marginals, a reddish-yellow dorsal longitudinal stripe in some, and a smooth posterior rim. The hingeless yellow plastron is either patternless or has a dark medial dendritic figure of varying size and shape. The upper jaw is medially notched and bordered on each side by a cusp. The crushing surface of the upper jaw lacks a ridge. Males have elongated foreclaws and longer tails than females. *Chrysemys* inhabits waters with little current, soft bottoms, and aquatic vegetation; including lakes, ponds, swamps, marshes, sloughs, and oxbows of rivers. They are basking turtles with omnivorous feeding habits.

Painted Turtles were originally described by Schneider (1783: 348) and assigned to the composite genus *Testudo*, but Wagler (1821: 135) used a specific generic name *Hydrochelys*. Due to its subsequent discontinuous use, *Hydrochelys* Wagler, 1821: 135 is considered a *nomen oblitum* (Gemel & Grillitsch, 2008: 188). Gray (1844: 27, 1856b: 32) placed Painted Turtles exclusively in the genus *Chrysemys*, recognizing two species: *C. picta* and *C. bellii*. Agassiz (1857) added the species *C. marginata* (p. 262) and *C. dorsalis* (p. 439). As noted earlier, Boulenger (1889: 69) expanded the genus *Chrysemys* to also include turtles currently recognized as the Chicken Turtle (*Deirochelys*), Cooters (*Pseudemys*), and Sliders (*Trachemys*). Stejneger & Barbour (1917: 118) returned to a restricted concept of *Chrysemys* which included two species, a monotypic *C. picta* and polytypic *C. marginata* (*C. m. marginata*, *C. m. dorsalis*, and *C. m. bellii*). Bishop & Schmidt (1931: 123) assigned Painted Turtles to a monotypic *Chrysemys*, including the four subspecies commonly recognized today: *C. p. picta* (Schneider, 1783: 348); *C. p. bellii* (Gray, 1831a: 12); *C. p. dorsalis*, Agassiz, 1857: 439; and *C. p. marginata* Agassiz, 1857: 262. As previously discussed, McDowell (1964) reverted back to an expanded concept of *Chrysemys* (similar to Boulenger, 1889: 69). Seidel & Smith (1986) restored *Chrysemys* to a monotypic genus including only the four subspecies of *C. picta*. In the United States, *C. p. picta* inhabits northeastern states, *C. p. marginata* ranges across the northcentral region, *C. p. bellii* inhabits western states, and the range of *C. p. dorsalis* is south-central. The three former subspecies also range into southern Canada, and an isolated population of *C. p. bellii* occurs in northern Mexico (Smith & Smith, 1979; Legler & Vogt, 2013). The subspecies of *C. picta* are characterized by differences in alignment of carapacial scutes, coloration, and markings on the plastron or carapace. Well-defined intergradation typically occurs where the geographic ranges are contiguous, although exact limits and ancestral dispersals have been argued. Norman Hartweg, in his 1934 Ph.D. dissertation, was the first to seriously study intergrade variation among the subspecies of *C. picta*. Other studies which have addressed morphological variation among subspecies include Babcock (1933), Cahn (1937), Bleakney (1958), Ernst (1967, 1970), Ernst & Ernst (1971), Ernst & Fowler (1977), Ernst et al. (2006, 2015), Gordon (1990), Groves (1983), Hartman (1958), Johnson (1954), Klemens (1978), MacCulloch (1981), Muir (1989), Pough & Pough (1968), Rhodin & Butler (1997), Seidel (1981), Ultsch et al. (2001), Waters (1964, 1969), and Wright & Andrews (2002). Over the last 20 years, the only taxonomic change proposed for *C. picta* has been elevation of *C. p. dorsalis* to full species status.

Fig. 47. Genus *Chrysemys*. Carapace of *Chrysemys picta picta,* and plastron of *Chrysemys p. picta.* Photos by Roger W. Barbour.

Based on analysis of DNA (mitochondrial control region) in more than 200 *C. picta* sampled thoughout the range, Starkey et al. (2003) found that *dorsalis* constitutes a sister taxon which is extensively divergent from the other three subspecies. Their recommendation to recognize it as a full species, *C. dorsalis*, adds phylogenetic information within *Chrysemys*, yet does not substantially disrupt taxonomic stability. However, McAllister et al. (2007) reported a record of *dorsalis* from Texas which matched *dorsalis* phenotypically but not genetically (sensu Starkey et al., 2003). The mitochondrial DNA sequence from the turtle was nearly identical to Haplotype 48 as reported by Starkey et al. (bootstrap > 95%); but it differed from other *dorsalis* haplotypes reported by Starkey et al. and from the complete mitochondrial sequence (GenBank AF069423; Mindell et al., 1999) by only a single substitution of cytosine for thymine in position 16205. McAllister et al. thought that this unique haplotype is unlikely confined to the northeast Texas population of *dorsalis*; confirmation pending further genetic analysis of *dorsalis* between the Sabine River and samples now available from eastern and southern Louisiana. Furthermore, genes in the mitochondrial control region of DNA examined by Starkey et al. (2003) may have little to do with speciation. “Speciation genes” impede mating between related organisms (such as *C. dorsalis* and the other three subspecies of *C. picta*), potentially keeping two nascent species apart or dividing one species into two. Such genes have now been discovered in several animals and plants (Nosil & Schluter, 2011; see also the review by Strain, 2011), but not in *C. dorsalis*, or other turtles. Until genes having this role are discovered in *C. dorsalis*, its species status is questionable.

Ernst et al. (2006) examined morphological variation of *Chrysemys* in Missouri and determined that *C. dorsalis* intergrades or “hybridizes” with *C. picta bellii and C. p. marginata* (also see Ernst, 1967, 1970). Ernst concluded that the geographic region of admixture among these turtles was too extensive to be explained by hybridization between species. Consequently, Ernst & Lovich (2009) treated *dorsalis* as a subspecies. The validity of *C. dorsalis* could be further tested by a detailed assessment of gene flow in areas where it is parapatric with subspecies of *C. picta*, especially northeastern Alabama, northern Louisiana, and southern Arkansas. Elevation of *dorsalis* to species rank has been accepted by Iverson et al. (2007, 2008); but not by Fritz & Havăs (2007), Turtle Taxonomy Working Group (TTWG) (2007, 2009), Buhlmann et al. (2008a), and Ernst & Lovich (2009). The most recent TTWG list (2014) presents both species and subspecies options for *dorsalis*. An additional study (Jensen et al., 2015), expanding sampling and inclusion of nuclear DNA character data, supports the “tentative” designation of *C. dorsalis* and *C. picta* (encompassing *C. p. picta*, *C. p. bellii*, and *C. p. marginata*) as separate species. Nevertheless, until further evidence is presented, continued recognition of *C. p. dorsalis* appears to be the more conservative and appropriate interpretation.

Jensen et al. (2013) analyzed genetic divergence of *C. picta bellii* in British Columbia using mitochondrial DNA haplotypic and microsatellite data. They revealed that this extreme northwestern group of Painted Turtles contained unique genetic diversity in the form of two novel haplotypes, compared to other populations in North America. Nevertheless, they made no mention of possible subspecific recognition.

Several factors may complicate subspecific identification of Painted Turtle subspecies or intergrades between them. Adults of both sexes of *C. picta bellii* often develop a dark net-like mosaic pigment pattern on their carapace termed reticulate melanism (Smith et al., 1969; Ernst & Barbour, 1972; Lovich et al., 1990; Ernst et al., 1994; Ernst & Lovich, 2009). The phenomenon is wide-spread over the range of the subspecies (Smith et al., 1969; Ernst & Ernst, 1973; MacCulloch, 1981; Schueler, 1983; Stuart, 1998; Gronke et al., 2006). It is the result of dendritic accumulations of melanin in the epidermal carapace scutes superimposed on a relatively unchanged underlying pattern, and also occurs in *Pseudemys rubriventris* (Lovich et al., 1990) and *Trachemys terrapen* (Seidel, 1988d). Reticulate melanism possibly represents an intermediate evolutionary step in the pathway to the full adult melanism found in the Slider Turtle, *Trachemys scripta*, and other species. Additionally, it it is known that shell color may vary between populations of *C. picta* occurring on different colored aquatic substrates. Painted Turtles can gradually change their shell color (probably under hormonal control) to match a dark or light substrate, and are capable of reversing this change (Porter et al., 2002; Ryan & Rowe, 2004; Howell et al., 2005; Rowe et al., 2006a, 2006b, 2009). In addition, diagnostic pigments of the plastron may be obscured by water chemistry, especially iron (Gibbons & Greene, 2009).

Life history components of *C. picta* may also have contributed to subspeciation (Lindeman, 1997). For instance, average plastron length of both sexes at maturity and the average clutch size increase with increasing latitude (Cagle, 1954; Fitch, 1985; Moll, 1973) and elevation (Christiansen & Moll, 1973). Iverson & Smith (1993) proposed several hypotheses, some following Moll (1973), for why the turtles’ body size and clutch size increase with both latitude and elevation. First, perhaps *dorsalis* is small due to character displacement resulting from competition with the several other sympatric emydid species across its southern range. Lindeman (1997) has challenged this, as the life history variation follows clinal patterns which predict low fecundity and small body size in southern populations of *C. picta* (i.e., *dorsalis* and *picta*). Iverson & Smith also suggested that there are advantages in larger body size and greater fecundity in northern, high-elevation habitats, and that larger size is adaptive for slowing heat loss, increasing storage of anabolic and catabolic products for overwintering (Elgar & Heaphy, 1989), and digging deeper nest cavities to better insulate overwintering hatchlings from freezing temperatures. That male body size varies geographically, as does female body size (Lindeman, 1997), supports Iverson & Smith’s hypothesis that body size increases for reasons of slowed heat loss or increased overwinter storage capacity. However, hatchling Canadian *C. picta* do not always overwinter (Lovich et al., 2014a; Riley et al., 2014).

Other environmental factors affecting the growth rate, size at maturity (Iverson et al., 1993), and total body size of *C. picta* were reported by Ernst & McDonald (1989); also reported by Gibbons et al. (1981). An organism encountering unavoidable stress resulting in an abnormal growth rate may alter its age and size at maturity along a trajectory that minimizes any reduction in fitness caused by this growth rate. This trajectory, along which age and size at maturity change as stress increases, is termed a plastic trajectory (Stearns, 1983). It is this trajectory, and neither a specific age nor size at maturity taken separately, that may be considered the character under selection. Ernst & McDonald (1989) studied this in two populations of *C. picta* in Charles County, Maryland. The test population was from a sewage disposal lagoon which had an artificially enriched organic bottom substrate that enhanced populations of algae and insect larvae living in the muck bottom on which the turtles fed, thus increasing their protein intake. This site also had warmer water temperatures resulting from the oxidation of the muck bottom that allowed the turtles to remain active and feed for more days during the year. As a control, they also studied turtles at a nearby wildlife management area where conditions were natural and the water lacked an enriched organic bottom. The turtles from the sewage lagoons grew both faster and larger, and matured at an earlier age than did those from the natural area. Gibbons (1967) reported similar results while comparing the growth rates of *C. picta* in Michigan where turtles from the polluted Kalamazoo River had much faster growth rates than those from the two other natural areas. These are examples of phenotypic variation which likely do not have a genetic basis. Broad geographic influence of environmental conditions on form and function may confound taxonomic recognition, especially at the subspecies level.

Ernst (1971, 1988) reviewed *Chrysemys* in the Catalogue of American Amphibians and Reptiles.

Graptemys AGASSIZ, 1857

Map Turtles, genus *Graptemys*: Agassiz, 1857: 252, inhabit rivers and streams of eastern and central North America, ranging from Ontario, Canada, Wisconsin, and Minnesota southward to Georgia, Alabama, Mississippi, Louisiana, and eastern Texas; with scattered populations in central Texas. Most species occur in waters with a current, but may also be found in quiet regions created by impoundment. *Graptemys* species are moderate to large sized basking turtles (more than 30 cm carapace length). The brown to green carapace is keeled, sometimes with spikes or knobs, has a serrate posterior rim, and varying patterns of yellow lines or blotches. The plastron is hingeless and patterned either with dark pigment along the seams sometimes with accompanying dark blotched pigment, and in one subspecies (*Graptemys pseudogeographica kohnii*) an intricate medial dark pattern. The skull is narrow in males; but large and often very broad in females. The crushing surface of the jaws is not ridged, but is very broad in females. They are predominately carnivorous, feeding mostly on mollusks and arthropods. They are the most taxonomically diverse genus in family Emydidae (Figs. 48a and 48b) and date at least from the Pleistocene (Jackson, 1975). Most of the known fossils of *Graptemys* have been assigned to species which are extant (Ernst & Lovich, 2009). However, a fossil species, *G. kerneri* Ehret & Bourque, 2011: 578, was recently described from the late Pleistocene (Rancholabrean), in northcentral Florida.

Species of Map Turtles have been classified in the following composite genera: *Testudo* (*T. geographica* Le Sueur, 1817: 86), *Terrapene* (*T. geographica* Bonaparte, 1831: 156), *Emys* (*E. geographica* Say, 1825: 204; *E. pseudogeographica* Gray, 1831b: 31), *Clemmys* (*C. geographica*, *C. pseudogeographica* Strauch 1862: 180), and *Malacoclemmys* (*M. geographica*, *M. pseudogeographica* Cope 1877: 53). Agassiz (1857: 252) was first to restrict Map Turtles to the genus *Graptemys*. Nevertheless, generic assignment remained somewhat unstable due to the inclusion of Map Turtles in the genus *Malaclemys* Gray, 1844: 28, along with its sister taxon the Diamondback Terrapin, *M. terrapin* (Hay, 1892; Hurter, 1911; McDowell, 1964). As discussed under *Relationships in the Subfamily Deirochelyinae*, subsequent works (Dobie, 1981; Lamb & Osentoski, 1997) justified reversion back to *Graptemys* (sensu Agassiz, 1857) for Map Turtles.

During the nineteenth century, five species of *Graptemys* were recognized: *G. geographica* (Le Sueur, 1817: 86) in the central and eastern United States, *G. pseudogeographica* (Gray, 1831b: 31) in the upper Mississippi drainage system, *G.* (*p.*) *kohnii* (Baur, 1890: 263) in the lower Mississippi system, and *G. oculifera* (Baur, 1890: 262) and *G. pulchra* Baur (1893b: 675) in the Gulf drainage systems of Mississippi and Alabama. In the early twentieth century, Stejneger (1925: 463) described a new subspecies of Map Turtle, *G. pseudogeographica versa* (later elevated to *G. versa* by Smith 1946: 60) endemic to the Colorado River system of central Texas. In 1941 field work by Archie Carr and Lewis Marchand substantiated the presence of a previously undescribed Map Turtle, *G. barbouri* (Carr & Marchand, 1942: 98), in the Apalachicola River system of the Florida panhandle. During the next decade the well known turtle biologist at Tulane University, Fred Cagle, conducted extensive field surveys of rivers along the northern Coastal Plain of the Gulf of Mexico. His taxonomic work involved the first attempt to understand evolutionary relationships among species of *Graptemys* (Cagle, 1952, 1953a, 1953b, 1954). Based on skull structure he (1953b) proposed that *G. oculifera* may be related to *G. kohnii*. Cagle (1952) also noted a close relationship between *G. pulchra* and *G. barbouri* based on shared head markings and the broad head of adult females. In 1953a: 2, Cagle described two new subspecies of *G. pseudogeographica*: *G. p. ouachitensis* in drainages of the Mississippi River system of Louisiana, northern Texas, Oklahoma, Arkansas, and Kansas; and *G. p. sabinensis* in the Sabine River system along the border of Louisiana and Texas. In 1954, Cagle also described two new species, *G. flavimaculata* (p. 167) and *G. nigrinoda* (p. 173), which he indicated are closely related to *G. oculifera* found in the Pearl River. *Graptemys flavimaculata* inhabits the Pascagoula River and its major tributaries while *G. nigrinoda* occurs in the Alabama-Tombigbee river system. Cagle (1954) recognized these three turtles as a complex of allopatric forms occurring in adjacent river systems. Thus, he could not test their biological species identity. Based on shared

Fig. 48a. Genus *Graptemys*. Row 1: Carapace of *Graptemys geographica,* plastron of juvenile *Graptemys geographica,* carapace of *Graptemys barbouri*, and plastron of juvenile *Graptemys barbouri*. Photos by Roger W. Barbour, Carl H. Ernst, Michael E. Seidel, and Carl H. Ernst, respectively. Row 2: Carapace of *Graptemys caglei,* head view of *Graptemys caglei,* carapace of *Graptemys ernsti,* and plastron of *Graptemys ernsti*. Photos of *G. caglei* by Dante Fenolio, and *G. ernsti* by Roger W. Barbour. Row 3: Carapace of *Graptemys*

flavimaculata, plastron of juvenile *Graptemys flavimaculata*, carapace of *Graptemys gibbonsi*, and plastron of juvenile *Graptemys gibbonsi*. Photos by Roger W. Barbour, Carl H. Ernst, Roger W. Barbour, and Richard D. Bartlett, respectively. Row 4: Carapace of *Graptemys nigrinoda nigrinoda,* plastron of *Graptemys n. nigrinoda*, carapace of *Graptemys oculifera,* and plastron of *Graptemys oculifera*. Photos of *G. n. nigrinoda* by Roger W. Barbour and *G. oculifera* by Carl H. Ernst.

Fig. 48b. Genus *Graptemys* (continued). Row 1: Carapace of *Graptemys ouachitensis ouachitensis*, plastron of *Graptemys o. ouachitensis*, carapace of *Graptemys pearlensis*, and plastron of *Graptemys pearlensis*. Photos of *G. o. ouachitensis* by Carl H. Ernst and *G. pearlensis* by Chris Hagen. Row 2: Carapace of *Graptemys pseudogeographica pseudogeographica*, carapace of *Graptemys p. kohnii*, plastron of

bright orange or yellow markings and morphology of the carapace, he noted an especially close relationship between *G. oculifera* and *G. flavimaculata*. Nevertheless, Cagle (1954) determined they are sufficiently distinct (without intermediates) to be recognized at the species level. Subsequently, Mertens & Wermuth (1955: 329) lumped the three as subspecies of *G. oculifera* but later reversed that decision (Wermuth & Mertens, 1977). Adding to specific characterization, Killebrew (1979) described three cranial characters which separate *G. flavimaculata* and *G. nigrinoda*. Chelonian specialists continued to recognize a very close relationship between *G. oculifera* and *G. flavimaculata*. More recently, Ennen et al. (2010a) comprehensively examined these two turtles applying multivariate morphological techniques and analysis of mitochondrial genes. Their mitochondrial data revealed only a limited amount of differentiation between *G. oculifera* and *G. flavimaculata*. However, their morphological results, in conjunction with recently published (Wiens et al., 2010) nuclear gene sequence data, supported the continued recognition of the two species. Selman et al. (2013) analyzed variation of microsatellite loci within *G. flavimaculata*. Their analysis strongly supported the recognition of two distinct populations (mainstem Pascagoula River vs. Escatawpa River) but subspecific partitioning was not suggested.

After Cagle (1954), no new forms of *Graptemys* were described for a decade and a half. In 1969: 677, Folkerts & Mount described a new subspecies of *G. nigrinoda*, *G. n. delticola*, from Mobile Bay drainages of Baldwin

Graptemys p. kohnii, and plastrons of juvenile *Graptemys p. kohnii.* Photo of plastrons of juvenile *Graptemys p. kohnii* by Carl H. Ernst; remaining photos by Roger W. Barbour. Row 3: Carapace of *Graptemys pulchra*, plastron of *Graptemys pulchra*, carapace of *Graptemys versa*, and plastron of *Graptemys versa*. Plastral view of *Graptemys pulchra* by Carl H. Ernst; remaining photos by Roger W. Barbour.

and Mobile counties, Alabama. This form was reported to differ from the nominate subspecies in having a more elongate plastral figure, darker soft parts, and a postorbital mark which is not strongly curved. Later, Lindeman (2000) reported that *delticola* has a wider alveolar (crushing surface of lower jaw) width compared to *G. n. nigrinoda.* Freeman (1970: 3) challenged subspecific partitioning of *G. nigrinoda* on theoretical grounds. Folkerts & Mount (1970: 3) countered by defining their concept of subspecies, and referring to the unique character states of *G. n. delticola*. Recently, Ennen et al. (2014) demonstrated extensive clinal variation throughout the range of *G. nigrinoda* based on mitochondrial DNA and morphological data. Their results appear to invalidate recognition of the two subspecies described by Folkerts & Mount.

In 1974: 143, Haynes & McKown reported on a previously unknown form of Map Turtle in the Guadalupe/San Antonio river system of Texas. This turtle, appropriately named *G. caglei*, is allopatric to all other congeners and extends the range of *Graptemys* into southern Texas. Based mostly on skull characters, Haynes & McKown (1974) concluded that *caglei* is closely related to *G. versa*, with which it is geographically proximal but not sympatric. *Graptemys versa* is the only Map Turtle inhabiting the Colorado River system to the north, separated from *G. caglei* by the intervening Lavaca/Navidad system which apparently has no *Graptemys* (Dixon, 1987: 184–187). Haynes & McKown also suggested a relationship between *G. caglei* and *G.* (*p.*) *kohnii*, which occurs in the Brazos River, adjacent to and north of the Colorado.

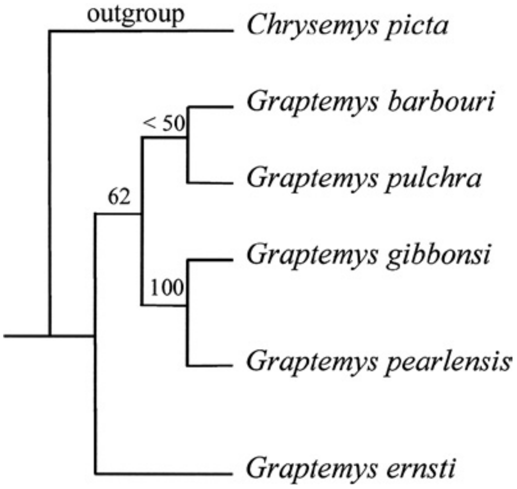


Fig. 49. Strict consensus tree of the two most parsimonious trees (consistency index = 0.86) showing phylogenetic relationships among the broad-headed species of *Graptemys*. Numerals at nodes represent maximum parsimony bootstrap values. The tree is based on sequence analysis of mitochondrial DNA (CR and ND4). Modified from Ennen et al. (2010b, fig. 4).

Bertl & Killebrew (1983) described seven skull characters which distinguish *G. caglei* from *G. versa*, thus strengthening species recognition. An additional Texas species was proposed by Ward (1980a: 302) in his Ph.D. dissertation. He elevated *G. pseudogeographica sabinensis* (inhabitant of the Sabine River and adjacent drainages along the eastern state border) to species level based on a unique feature of the cranium. He found that separation of its nasal bone by the prefrontals occurs along the entire length. However, Ward's unpublished recommendation did not receive much attention in the taxonomic literature (but see below). Similarly, Vogt (1980: 17) published a paper elevating *G. p. ouachitensis* to species rank. While this publication reported mostly on the natural history of Map Turtles, it referred to systematic analyses in his 1978 Ph.D. dissertation. Vogt's recognition of *G. ouachitensis* was accepted by subsequent authors (e.g. Iverson, 1986; Ernst & Barbour, 1989; King & Burke, 1989; Ernst et al., 2000; Ernst & Lovich, 2009; but see Obst, 1986 and Conant & Collins, 1991) even though his taxonomic justification for it was published much later (Vogt 1993).

In 1992: 293, Lovich & McCoy described two new species of *Graptemys*, *G. ernsti* and *G. gibbonsi*, which were previously considered geographic variants of *G. pulchra* (Tinkle, 1962; Shealy, 1973, 1976; Little, 1973). *Graptemys ernsti* inhabits the Escambia/Conecuh, the adjacent Yellow River, and the Pea River systems of Florida and Alabama (Godwin et al., 2014; Ennen et al., 2016). *Graptemys gibbonsi* was reported to occur in the Pascagoula and Pearl rivers of Mississippi and Louisiana. They were distinguished as species on the basis of their head, neck, and marginal scute markings. Subsequently, Ennen et al. (2010b: 104) split *G. gibbonsi*, recognizing populations in the Pearl River as a new species, *G. pearlensis*. These two species are diagnosed by differences in marginal scute coloration and divergence in their mitochondrial DNA. *Graptemys barbouri*, *G. ernsti*, *G. gibbonsi*, *G. pearlensis*, and *G. pulchra* form a complex of broad-headed Map Turtles that are distributed across northern Gulf coastal rivers. They are mostly allopatric but *G. ernsti* and *G. barbouri* reportedly occur sympatrically in a small portion of the Choctawatchee River system in Alabama, and may hybridize in that region (Godwin, 2002; Ennen et al., 2010b). Using *Chrysemys picta* as an outgroup, Ennen et al. (2010b) presented a phylogeny for the broad-headed clade of *Graptemys* based on mitochondrial DNA (Fig. 49). They found a sister group relationship between *G. barbouri* and *G. pulchra* which collectively form a sister group to *G. gibbonsi* and *G. pearlensis*. *Graptemys ernsti* was found to be the most divergent, sister to a clade of all the other broad-headed *Graptemys*.

The first attempt to comprehensively define relationships among all Map Turtles was by Ronald McKown (1972) a student of W. Frank Blair at the University of Texas, Austin. McKown (1972) presented his results in a Ph.D. dissertation which described relationships of *Graptemys* based on morphology, karyology, and protein electrophoresis (Fig. 50). The latter two data sets proved to be mostly conservative and thus only marginally informative at the species level. Nevertheless, he observed that *G. barbouri* and *G. pulchra* share a unique diploid chromosome number of 52. This finding was very surprising because all other emydid turtles have been reported to have a diploid number of 50 (Van Brink, 1959; Forbes, 1966; Stock, 1972; Bickham & Carr, 1983). In Killebrew's 1977 analysis of Map Turtle karyology he stated that "the diploid number of 52 for *Graptemys barbouri* and *Graptemys pulchra* (sensu McKown, 1972) are not supported by this study." It appears likely that McKown rescinded on his report of 52, because Killebrew (1977) acknowledged him for assistance and support throughout the study. The only protein variant which McKown (1972) detected was a slow migrating form of hemoglobin uniquely shared by *G. barbouri*, *G. caglei*, *G. kohnii*, *G. pulchra*, and *G. versa.* However, Seidel (2002b) examined hemoglobin polymorphism by isoelectric focusing and found no variation among *Graptemys* species. Based on skull morphology, McKown identified two major lineages: a broad-headed group which included *G. barbouri*, *G. geographica*, *G. kohnii*, and *G. pulchra*; and a narrow-headed group comprised of the remaining species (Fig. 50). He also suggested that *G. geographica* may approximate the ancestral condition considering its morphological similarities to *Trachemys* Agassiz, 1857: 252. This hypothesis has been upheld by subsequent DNA analyses (e.g. Lamb et al., 1994; Stephens & Wiens, 2003).

The importance of head and alveolar width in the evolution of Map Turtle species has been studied extensively by Lindeman (2000, 2013). He has statistically demonstrated that cephalic width is associated with the degree of molluscivory, especially in adult females (Lindeman & Sharkey, 2001). It has been suggested that

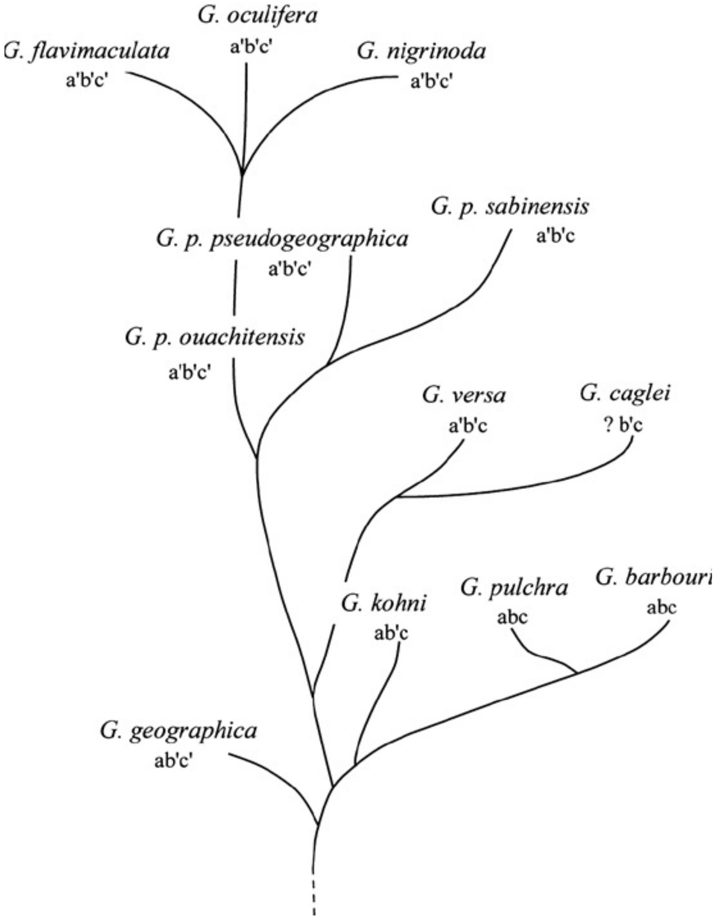


Fig. 50. A proposed theory of evolution in the genus *Graptemys* based on morphology, karyology, and protein electrophoresis (McKown 1972, fig. 8). The following character states are indicated by letters under each taxon: a) large heads, b) 52 chromosomes, c) slow hemoglobin phenotype, a') small heads, b') 50 chromosomes, c') fast hemoglobin phenotype. The presence of 52 chromosomes was not supported in subsequent analysis.

broadening of the head in turtles (a developmental process) may not be genetic, but rather a result of the absorption of calcium from molluscan prey and the muscular activity of crushing their shells (Fachin Teran et al., 1995). However, interspecific differences in head width of *Graptemys* hatchlings suggests otherwise (Lindeman, 2000). The development of megacephaly appears to be a primitive condition in the evolutionary history of the genus. The appearance of a reduced head width related to stronger dependence on insectivory is presumably the derived condition seen in *G. ouachitensis*, *G. flavimaculata*, *G. oculifera*, and perhaps independently derived in *G. nigrinoda* (Lindeman, 2000, 2013). Lindeman also pointed out that vicariance events (sea-level changes and stream capture) in the early evolutionary history of *Graptemys* probably promoted character assortment of mega-, meso -, and microcephaly.

Classification of False Map Turtles belonging to the *G. pseudogeographica* group presented a serious taxonomic problem for most of the twentieth century. In their checklists, Stejneger & Barbour (1917: 117–118) recognized the subspecies *G. p. pseudogeographica*, *G. p. kohnii*, and *G. p. oculifera*. In 1933: 145 they added *G. p. versa* and in 1939: 161 they elevated *oculifera* to species level. Carr (1949: 9) expressed doubt that *kohnii* is a valid taxon and suggested it may merely be a geographic variant of *G. pseudogeographica*. Acknowledging that *G. p. kohnii* can be distinguished from conspecifics by its broad head, Carr theorized this feature may be a phenotypic response to feeding in regions where bivalve mollusks are plentiful. Nevertheless, Carr (1952: 207) in his classic Handbook of Turtles, and Schmidt (1953: 98) in his Check List, recognized *G. p. kohnii* (sensu Stejneger & Barbour, 1939), followed by Cagle's (1953a) addition of *G. p. ouachitensis* and *G. p. sabinensis*. Cagle also determined that polytypic *G. pseudogeographica* is primarily a narrow-headed species compared to the presumably heritable broad-headed condition seen in *G. barbouri*, *G. geographica*, and *G. pulchra*. On the basis of its wide head, Cagle (1953a: 16) elevated *kohnii* to species level and considered it related to the other broad-headed Map Turtles (Lindeman, 2000, 2013). Curiously, neither Carr, Schmidt, nor Cagle followed Smith's (1946: 60) elevation of *G. p. versa* to species rank. While Cagle (1953a: 16) noted that *ouachitensis* and *pseudogeographica* appear to intergrade where their ranges overlap, he also noted later on that page that intermediates between *kohnii* and *pseudogeographica* occur and suggested they may all be conspecific. In a paper published later the same year (1953b: 138), without explanation, Cagle elevated *versa* to species level (sensu Smith, 1946: 60) and relegated *kohnii* back to a subspecies of *G. pseudogeographica*. The next year he reversed again and gave *kohnii* full species rank (Cagle, 1954: 181). Clearly Cagle was perplexed about the relationship of *kohnii* to other Map Turtles. Philip W. Smith

(1961: 148, 150) observed a troublesome amount of variation in the diagnostic head patterns of *G. pseudogeographica* in Illinois. He noted that some turtles had markings similar to *G. versa* while others had markings typical of *G. kohnii*. Smith stated: "A study of substantial series of these turtles from the Illinois and Mississippi rivers might resolve the problem involved; this is one of the most urgent problems in the herpetological taxonomy of eastern United States." In contrast, Cahn (1937) did not report *G. p. kohnii* from Illinois in his monograph on that state's turtles. Dundee (1974: 540–542) examined skulls of the *G. pseudogeographica* complex and concluded that *G. kohnii* is a valid species, later accepted by Dixon in 1987: 82. Minton (1972: 174–175) added to the taxonomic uncertainty of *G. pseudogeographica*. Based on specimens in Indiana, he concluded that *G. p. ouachitensis* is not recognizable as a valid taxon. During the next two decades the taxonomy of *G. pseudogeographica* remained quite unstable. By applying the only available diagnostic characters (primarily head makings), species and subspecies identification was extremely difficult. In 1979, Michael Ewert published his work on turtle embryology which described some taxonomically relevant examples of color pattern induction. Specifically, he found that incubation temperature can alter the diagnostic markings of *G. pseudogeographica* and *G. kohnii*. This raised even more doubt about genetic divergence in this species complex, not to mention a nomenclatural problem with the name itself (*pseudogeographica*). *Emys lesueurii* Gray, 1831a: 9, was long considered a junior synonym of *G. pseudogeograhica*, but its type specimen is in reality a *G. geographica*, so the taxon is actually a junior synonym of the latter species (Bour & Dubois, 1983: 42).

Vogt (1993) published a paper, mostly extracted from his 1978 Ph.D. dissertation, which addressed taxonomic problems in the *G. pseudogeographica* complex. This study included discriminant analysis of morphology, protein electrophoresis, and observations of courtship behavior. Vogt's early field work (1970–71) along the Mississippi River in Wisconsin suggested that several members of this species complex may be sympatric in the region. Following conventional practice, he stated that his tentative identifications were based on "The supposedly diagnostic head marking." To initially test his hypothesis, Vogt collected and incubated numerous clutches of eggs laid by alleged False Map Turtles from his study area. He discovered that hatchlings with head markings reputedly characteristic of four different taxa emerged; in some cases multiple "morphotypes" hatched from a single clutch. Ewert (1979) had found that diagnostic markings attributed to *G. ouachitensis* (i.e. reduced plastral figure, broad postorbital marks and head stripes) can be induced in hatchlings of *G. pseudogeographica* by low (25°C) egg incubation temperatures. Vogt (1993) found similar results when he altered incubation temperatures, and concluded that "The basic pattern can be modified to the extent that *G. ouachitensis* incubated at high temperatures (30–35°C) resemble *G. pseudogeographica*." Thus, Vogt also found that traditional morphological characters (including head markings) did not adequately distinguish members of the *pseudogeographica* complex. However, he did find that area or size (not necessarily shape) of the postorbital, subocular, and mandibular spots was a characteristic which could separate *ouachitensis* from *pseudogeographica*. These light yellow markings of the head region are considerably larger in *ouachitensis* than in *pseudogeographica*.

A subtle but consistent difference in courtship behavior also emerged to support distinction of these two turtles. All members of the *pseudogeographica* complex apparently utilize titillation courtship (Seidel & Fritz, 1997). However, Vogt noted that during initiation of foreclaw vibration, the head of male *pseudogeographica* is bobbed in a vertical plane, and that of *ouachitensis* is held stationary. In addition, he noted the speed of vibration strokes (foreclaws of male against the ocular region of the female) in *pseudogeographica* was about double that of *ouachitensis*. Both these differences had previously been reported by Ernst (1974). These differences in courtship combined with differences in area of light head markings prompted Vogt (1993) to recognize these two as species, which occur sympatrically (along with *G. geographica*) in the upper Mississippi River. Vogt further recognized bitypic geographic variation throughout their ranges which justified retention of the subspecies *G. p. kohnii* and *G. o. sabinensis*. This arrangement was followed by Ernst et al. (1994), Dixon (2000), and Ernst & Lovich (2009), among many others.

Vogt's (1993) study was thorough and comprehensive. It applied the commonly accepted technique at that time (discriminant canonical analysis) to test the validity of populations of *G. ouachitensis* and *G. pseudogeographica*. A limitation of that procedure is that individuals are assigned *a priori* to a group or species based on traditional and sometimes questionable diagnostic features. It is a powerful discriminating technique which weights variables (characters) to find maximum separation between groups. To avoid any possible bias of population or species assignment, more recent studies apply the technique of principal components analysis (PCA). PCA does not depend on assumptions of individual identification based on questionable diagnostic characters. If *G. ouachitensis* and *G. pseudogeographica* can be separated by PCA using Vogt's morphological characters, their taxonomic identity would be more convincing. Vogt's conclusions, nevertheless, were corroborated by Lamb et al.'s (1994) mitochondrial DNA sequence data. These authors, using *Malaclemys terrapin* as an outgroup, found that *G. o. ouachitensis* and *G. o. sabinensis* form a lineage (clade) which is distinct from *G. p. pseudogeographica* and *G. p. kohnii* (Fig. 51). Lamb et al. (1994) further concluded that the broad-headed condition (female megacephaly), which is common in *G. p. kohnii*, represents character convergence with the other broad-headed Map Turtles *G. pulchra* and *G. barbouri* (see comments by Dobie, 1981 and Lindeman, 2000). Lamb

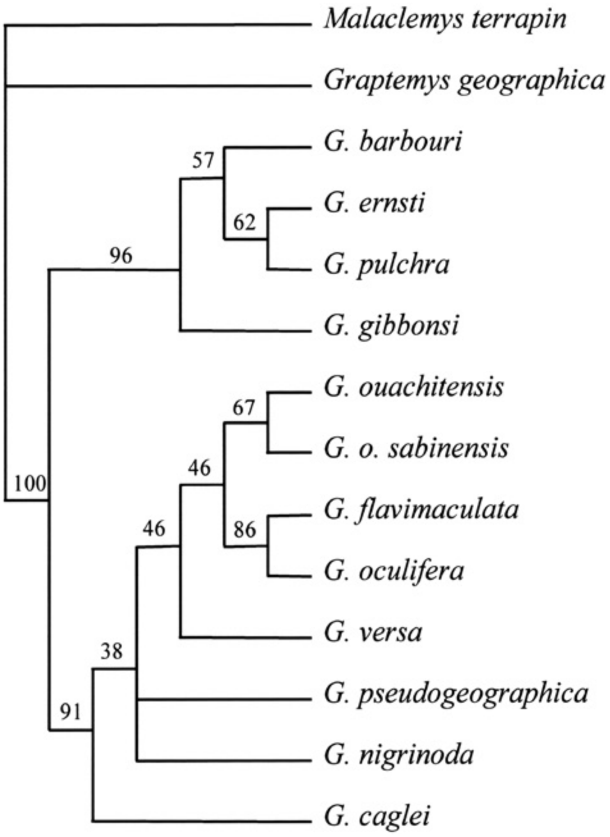


Fig. 51. Strict consensus tree for the genus *Graptemys* based on mitochondrial DNA (restriction site and sequence data combined). The consensus is derived from two equally parsimonious trees. Numbers above the branches indicate the proportion of 100 bootstrap replicates that support the nodes. Modified from Lamb et al. (1994, fig. 6).

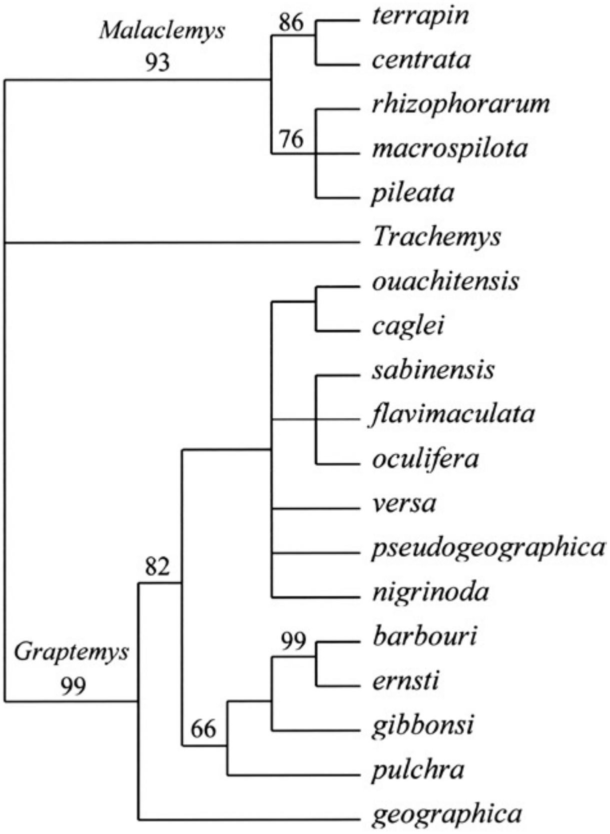


Fig. 52. Strict consensus tree for *Malaclemys* and *Graptemys* (based on mitochondrial DNA) derived from 32 equally parsimonious trees (Lamb and Osentoski 1997, fig. 3). Numbers above nodes are bootstrap values; only values greater than 60 are shown.

joined Osentoski (1997) to report again on phylogenetic relationships in *Graptemys* using DNA sequence data (Fig. 52), but in this analysis he used a broader outgroup that included *Malaclemys* and *Trachemys*. More recently, Myers (2008) analyzed relationships in *Graptemys* based on DNA sequencing (mitochondrial and nuclear), designating *Chrysemys picta* and *Malaclemys terrapin* as outgroups. These two studies produced similar major clades, but neither offer clear support for the *G. pseudogeographic*a complex. Support is also lacking in recent phylogenetic analyses which include morphological characters (i.e. Stephens & Wiens, 2003, 2008; Iverson et al., 2007); although Lindeman (2003) was able to distinguish between G. *pseudogeographica* and G. *ouachitensis* in the lower Tennessee River based on eye color (iris markings) and head, alveolar surface, and gular scute widths.

Myers' (2008) DNA data indicated a polytomous relationship of *sabinensis* with a clade of other members of the *pseudogeographica* complex and to *G. flavimaculata* and *G. oculifera* (Fig. 53). The nuclear DNA data of Wiens et al. (2010; Fig. 31) suggested that *G. ouachitensis* is paraphyletic and that *G. o. sabinensis* is the sister taxon of *G. geographica*. Sanders et al. (2010) reported a concentration of orange or reddish pigmentation in the diagnostic markings of *sabinensis*. This resemblance to *G. oculifera* and *G. flavimaculata* (if genetically based) again suggests divergence from *ouachitensis*. Vetter (2004) and Buhlmann et al. (2008a) elevated the Sabine Map Turtle to species status, *G. sabinensis* (sensu Ward, 1980a: 302). The Turtle Taxonomy Working Group (2007) and Iverson et al. (2012) stated that further study may warrant elevation of the sympatric taxon *sabinensis* to full species status. Nevertheless, Vogt's taxonomy of the *pseudogeographica* complex (including *G. o. sabinensis* and *G. p. kohnii*) has continued to receive acceptance (Fritz & Havăs, 2007; Turtle Taxonomy Working Group, 2007, 2009; Iverson et al., 2008, 2012; Collins & Taggart, 2009; Ernst & Lovich, 2009).

Brown et al. (2012) conducted the most recent analysis of DNA (mitochondrial) sequencing for *G. ouachitensis* (including *sabinensis*) and *G. pseudogeographica*. Their maximum-likelihood tree of haplotypes indicates *sabinensis* on a separate lineage (Fig. 54), which presumably resulted from their isolation in the Sabine River and adjacent minor drainages. Brown et al. (2012) also reported limited differentiation (1.16%) between *pseudogeographica* and *ouachitensis*. They concluded (p. 305)

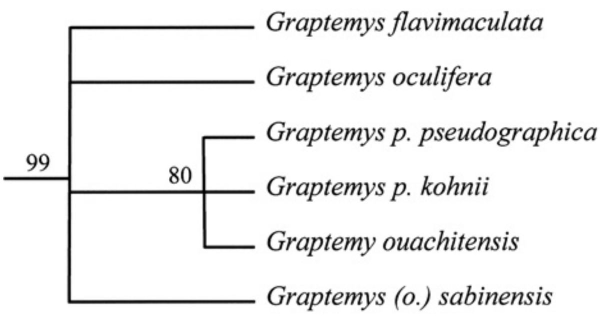


Fig. 53. A theory of relationships among forms of *Graptemys* in the *pseudogeographica* complex. Bootstrap consensus topology recovered in maximum parsimony analysis based on sequencing three mitochondrial genes (including cytochrome b) and one nuclear (recombinant activity gene). Values at the nodes indicate bootstrap support. Modified from Myers (2008, fig. 2.3A).

"Additional studies that combine both genetics and morphology, particularly in areas of sympatry, are needed to clarify the limits of these species and other members of the *pseudogeographica* group." Recently, Lindeman (2013: 255) presented a convincing case for elevating *sabinensis* to a full species endemic to the Sabine-Neches, Calcasieu, and Mermentau drainages in eastern Texas and southwestern Louisiana. He cited evidence that it is allopatric to *G. ouachitensis*, and has unique cranial features not shared with that species. Lindeman (2013) also pointed out that "… various combined analyses of morphological and molecular data placed *sabinensis* as a close relative of *caglei* and/or *versa* but not as a particularly close relative of *ouachitensis*." He also reported that *sabinensis* has an unusually small clutch size (mean of two eggs) compared to other *Graptemys*. It appears that broad acceptance of species status for *sabinensis* is imminent (e.g. Iverson et al., 2014; Turtle Taxonomy Working Group, 2014) and we follow that consensus. An additional variant Map Turtle in southwestern Louisiana has recently been noted. Lindeman et al. (2015) reported that *G. pseudogeographica* in the Calcasieu system is morphologically distinct based on dark pigmentation of the eye (iris) and markings on the chin. The authors mentioned that further study of this population might support taxonomic recognition.

When all molecular and morphological data are evaluated (Lamb et al., 1994; Lamb & Osentoski, 1997; Lindeman, 2000, 2013; Stephens & Wiens, 2003; Myers, 2008; Ennen et al., 2010a; Thomson & Shaffer, 2010; Wiens et al., 2010) it appears that *G. geographica* is basal to all other *Graptemys* which form two major clades (species complexes): a broad-headed group consisting of *G. barbouri*, *G. ernsti*, *G. gibbonsi*, *G. pearlensis*, and *G. pulchra*; and a narrow-headed group (including mesocephalic forms) comprised of *G. caglei*, *G. flavimaculata*, *G. nigrinoda*, *G. oculifera*, *G. ouachitensis*, *G. pseudogeographica*, and *G. versa*. Although female *G. p. kohnii* often have a broad head, they share character states (synapomorphies) with the narrow-headed clade. *Graptemys geographica* also tends to be broad-headed, while molecular and morphological data indicate that it occupies a basal (ancestral?) position to all other congeners. There is strong evidence for a sister group relationship between *G. flavimaculata* (endemic to the Pascagoula River system) and *G. oculifera* (endemic to the Pearl River system). Ennen et al. (2007, 2010a, 2010b) found greater molecular similarity between these two species than they found comparing *G. gibbonsi* in the Pascagoula River to *G. pearlensis* in the Pearl River. Wiens et al. (2010) found strong evidence based on nuclear DNA for a Texas endemic clade of *G. versa* and *G. caglei*. Other phylogenetic relationships within the narrow-headed clade of *Graptemys* remain mostly unresolved. Thomson & Shaffer (2010) included 12 species of *Graptemys* in their reconstruction of turtle phylogenies based on large sequence databases, sparse supermatrices from GenBank. Compared to most species groups in Emydidae, relationships in *Graptemys* are poorly resolved.

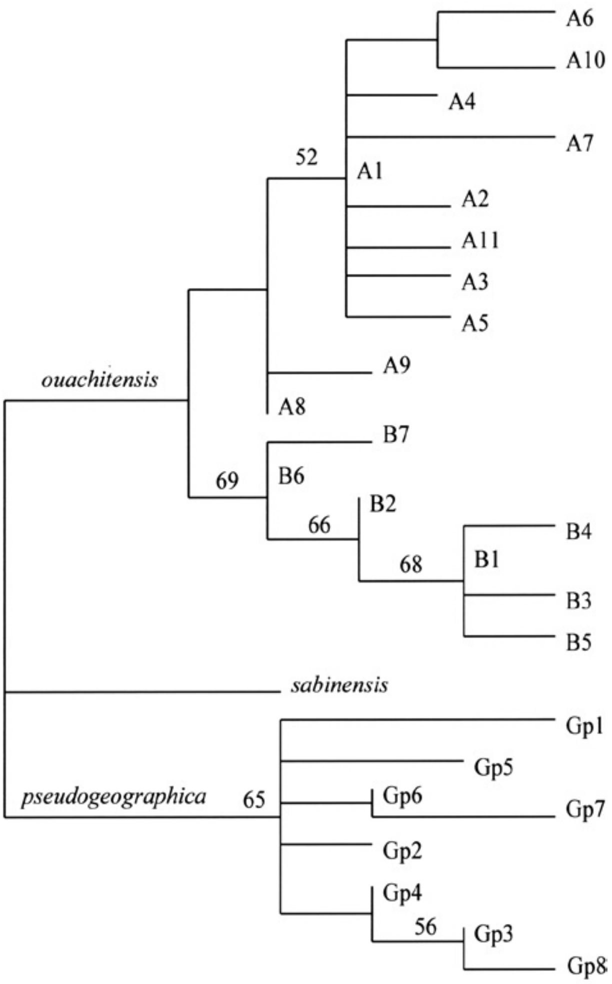


Fig. 54. Maximum-likelihood tree of haplotypes observed in *Graptemys ouachitensis* (A1-A11, B1-B7), *G. pseudogeographica* (Gp1-Gp8), and *G. o. sabinensis* (Brown et al. 2012, fig. 2). Only bootstrap values greater than 50 are reported.

Lindeman (2013) summarized our knowledge of systematic relationships in *Graptemys* by stating "Intrageneric relationships appear to be best known for early divergences; more recent divergences are more uncertain, with lower levels of bootstrap support and conflicting results among studies." Introgression is likely a complicating factor in resolving species relationships. *Graptemys ernsti* X *G. barbouri* hybrids have been reported by Godwin et al. (2014). Fritz (1995a) has reported natural and captive hybrids between *G. geographica* x *G. o. ouachitensis*, *G. geographica* x *G. p. pseudogeographica*, *G. oculifera* x *G. barbouri*, and *G. p. pseudogeographica* x *G. p. kohnii.*

The following accounts of *Graptemys* have appeared in the Catalogue of American Amphibians and Reptiles (CAAR) and Conservation Biology of Freshwater Turtles and Tortoises (CBFTT): *G. caglei* (Haynes 1976, CAAR), *G. versa* (Vogt 1981, CAAR), *G. pulchra* (Lovich 1985, CAAR; Lovich et al. 2014b, CBFTT), *G. nigrinoda* (Lahanas 1986, CAAR; Blankenship et al. 2008, CBFFT), *G. flavimaculata* (McCoy & Vogt 1987, CAAR; Selman & Jones 2011, CBFTT), *G. barbouri* (Sanderson & Lovich 1988, CAAR), *G. oculifera* (McCoy & Vogt 1988, CAAR; Jones & Selman 2009, CBFTT), *G. geographica* (McCoy & Vogt 1990, CAAR), *Graptemys* generic (McCoy & Vogt 1994, CAAR), *G. ernsti* (Lovich & McCoy 1994a, CAAR; Lovich et al. 2011, CBFTT), *G. gibbonsi* (Lovich & McCoy 1994b, CAAR; Lovich et al. 2009, CBFTT), *G. ouachitensis* (Vogt 1995a, CAAR), *G. pseudogeographica* (Vogt 1995b, CAAR), and *G. pearlensis* (Ennen et al. 2012, CAAR). *Graptemys barbouri* and *G. ernsti* were also reviewed in Chelonian Research Monograph 3 by Ewert et al. (2006b) and Aresco & Shealy (2006), respectively. A comprehensive review of the identification and natural history of *Graptemys* species is presented by Lindeman (2013).

Keys for the genus *Graptemys* have been presented by Carr (1952), Cagle (1954, 1968), Wermuth & Mertens (1961), Ernst & Barbour (1972), Iverson (1992), McCoy & Vogt (1994), Ernst et al. (1994), Powell et al. (1998), and Ernst & Lovich (2009).

Malaclemys Gray, 1844

The genus *Malaclemys* Gray, 1844: 28 is monotypic, containing only the Diamondback Terrapin, *Malaclemys terrapin* (Schoepff, 1793: 64), which ranges throughout coastal marshes from Cape Cod, Massachusetts to Corpus Christi, Texas. Possible occurrence of this species in northeastern Mexico was discussed by Smith & Smith (1980: 525), but there is no credible evidence that the species occurs there. Parham et al. (2008) discovered a population of *Malaclemys* on Bermuda. Based on fossil and genetic data, they suggested it could be of natural origin. Ehret & Atkinson (2012) established its presence throughout the coastal southeastern United States during the Late Pleistocene. *Malaclemys terrapin* exclusively utilizes tidal estuaries (including coastal marshes, mangrove thickets, bays, and tidal creeks) and thus has a limited area of natural habitat. Terrapins are moderate-sized turtles (greater than 20 cm carapace length) with pronounced sexual dimorphism as mature females are larger than mature males and usually have a very broad head (Fig. 55). Usually gray in color, the keeled carapace bears either light concentric markings or a large light blotch on the vertebral and pleural scutes. The medial keel may bear low to prominent knobs. The skin is gray to black and usually lacks stripes. The hingeless plastron is yellowish with mottling. The jaws are light colored, and the limbs unstriped. The upper jaw is either not or slightly notched. The triturating surface of the upper jaw is smooth (lacking a ridge) and wide in females but narrow in males. They are primarily carnivorous, feeding mostly on arthropods and mollusks. Pleistocene fossils are known from Florida and South Carolina (Ernst & Lovich, 2009).

The species was initially described as *Testudo terrapin* by Schoepff (1793: 64) and subsequently was classified in the composite genus *Emys* (Duméril, 1805: 76, Link, 1807: 52). As discussed earlier, *Malaclemys* has sporadically been considered a polytypic genus (sensu Boulenger, 1889: 88; Shufeldt, 1920: 55; McDowell, 1964: 274) which also included species currently placed in the genus *Graptemys*. The species name has changed several times, i.e. *Testudo concentrica* (Shaw, 1802: 43), *T. ocellata* (Link, 1807: 52), *Emys macrocephalus* (Gray, 1844: 26), and *Malaclemys tuberculifera* (Gray, 1844: 29). Seven subspecies of *M. terrapin* are recognized, four of which were initially described as full species: *T. centrata* Latreille, *in* Sonnini & Latreille (east coast from North Carolina to northern Florida), 1802: 145; *E. pileata* Wied-Neuwied, 1865: 17 (Gulf coast from Florida panhandle to western Louisiana); *M. macrospilota* Hay, 1904: 16 (Florida west coast); and *M. littoralis* Hay, 1904: 18 (coastal Texas). In addition to the nominate subspecies *M. t. terrapin* (Schoepff, 1793: 64) (Massachusetts to North Carolina), two additional races were described from Florida: *M. t.* (*littoralis*) *rhizophorarum* Fowler, 1906: 112 (Florida Keys) and *M. t. tequesta* Schwartz, 1955: 158 (east coast of Florida). It is likely that the number of recognized taxa for *Malaclemys* will be reduced based on genetic studies (e.g. Hart et al., 2014).

Schoepff (1793: 64) chose the specific name *terrapin* for Diamondback Terrapins. Although both his description and plate figure appear to be of the subspecies *centrata*, Schoepff makes it clear that his data and illustration are of specimens he and Muhlenberg personally collected around Philadelphia and the coastal waters of Long Island. Both Mittleman (1944, 1945) and Stejneger (1936: 115) thought *centrata* should have precedence over *terrapin* as the species name. They also considered the name *terrapen* (= T*estudo terrapen* Lacépède, 1788: 129) of Jamaica as a possible spelling error of *terrapin*, but that species is from the Carribean and also belongs to a different genus, *Trachemys* (see the discussions in their papers). Therefore, *terrapin* is the proper specific name for the Diamondback Terrapin, and the nominate subspecies is therefore *M. t. terrapin* as first used by Lindholm (1929: 294).

Fig. 55. Genus *Malaclemys*. Carapace of *Malaclemys terrapin terrapin,* and plastron of *Malaclemys t. pileata*. Photos by Roger W. Barbour and Carl H. Ernst.

Siebenrock (1909: 471–473) recognized variant forms of *Malaclemys* as subspecies and this arrangement has persisted to present. The subspecies are differentiated by carapace shape, presence or shape of knobs on the carapace keel, pigmentation of the plastron and carapace, and markings of the head and neck. The different forms of *M. terrapin* typically intergrade where their ranges contact or overlap. Carr (1946: 170) discussed the variation and status of the subspecies, exclusive of *M. t. tequesta*, and concluded that they are valid. It should be noted that in the distribution map provided by Ernst & Bury (1982: 1), several of the label numbers identifying the seven subspecies were inadvertently switched. Wood (1994) proposed an eighth subspecies of *M. terrapin*, *M. t. fordorum*, from the northern Florida Keys. However, subsequent investigators have not found a distinction between *M. t. fordorum* and *M. t. rhizophorarum* in the southern Keys (Ernst & Lovich, 2009). Furthermore, Wood did not present a description of the latter subspecies; therefore, *fordorum* remains a *nomen nudum*.

Ernst & Hartsell (2000a: 8, 2000b: 887) examined the type specimen of *Malaclemys tuberculifera* Gray, 1844: 29 at the Natural History Museum, London, and found it to be a *M. t. rhizophorarum* Fowler, 1906: 112. Because it pre-dates Fowler's (1906) description, it is the earliest name for that subspecies, but it has not been used since 1844 while *rhizophorarum* has been the designated subspecies continuously since 1906, making *M. tuberculifera* Gray, 1844: 29 a *nomen oblitum.*

Some morphological characteristics differ among the seven subspecies of *M. terrapin* (Hartsell, 2001). Hartsell & Ernst (2004) found that the ranges of the seven subspecies correspond closely to the six major physiographic regions of the United States Atlantic and Gulf coasts, but zones of intergradation occur where the subspecies' ranges meet. Molecular studies by Trip Lamb have supported some degree of subspecies partitioning. Lamb & Avise (1992) found well-defined mitochondrial DNA divergence between *M. t. centrata* (which ranges along the Atlantic coast of Florida from the Georgia state line south to Volusia County) and *M. t. tequesta* (which ranges from Volusia County south to Miami). This break is also congruent with the abrupt morphological distinction between *M. t. tequesta* which has knobs on the carapace keel and *M. t. centrata* which lacks such knobs (Butler et al., 2006). Lamb & Osentoski (1997) reported mitochondrial DNA divergence (Fig. 52) between Atlantic subspecies (*terrapin* and *centrata*) and the Gulf forms (*rhizophorarum*, *macrospilota*, and *pileata*). More recent microsatellite DNA analyses have not provided strong support for taxonomic partitioning in *M. terrapin* (Hauswaldt & Glenn, 2003, 2005; Hart, 2005; Hart et al., 2014). Hart et al. (2014) reported three zones of genetic discontinuity in the geographic range of *M. terrapin*, resulting in four discrete populations. However, the boundaries of these populations did not correspond to current subspecies limits. Some of the presently recognized subspecies may be placed in synonymy due to weak diagnostic characters and genetic differences which may be a product of clinal variation (Ernst et al., 1994; Butler et al., 2006).

A contribution to subspecific confusion was the practice of translocating and then "hybridizing" several Gulf Coast races of *M. terrapin* in captivity at Beaufort, North Carolina (Coker, 1906; Hildebrand, 1929, 1933; Hildebrand & Hatsel, 1926; Hildebrand & Prytherch, 1947). Some cross-bred turtles escaped, or possibly were released, and introduced their genes into the Atlantic Coast populations of *M. terrapin.* The genus and species *M. terrapin* were reviewed in the Catalogue of American Amphibians and Reptiles by Ernst & Bury (1982), and in Chelonian Monograph 3 by Butler et al. (2006).

Pseudemys Gray, 1856a

Cooter and Red-bellied Turtles, genus *Pseudemys* Gray, 1856a: 197, date from the Pleistocene (Seidel & Ernst, 1996). They occur in the eastern, central, and southwestern United States. There are isolated populations in southeastern Massachusetts, but the continuous range extends from central New Jersey south through Florida and west to southeastern Kansas, Oklahoma, and Texas. In the extreme southwestern part of the range, they inhabit the Rio Grande/ Pecos system of New Mexico, Texas, and Mexico. Cooters occur in lakes, rivers, streams, large springs, and canals; preferring relatively clear water with abundant vegetation. *Pseudemys* species are relatively large (reaching over 40 cm carapace length). The brown to olive carapace has a medial keel and a serrate posterior rim in juveniles; the adult carapace is more flattened with a low keel at best. Its vertebral and pleural scutes are patterned with cream, yellow, or orange markings. The hingeless, yellow to red plastron bears a variable pattern of dark marks, especially anteriorly. The skin is brown to black with yellow stripes on the neck and limbs. The upper jaw is medially notched in most species, and its crushing surface bears a ridge or row of tubercles. Males have elongated foreclaws and elongated tails. Basking behavior is well-developed and adults are herbivorous (Fig. 56).

Historically, Cooters have been classified in the following composite genera: *Testudo* (*T. concinna*, *T. floridana*, and *T. rubriventris*; Le Conte, 1830: 100, 101, 106), *Clemmys* (Fitzinger, 1835: 124; Strauch, 1862: 32), *Emys* (Duméril & Bibron, 1835: 285; addition of *E. hieroglyphica* and *E. mobilensis* by Holbrook, 1836: 47, 53), and *Pseudemys* (Gray, 1856a: 197). Agassiz (1857: 431) taxonomically separated Cooter and Red-bellied Turtles from other species by placing them (and a newly described form, *P. hoyi*, p. 433) exclusively in the genus *Ptychemys* (p. 252). In volume 2 of the same publication, Agassiz (1857: 642) introduced the name *Nectemys* (a *nomen novem* pro *Ptychemys* Agassiz, 1857: 252), now recognized as a senior synonym of *Ptychemys.* Boulenger (1889: 69), however, reverted back to a composite genus, *Chrysemys*, which also included Painted Turtles and Sliders. Subsequently, Baur (1893a: 223–224), Babcock (1937: 293), and Carr (1938a: 105, 1938b: 131, 1938c: 305) included Cooter and Red-bellied Turtles in the genus *Pseudemys*, along with Slider Turtles. These authors described six additional taxa: *P. alabamensis*, *P. texana* (Baur, 1893a: 223–224), *P. rubriventris bangsi* (Babcock, 1937: 293), *P. concinna suwanniensis* (Carr, 1937: 4), *P. nelsoni* (Carr, 1938c: 307), and *P. floridana peninsularis* (Carr, 1938a: 105). Cagle (1968: 224–226) included *Trachemys scripta* in his list of *Pseudemys*, along with the species *alabamensis*, *concinna*, *floridana*, *nelsoni*, and *rubriventris*. Generic assignment was unstable (see McDowell, 1964) until Seidel & Smith (1986: 242) placed Cooter and Red-bellied Turtles in a restricted genus *Pseudemys* (= *Ptychemys* sensu Agassiz, 1857: 252).

Species relationships in *Pseudemys* have had a long confusing history and represent one of the most perplexing topics in turtle taxonomy. Frequently in areas where species of *Pseudemys* are sympatric, evidence of sporadic hybridization (or limited introgression) has been observed (e.g. Crenshaw, 1965). Some populations with intermediate (hybrid?) characters are widely distributed, which suggests subspecific relationships. These interactions have been examined in Florida (Crenshaw, 1955), Louisiana (Fahey, 1980), and North Carolina (Seidel & Palmer, 1991). Part of the problem stemmed from the absence of clearly defined, quantifiable characters which separate the different forms of *Pseudemys*. Ward (1984) presented one of the broader analyses of the genus and described two new subspecies: *Pseudemys concinna metteri* (p. 34) and *P. c. gorzugi* (p. 29). His analysis relied heavily on cranial musculature and osteology, which unfortunately are of little use in field identification or evaluation of fluid-preserved museum material. Seidel (1981), Iverson & Graham (1990), and Seidel & Palmer (1991) characterized the morphology of *P. rubriventris*, *P. concinna*, and *P. floridana* in the eastern United States. They examined relatively large series of specimens using external morphometric characters. However, throughout much of the range of *Pseudemys*, the taxonomic status of species and subspecies remained unstable. During the latter half of the twentieth century, the following taxa were recognized (but not uniformly accepted) by authors: *P. alabamensis* (southern Alabama), *P. nelsoni* (Florida and southern Georgia), *P. rubriventris rubriventris* (Atlantic slope from New Jersey to North Carolina), *P. r. bangsi* (eastern Massachusetts), *P. concinna concinna* (Atlantic slope from Virginia to Georgia), *P. c. hieroglyphica* (central United States, Mississippi drainage system), *P. c. metteri* (west-central United States, Mississippi drainage system), *P. c. mobilensis* (southern United States, drainages into Gulf of Mexico), *P. c. suwanniensis* (northwestern peninsular Florida), *P. c. gorzugi* (Rio Grande and Pecos systems of Texas and New Mexico), *P.c. texana* (Colorado River system of central Texas), *P. floridana floridana* (Atlantic slope from Virginia to Georgia), *P. f. hoyi* (central United States, Mississippi drainage system), and *P. f. peninsularis* (Florida); (Carr, 1952; Ernst & Barbour, 1972; Conant, 1975; Ward, 1984; Iverson, 1992; Ernst et al., 1994).

Red-bellied Turtles (*P. rubriventrisis*, *P. nelsoni*, and *P. alabamensis*) have collectively been treated as subspecies of *P. rubriventris* (Le Conte, 1829: 101) by some authors (Wermuth & Mertens, 1977: 57–58; Obst, 1985: 20; Müller 1987: 82) but most have considered them separate species. Carr (1952: 266) recognized a "*rubriventris* section" which included *P. r. rubriventris* in Atlantic drainages from New Jersey south to North Carolina, *P. r. bangsi* from isolated populations in eastern Massachusetts, and *P. nelsoni* native to peninsular Florida. He described this group by their deeply notched upper jaw flanked by strong cusps (Fig. 57), and their reddish orange or coral markings on the shell. In the *rubriventris* section, Carr & Crenshaw (1957: 25) later included *P. alabamensis* from southern Alabama which had formerly been considered a variant of *P. c. mobilensis* (= *Emys mobilensis* Holbrook, 1838: 53) (Carr, 1938a: 1). Carr & Crenshaw (1957) also described a "prefrontal arrow" in Red-bellied Turtles formed from the meeting of the sagital head stripe with the supratemporal stripes (Fig. 57). In addition to Carr's characters, McDowell (1964) found that the three species, which he called the "*rubriventris* series," (p. 18) can be distinguished from other *Pseudemys* ("*floridana* series" p. 18) by their cranial features.They share a unique vomerine bone which contributes to the triturating (crushing) sur-

Fig. 56. Genus *Pseudemys*. Row 1: Carapace of *Pseudemys concinna concinna*, plastron of *Pseudemys c. concinna*, carapace of *Pseudemys alabamensis*, and plastron of *Pseudemys alabamensis*. Photos by Carl H. Ernst, Kenneth Nemuras, Roger W. Barbour, and Carl H. Ernst, respectively. Row 2: Carapace of *Pseudemys gorzugi*, plastron of *Pseudemys gorzugi*, carapace of *Pseudemys nelsoni*, and plastron of *Pseudemys nelsoni*. Photos of *P. gorzugi* by Charles W. Painter, and *P. nelsoni* by Roger W. Barbour and Richard D. Bartlett.

Row 3: Carapace of *Pseudemys peninsularis*, plastron of *Pseudemys peninsularis*, carapace of juvenile *Pseudemys rubriventris*, and plastron of *Pseudemys rubriventris*. Photos of *Pseudemys peninsularis* by Roger W. Barbour and Michael E. Seidel, and photos of *Pseudemys rubriventris* by Carl H. Ernst. Row 4: Carapace of *Pseudemys suwanniensis*, plastron of *Pseudemys suwanniensis*, carapace of *Pseudemys texana*, and plastron of *Pseudemys texana*. Photos of *Pseudemys suwanniensis* by Carl H. Ernst, and *Pseudemys texana* by Michael E. Seidel.

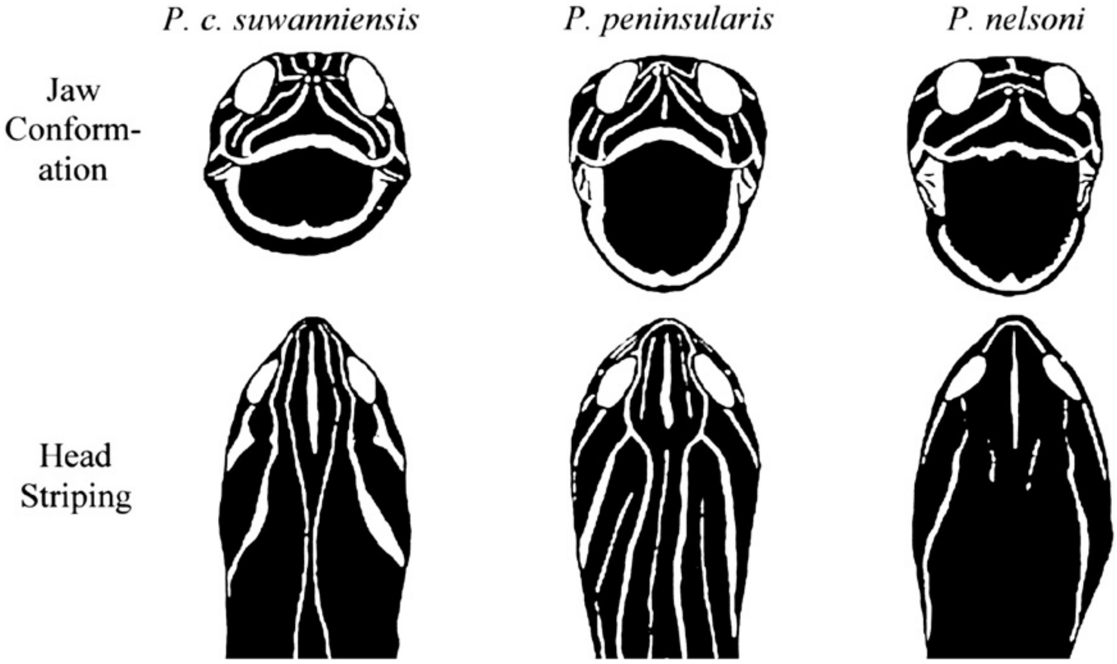


Fig. 57. Comparison of three Florida turtles of the genus *Pseudemys* with respect to upper jaw conformation and head striping (Carr and Crenshaw 1957, fig. 2).

face of the upper jaw (Fig. 58). Weaver & Rose (1967) found several additional characters which distinguish the *rubriventris* group, including a long cervical scute underlap and rugose plastron. Another distinction between Red-bellied Turtles and Cooters is their nesting behavior. Some Cooters (*P. floridana and P. concinna*) have been reported to dig one or two shallow or "false" holes on either side of the major excavation (Jackson & Walker, 1997; Buhlmann et al., 2008a). These satellite nest holes have never been reported in the *rubriventris* series (Dale Jackson, pers. comm.). Ward (1984: 42) taxonomically separated Red-bellied Turtles from Cooters by placing them in the subgenus *Ptychemys*, in which he also placed *P.* [*c.*] *texana*, a turtle which inhabits rivers of central Texas. Ward's inclusion of *texana* in the subgenus was apparently based on its orange shell markings and notch with cusps on the upper tomium, a feature previously noted by Carr & Crenshaw (1957). Using multivariate analysis of morphometric characters, Iverson & Graham (1990: 13) determined that *P. r. bangsi* Babcock (1937: 293) is not a valid taxon and placed it in the synonymy of *P. r. rubriventris*. Iverson (1992: 196) also questioned the relationship of *P. texana* to Red-bellied Turtles (subgenus *Ptychemys*). Seidel (1994) examined additional characters (morphological and biochemical) useful in separating taxa of *Pseudemys* across their entire range. He evaluated variation or divergence among taxa by principal components, cluster, and cladistic analysis which produced a theory of phylogenetic relationships (Fig. 59). Seidel (1994: 117) found that Red-bellied Turtles (*P. alabamensis*, *P. nelsoni*, *and P. rubriventris*) are morphometrically distinct (divergent) from all Cooters, including *P. texana*. Therefore, Seidel rejected (p. 123) Ward's inclusion of the latter in *Ptychemys*. He found that some of the character states that Ward (1984) used to diagnose *Ptychemys* are not present in *P. texana* (i.e. "carapace strongly rugose…posterior marginals without notch"). The similarities in cranial morphology of these turtles (which Ward emphasized), including cusps on the upper jaw, may have arisen as homoplasies resulting from convergent trophic habits (Jackson, 1978b). Seidel's report of a derived liver protein (isoelectric point = 8.2) unique to *P. rubriventris*, *P. nelsoni*, and *P. alabamensis* (absent in *texana*) supports the thesis that the three Red-bellied species form a monophyletic group (subgenus *Ptychemys*, Iverson 1992). Evidence presented by Wiens et al. (2010) based on nuclear DNA, provides additional support for this relationship (Fig. 31), although *P. alabamensis* was not sampled. T. G. Jackson et al. (2012) reported on phylogenetic relationships among all forms of *Pseudemys*, based on analysis of mitochondrial DNA (control region cytochrome *b* gene). Surprisingly, their evidence did not support a clade (monophyly) formed of *P. rubriventris*, *P. nelsoni* and *P. alabamensis* (Fig. 60).

Morphological overlap occurs among the three Red-bellied Turtles but they appeared distinct enough for Seidel (1994) to retain them as separate species. That decision is further supported by their broadly disjunct geographic ranges (Iverson, 1992). Leary et al. (2003) reported isolated populations of *P. alabamensis* in Mississippi, which extended the species range 100 km west of Mobile Bay. Their principal components analysis (p. 639) of morphometric characters indicated that the Mississippi populations are not sufficiently distinct to warrant separate taxonomic status. The reported range of *P. nelsoni* has also been expanded to southern Georgia and the Apalachicola region of Florida (Buhlmann et al.,

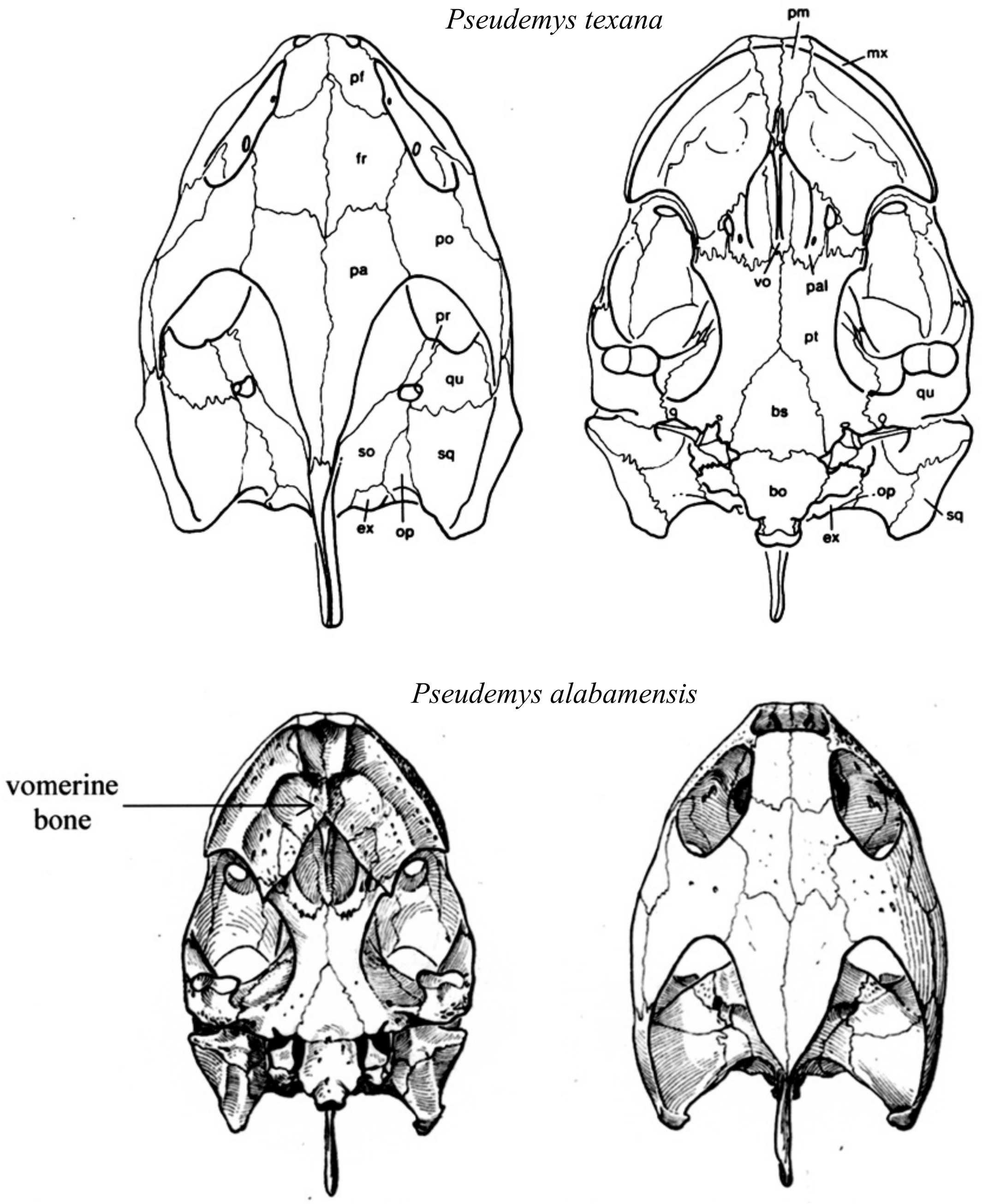


Fig. 58. Illustrations of the cranium in *Pseudemys*. The specialized condition of Red-bellied turtles (contribution of vomer to triturating surface) is indicated in *P. alabamensis* below (McDowell 1964, fig. 6) and the alternate condition appears in *P. texana* above (Gaffney 1979, fig. 229).

2008a). Presumably introduced populations have been reported in Liberty County (Seidel, 1994) and Hays County (Rose et al., 1998), Texas.

Within the subgenus *Pseudemys* (sensu Ward, 1984), geographic variation in the River Cooter, *P. concinna*, has been a frequent topic of debate. Subspecies have been described mostly on the basis of color-pattern markings and tend to show clinal variation over a broad geographic range. Mount (1975: 289–290) found that he could not separate the three subspecies of *P. concinna* which reportedly occur in Alabama (*concinna*, *hieroglyphica*, *mobilensis*) and recommended that they, along with *P. c. suwanniensis* Carr, 1937: 348, be placed in the synonymy of *P. concinna*. Ward (1984: 38) placed *P. floridana hoyi* and *P. c. mobilensis* in the synonymy of *P. c. hieroglyphica*. He defined a broad region from Texas and Missouri to Georgia and Florida as a zone of intergradation for *P. c. metteri*, *P. c. hieroglyphica*, and *P. c. concinna*. As pointed out by Frost & Hillis (1990: 93–94), this area of reported intergradation is larger than the defined ranges of each subspecies and therefore taxonomic recognition is unwarranted. Although the appearance of River Cooters from opposite ends of their range (i.e. Texas and Virginia) is quite different, delineation of range limits for the variants is essentially impossible. As discussed for *Chrysemys*, over such a broad range it is difficult

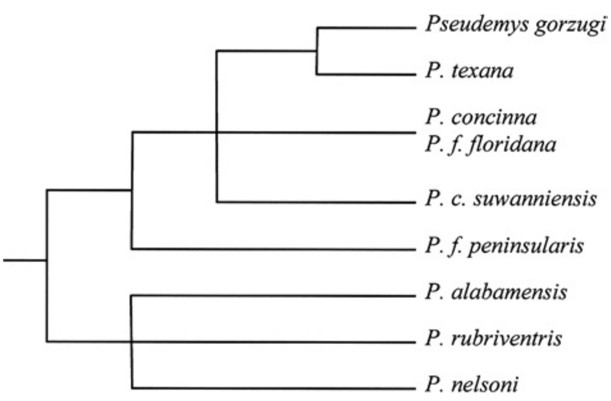


Fig. 59. Strict consensus tree expressing phylogenetic relationships among species of *Pseudemys* based on one protein and 14 morphometric characters (Seidel 1994, fig. 8). The consistency index is 0.70 and the tree is rooted with an outgroup of *Trachemys* and *Graptemys*.

to evaluate whether phenotypic variation is genetically controlled or the result of environmental influence on development. Based on extensive morphometric overlap, Seidel (1994: 125) found relatively little morphological distinction among several of Ward's subspecies, and recommended that *P. c. metteri* and *P. c. hieroglyphica* be placed in the synonymy of *P. c. concinna*.

In the southwestern extreme of the range, two additional subspecies of *P. concinna* have been recognized: *P. c. texana*, endemic to the Brazos, Colorado, and San Antonio river systems of central Texas; and *P. c. gorzugi*, endemic to the lower Rio Grande and Pecos river systems of northeastern Mexico, Texas, and New Mexico. *Pseudemys texana* was described as a new species by Baur (1893a: 223) but relegated to a subspecies of *P. floridana* by Carr (1938a: 108). Ward (1984: 45) resurrected *texana* to species level based on its distinctive cranial features and allopatry to other *Pseudemys*. This interpretation was generally accepted (Dixon, 1987; Fritz, 1989a; King & Burke, 1989; Conant & Collins, 1991; Iverson, 1992) and later substantiated by Seidel (1994). James R. Dixon, Professor Emeritus at Texas A&M University, has observed (pers. comm.) that populations of *P. texana* in the Colorado River system above the city of Austin, Texas are morphologically distinct from populations downstream. The extent of this variation may justify recognition of two subspecies (Seidel, unpubl. observ.). *Pseudemys c. gorzugi*, another allopatric Cooter in the southwest, was originally described by Ward (1984: 29). Ernst (1990a: 1), in his review for The Catalogue of American Amphibians and Reptiles, elevated it to species level. However, Iverson (1992: 192) was initially critical of recognizing *P. gorzugi* because it was done without analysis. Subsequently, Seidel's (1994) taxonomic study of *Pseudemys* demonstrated that *P. gorzugi* is morphologically divergent from all other congeners. In addition, Davis's (1994) mitochondrial DNA analysis (cited by Seidel, 1995) identified only one separate lineage in the genus, that being *P. gorzugi*. Species status has now been broadly accepted. Seidel's (1994: 123, 126) morphological analysis revealed that *P. texana* and *P. gorzugi* are sister species. This relationship, which is certainly congruent with their proximal geographic distribution, has more recently been substantiated by phylogenetic analysis based on nuclear DNA (Wiens et al., 2010). Most recently, the comprehensive mitochondrial DNA analysis by T. G. Jackson et al. (2012) does not support a sister group of the two endemic Texas species. However, it does provide evidence that *P. gorzugi* and *P. texana* are monophyletic taxa compared to other forms of *Pseudemys* (Fig. 60).

In the eastern United States, the only subspecies of River Cooter which Seidel (1994: 124) found distinct from *P. concinna concinna* was *P. c. suwanniensis* Carr. This turtle inhabits northern peninsular Florida and is characterized by having a short underlap of the cervical scute (ventral length less than 35% of dorsal length), nuchal bone not projected forward, recession of cervical scute deep (greater than 2% of carapace length), and epiplastral lip curved. Pritchard (1979) had suggested that movement patterns of *suwanniensis* are unique among *Pseudemys*: limited terrestrial activity, cryptic nesting, and "migration" from rivers to open sea water. Because *P. c. suwanniensis* may be allopatric to (Conant & Collins, 1991) and morphologically distinct from other River Cooters, Frost & Hillis (1990: 93–94) suggested that it be considered a separate species. Seidel (1994: 124) accepted that recommendation and described the range of *P. suwanniensis* as limited to Gulf drainages of northern peninsular Florida, including the Santa Fe, lower Suwannee, and smaller rivers north of Tampa Bay. Subsequently, D. R. Jackson (1995) refuted species status for *P. c. suwanniensis* on several grounds. He considered Pritchard's (1979) report of unique behaviors merely conjecture, Seidel's (1994) morphological distinctions weak, and Conant & Collins's (1991) purported allopatry inaccurate. Seidel's (1995) rebuttal pointed out that Jackson provided no substantial data or evidence to support these claims. However, in 2002, Jackson provided some geographic and morphological information which did suggest intergradation in Florida Gulf drainages farther to the north (Jackson, *in* Ward & Jackson, 2008). Seidel & Dreslik (1996: 5) treated *suwanniensis* as a subspecies of *P. concinna*. Jackson (1995, 2002) considered the range of *P. c. suwanniensis* to extend west along the Florida panhandle to the Ochlockonee River. Later, when making reference to the two Florida subspecies *P. c. concinna* and *P. c. suwanniensis*, Jackson (2006b) acknowledged that "… their potential degree of intergradation has not been studied closely." A rigorous morphological comparison of River Cooters in the Apalachicola system to Cooters in the Ochlockonee system would help elucidate presence or absence of species differentiation. In their recent checklists of turtles, Iverson et al. (2008), Collins & Taggart (2009), and Ernst & Lovich (2009) treat *suwanniensis* as a species whereas Bonin et al. (2006), Fritz & Havăs (2007), and Turtle Taxonomy Working Group (2007,

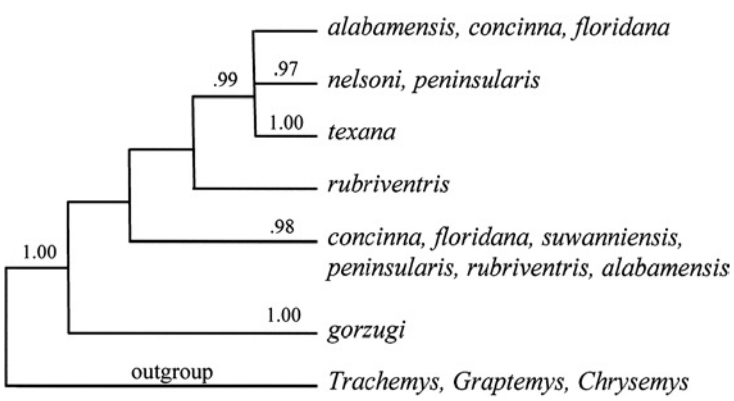


Fig. 60. Bayesian analysis showing phylogenetic relationships in *Pseudemys* based on sequencing two regions of mitochondrial DNA (control and cytochrome b). Numbers above branches correspond to posterior probabilities greater than 0.90 for each recovered relationship. Modified from T. G. Jackson et al. (2012, fig. 3).

2009) list it as a subspecies of *P. concinna*. Clearly, its taxonomic status is unsettled.

The Peninsula Cooter, *P. f. peninsularis*, was originally described as a Florida subspecies by Carr (1938a: 105). Based on phylogenetic and cluster analyses, Seidel (1994) demonstrated that it has a number of character states (e.g. upper tomium entirely rounded, nuchal bone projected forward, posterior border of cervical scute wide) which separate it from all other *Pseudemys*, and that it does not overlap morphologically (intergrade) with *P. f. floridana* in northern Florida. Accordingly, he elevated it to full species status, *P. peninsularis* (p. 125). This turtle clearly ranges throughout peninsular Florida (Seidel & Ernst, 1998), but its western limits in the panhandle region remain undetermined. Jackson (1995) disagreed with Seidel's results and claimed that *P. f. peninsularis* intergrades with *P. f. floridana* in northern Florida. Meylan (2006a) also stated that "*Pseudemys floridana floridana* has a wide area over which it intergrades with *Pseudemys floridana peninsularis* between Ocala and Tallahassee." However, there have been no morphological or genetic data presented to support these assertions. An alternative hypothesis is that the turtles Meylan (2006a) and Jackson (1995, 2006b) refer to as *P. f. floridana* in western Florida are the same taxon as (indistinguishable from) Seidel's (1995) *P. peninsularis*. If so, the range limit for *P. peninsularis* should be extended into the panhandle region and this could explain why Meylan & Jackson have reported *P. concinna* and *P. "floridana"* (= *peninsularis*) in the same rivers of that area. Nevertheless, specific or subspecific status of the Peninsula Cooter presently remains unstable. Meylan (2006a), Fritz & Havăs (2007), Thomas & Jansen (2006), and Buhlman et al. (2008) list it as *P. f. peninsularis*. On the other hand, Turtle Taxonomy Working Group (TTWG) (2007, 2009), Iverson et al. (2008), Collins & Taggart (2009), and Ernst & Lovich (2009) list it as *P. peninsularis*. In later versions of TTWG (e.g. 2011, 2014) the Peninsula Cooter is listed *P. peninsularis* or *P. floridana peninsularis.*

Distinction between the Florida Cooter, *P. f. floridana* (LeConte, 1829 [1830]: 100), and River Cooter, *P. concinna* (LeConte, 1829 [1830]: 106), in northern portions of their collective range has presented the most difficult problem in *Pseudemys* taxonomy. Carr (1952) considered *concinna* and *floridana* to be conspecific. However, his doctoral student John Crenshaw (1955) disagreed and treated them as separate macrosympatric species. The deeper, more domed (arched) shell of *floridana* has traditionally been cited as a character state which separates it from *concinna* (Carr, 1952; Crenshaw, 1955; Ward, 1984; Palmer & Braswell, 1995). *Pseudemys concinna* tends to utilize more lotic habitats while *P. floridana* is more lentic. These turtles range north along the Atlantic Coastal Plain and Piedmont to the James River in Virginia and north in the Mississippi drainage system throughout the southern Great Plains and Ohio River system. Their identification has been problematic in many areas including drainages of Illinois (Smith, 1961), Indiana (Minton, 1972), Arkansas (Trauth et al., 2004), Louisiana (Dundee & Rossman, 1989), Kentucky (Barbour, 1971), Alabama (Mount, 1975), Georgia (Jensen et al., 2008), North Carolina (Palmer & Braswell, 1995), Virginia (Mitchell, 1994), and West Virginia (Bayless, 1972; Seidel, 1981, 1982; Seidel & Green, 1982). In addition to shell depth, *Pseudemys floridana* in southern portions of the range is generally distinguished from *P. concinna* by absence of a dark dendritic plastral pattern and light lines on the carapace which form concentric or wavy semi-circles. However, these diagnostic markings are highly variable in more northern populations. Seidel & Palmer (1991) were unable to separate *P. concinna* and *P. floridana* in the central Atlantic drainages using morphometric characters and indicated that they might be conspecific. Subsequently, Seidel (1994) examined many additional turtles from more southern and western portions of the range, but still could not clearly distinguish these species. He pointed out that assignment of some individuals to *P. concinna* or *P. floridana* is impossible using all of the reported key characteristics. Local populations are sometimes polymorphic, demonstrating a full range of character state gradients across both species. Hatchlings from a single clutch of eggs may have a full assortment of "interspecific" traits, especially regarding plastral pattern (Seidel & Palmer, 1991; Seidel & Dreslik, 1996). Along the Atlantic slope drainages, there is a *P. c. concinna* morphotype (shallow carapace with swirl marking, plastron with dark central figure, and head with more than 11 head stripes) which inhabits Piedmont sections of rivers. It is easily distinguished by color pattern/markings from a *P. f. floridana* morphotype (deep carapace with wavy light bars on costal scutes and no markings on plastron) which occurs in the Coastal Plain (Seidel & Palmer, 1991). However, these turtles are not morphometrically distinct, and based on their markings, they appear to intergrade along some regions of the Fall Line in North Carolina, South Carolina, and Georgia (Seidel, 1994; Palmer & Braswell, 1995). In other regions near the Fall Line and upper Coastal Plain of these states, turtles with distinct *P. concinna* features inhabit portions of rivers (e.g. Savannah River) in close proximity to lentic waters inhabited by turtles with very typical *P. floridana* markings (e.g. Carolina bays near Aiken, South Carolina). Nevertheless, the two distinct forms (color pattern morphotypes) do not seem to occur in the same body of water (microsympatry). Perhaps different habitat preferences are sufficient to maintain reproductive isolation in some regions, but not in others where they intergrade. Thus, gene flow may be intermittent. Accounts of similar relationships have been reported along the Gulf Coastal Plain and Piedmonts of Alabama (Mount, 1975) and Louisiana (Fahey, 1980; Dundee & Rossman, 1989).

Buhlman et al. (2008) pointed out that natural barriers at one time may have limited gene flow between *P. concinna and P. floridana*, but are now likely weakened. Impoundment of rivers and streams has apparently brought the two forms into extensive contact (microsympatry) and promoted gene exchange (Jensen et al., 2008, p. 489). If this theory is correct, the direction or "reversal" of species divergence (reticulation) would seem to favor recognition of *concinna* and *floridana* as conspecifics. In addition, it is possible that some or all cases of phenotypic variation between these turtles are not directly a product of genetic control. The influence of stream habitat (lentic or lotic) may play an important role in the presumptive differences between *concinna* and *floridana.* Aresco & Dobie (2000) and Rivera (2008) found marked differences in carapace height comparing *P. concinna* from lotic environments of the Piedmont to populations from the Coastal Plain of Gulf and Atlantic drainages. River Cooters with flatter shells were found in the faster flowing waters of the Piedmont. In contrast, Cooters inhabiting slower flowing portions of rivers had a more domed shell (*floridana*-like) with a gradient of individuals in the region of the Fall Line. Similar correlates between shell morphology and stream flow have been observed in other riverine emydids (e.g. *G. nigrinoda*, Ennen et al. 2014; *Actinemys marmorata*, Lubcke & Wilson 2007). For all of these species, it has been suggested that variation in shell morphology, along with other phenotypic conditions, may be a direct developmental response to stream flow rather than a genetic condition resulting from selection. Although this hypothesis seems reasonable, it has not been experimentally tested (e.g. raising hatchling turtles under variably controlled flow regimes). An alternative or co- hypothesis is that greater shell depth in *Pseudemys* is an adaptation to the selective pressures of predation by alligators. A stronger high arched shell could be an advantage in lentic waters where alligators are more prevalent (D. R. Jackson, 2006a, 2006b, pers. comm.).

Based on DNA analysis of *Pseudemys concinna*, *P. peninsularis*, and *P. nelsoni*; Thomson & Shaffer (2010) suggested that nonmonophyletic relationships in *Pseudemys* may be due to a history of hybridization. Seidel (1994) concluded that *concinna* and *floridana* are best treated as subspecies of *P. concinna*. D. R. Jackson (1995) again disagreed with that interpretation and Seidel (1995) presented a rebuttal. Clearly, the relationship between *concinna* and *floridana* challenges our concepts of species taxonomy. In contemporary checklists these turtles have been recognized as conspecific subspecies by Turtle Taxonomy Working Group (2007, 2009; but as either separate species or subspecies in 2010 onward), Iverson et al. (2008, 2012), and Ernst & Lovich (2009); whereas Fritz & Havăs (2007) and Collins & Taggart (2009) treat them as separate species. Whether it is recognized at the species or subspecies level, a problem with the type location for *floridana* exists. Carr (1935: 148), Ward (1984: 42), and Bour (2003a: 540) have all pointed out that Le Conte's (1829: 100) type locality "St Johns's River of east Florida," without designated type specimens, is in a region of intergradation. Now this location may be viewed as a region of parapatry for *P. peninsularis* to the south and *P. c. floridana* (or *P. floridana*) to the north. Bour (2003a: 540) located the shell (MNHN 9170) of a turtle he believes was part of Le Conte's type series, but because its specific identification was uncertain, he considered it only as a syntype, and suggested the type locality should be restricted to the "lower reaches of the St. John's River (Duval County), Florida. Clearly this problem needs to be addressed if *floridana* continues to be recognized as a valid taxon.

Thus far, molecular data have failed to resolve species questions in *Pseudemys*. Preliminary DNA analyses by Davis (1994) and Lydeard (1995) indicated that intrageneric divergence is conservative and not easily resolved. Spinks et al. (2009a) examined nuclear and mitochondrial DNA in four species: *P. concinna* (LeConte, 1829: 106); *P. floridana* (LeConte, 1829: 100); *P. peninsularis* Carr, 1938a: 105; and *P. nelsoni* Carr, 1938c: 307. Based on poor resolution, they referred to them collectively as "the exceedingly problematic genus *Pseudemys.*" T. G. Jackson et al.'s (2012) analysis of mitochondrial DNA from 86 *Pseudemys* (representing all extant taxa) showed limited resolution; and most taxa were not recovered as monophyletic, other than *P. gorzugi* Ward, 1984: 29 and *P. texana* Baur, 1893a: 223, similar to results from Bailey et al. (2004). Not only were Jackson et al. unable to demonstrate species status for *concinna*, *floridana*, *suwanniensis* Carr, 1937: 4, and *peninsularis*; but the Red-bellied subgroup [*nelsoni*, *rubriventris* (LeConte, 1829: 101), and *alabamensis* Baur, 1893: 224], as noted earlier, appeared paraphyletic (Fig. 60). T. G. Jackson et al. (2012) did recover a clade of *P. peninsularis* and *P. nelsoni* in Florida. The only outlier was a single *peninsularis* specimen which was represented by an incomplete data set. Curiously, these two species are exclusively sympatric throughout most of peninsular Florida, and have been reported to hybridize (Carr, 1952 and Crenshaw, 1955). Based on haplotypes, their appearance as a monophyletic lineage (Fig. 60) could be the result of introgression. However, Dale Jackson (pers. observ. and discussions with J. W. Crenshaw) does not believe hybridization between *nelsoni* and *peninsularis* is common. T. G. Jackson et al. (2012) concluded that "Phylogenetic relationships within *Pseudemys* are highly complex, likely as a result of retained ancestral polymorphism and possibly recent hybrid swarms." This is consistent with the very volatile and unstable taxonomy of these turtles, highlighted by the vigorous debate between D. R. Jackson (1995) and and M. E. Seidel (1995).

Most recently, Spinks et al. (2013) examined 10 nuclear and 3 mitochondrial genes in *Pseudemys.* Their population-genetic and phylogenetic analyses were comprehensive, including 86-individual data sets representing all currently recognized taxa. Even with the addition of nuclear loci, they were unable to recover clades representing recognized species and subspecies, including diagnosis of the subgroups *rubriventris* and *concinna.* In their analysis based on gene sequences (source GenBank), Rödder et al. (2013) also were unable to resolve separate monophyletic clades for Cooter and Red-bellied Turtles. As possible explanations for these results, Spinks et al. (2013) suggested that *Pseudemys* is an overly split taxon; or alternatively their data could not delineate species due to extensive hybridization and introgression. Another reasonable interpretation is that much of the genetic variation observed thus far evolved in a wide-ranging ancestral form of *Pseudemys*, and is now sporadically retained throughout the genus (Seidel & Spinks, intercommunication). This is consistent with T. G. Jackson et al.'s (2012) conclusion that "Phylogenetic relationships within *Pseudemys* are highly complex, likely as a result of retained ancestral [primitive] polymorphism." Perhaps radiation (divergence) within *Pseudemys* is relatively recent, resulting from a subtle but complex biogeographic history which lead to partial reproductive isolation. A small number of comparatively new mutations may be exerting a major influence on morphological development and "species" boundaries. Therefore, it may not be surprising that populations (species) of *Pseudemys* appear to be most morphologically distinct in areas where they are allopatric to all other congeners; e.g. *P. gorzugi* and *P. texana* in Texas, and *P. rubriventris* in New Jersey and Massachusetts (Seidel, pers. observ.). In other regions, levels of introgression likely challenge our conventional taxonomic practice. Additional analyses of *Pseudemys* must be species comprehensive and geographically broad. Spinks et al. (2013) emphasize that future study should examine morphological and genetic data from an identical set of individuals, ideally using a high density of molecular markers. T. G. Jackson et al. (2012) add that "… consideration of molecular markers with differential mutational rates (mtDNA/nucDNA, vs. microsatellites) coupled with fossil calibration points will be necessary to better comprehend underlying evolutionary processes from different points in time." When all this is accomplished, taxonomically *Pseudemys* Gray, 1856a: 197 may become the most intensively studied turtle genus, but certainly not the best understood.

The following accounts concerning *Pseudemys* have appeared in the Catalogue of American Amphibians and Reptiles: *P. nelsoni* (Jackson, 1978a), *P. alabamensis* (McCoy & Vogt, 1985), *P. gorzugi* (Ernst, 1990a), *P. texana* (Etchberger and Iverson, 1990), *P. rubriventris* (Graham, 1991), *P. concinna* (Seidel & Dreslik, 1996), and *P. peninsularis* (Seidel & Ernst, 1998). Jackson (2006a, 2006b) and Thomas & Jansen (2006) published accounts of *Pseudemys nelsoni*, *P. concinna*, and *P. floridana* in Chelonian Research Monograph 3. In Conservation Biology of Freshwater Turtles and Tortoises, Leary et al. (2008) authored an account of *P. alabamensis*, Ward & Jackson (2008) authored an account of *P. concinna*, and Jackson (2010) authored an account of *P. nelsoni.*

Seidel & Ernst (1996, Catalogue of American Amphibians and Reptiles) and Ernst & Lovich (2009) reviewed the genus *Pseudemys* and presented dichotomous keys for the species of Cooters.

Trachemys AGASSIZ, 1857

Sliders, genus *Trachemys* Agassiz, 1857: 252, have the broadest distribution of all emydid turtles (Buhlmann et al., 2009), and represent one of the most intensely studied of reptilian genera. The distribution of turtles in the genus *Trachemys* has been complicated by the release of several species into unnatural areas around the World (Rödder et al., 2009), an artifact of the pet and food trades (Seidel & Ernst, 2012). The natural range of the genus extends from the central United States and Atlantic Coastal Plain of the United States southward through Mexico and Central America, where species populations occur on both coasts, to Venezuela and Colombia, with isolated populations in Brazil, Argentina, and Uruguay. Several species inhabit the Greater Antilles in the West Indies. *Trachemys* inhabits a very broad diversity of aquatic habitats including ponds, lakes, rivers, swamps, and temporary pools. At least some of the forms are tolerant of varying salinities (Moll & Legler, 1971; Dunson & Seidel, 1986) and polluted conditions (M.E.S., pers. observ.). Sliders are relatively large (some taxa exceeding 50 cm carapace length). The rugose carapace of adults is notched and serrate posteriorly with some indication of a medial keel. It is green to brown or black with a combination of ocelli or wavy yellow stripes. The hingeless, yellow plastron has a variety of dark blotches or a large central figure. The skin is green to brown with yellow stripes. A prominent yellow, orange or red postorbital stripe is present, which may be continuous or separated from the orbit. Older males lose most of their diagnostic markings which are replaced by black pigment or a brown mottled pattern. The upper jaw has a notch-like medial angle, and its crushing surface lacks tuberculate denticles. Males of some species have elongated foreclaws, and all have longer tails than females. *Trachemys* contains mostly aquatic species with strong basking habits and omnivorous feeding (Figs. 61a and 61b).

Sliders have been classified in the composite genera *Testudo* (Schoepff, 1792: 16), *Emys* (Gray, 1831a: 11; Duméril & Bibron, 1835: 272), *Clemmys* (Fitzinger, 1835 [1836]: 124; Strauch, 1862: 32), *Pseudemys* (Cope, 1877: 53), and *Chrysemys* (Boulenger, 1889: 71). Agassiz (1857: 434) restricted Sliders to the genus *Trachemys* Agassiz, 1857: 252, a separation from Cooters (*Pseudemys* Gray, 1856a: 197) and Painted Turtles (*Chrysemys* Gray, 1844: 27) which later was substantiated by Ward (1980a, 1984) and Seidel & Smith (1986). Although *Trachemys* (sensu Agassiz, 1857: 252) became stabilized as the genus for Slider Turtles, a problem persisted regarding the type-species. Agassiz (1857: 434) described *Trachemys scabra* [= *T. scripta* (Thunberg, *in* Schoepff, 1792: 16) in part] based on *Testudo scabra* of Linnaeus (1758: 198), a composite poorly defined taxon variously referred to several different nominal taxa (see Rhodin & Carr, 2009). Prior to Agassiz (1857), Schoepff (1792: 12) had split *Testudo scabra* into the pelomedusid, *T. galeata* [= *Pelomedusa subrufa* (Lacépède, 1788: 13)] and the slider, *T. scripta.* The latter was based on an illustration and description by C. P. Thunberg (p. 16), although a type specimen for *scripta* was not formally designated at that time. Because it was unclear which specimens of "*scabra"* (if any) were examined by Agassiz, *T. scabra* Linnaeus, 1758: 198 was declared a *nomen dubium* (by Smith & Smith, 1980: 437). Recently, however, Rhodin & Carr (2009) located and examined the previously unexamined holotype of *Testudo scabra* Linnaeus 1758, and it in fact represents the geoemydid turtle *Rhinoclemmys punctularia*, further invalidating *Testudo scabra* as the type of *Trachemys.* Smith & Smith (1980: 438) proposed that *Emys troostii* Holbrook (1836: 55) be designated as the type species for *Trachemys*, following Lindholm's (1929: 280) original description. Until recently, no holotype for *Trachemys scripta* was known, and the type-species for *Trachemys* was assigned to *Emys troostii* (Iverson, 1992; Seidel & Ernst, 2006, 2012). Subsequently, A. Rhodin examined the Uppsala University Zoological Museum's original Linnaean and Thunbergian collections. As reported in Rhodin & Carr (2009), he discovered and described the long lost holotype of *Testudo scripta* Thunberg, *in* Schoepff 1792: 16 (UUZM 7455). This specimen, a dried hatchling, matches the description and individual markings of the turtle illustrated in Schoepff (1792; pl. 3, figs. 4–5) and is clearly a *Trachemys scripta.* Thus, *Testudo scripta* is the appropriate type-species for genus *Trachemys* and authorship of the species should be *Testudo scripta* Thunberg, *in* Schoepff 1792: 16. Detailed fossil histories are presented in Ernst & Lovich (2009) and Seidel & Ernst (2012). Known fossil remains of the genus date back to the Upper Miocene (Seidel & Ernst 2012).

Species and subspecies definitions in *Trachemys* have had a complicated taxonomic history. Early workers described new Slider turtles at the species level: *Testudo terrapen* from Jamaica (Lacépède, 1788: 129, but see Iverson's 1992 reference to Bonnaterre, 1789: 30); *T. scripta* from the eastern United States (Thunberg, *in* Schoepff, 1792: 16); *T. panama* (= *venusta*) from Central America (Perry, 1810: page unnumbered); *Emys decussata* from Cuba and *E. ornata* from Sinaloa, Mexico (Gray, 1831a: 11–12); *E. dorbigni* from Argentina (Duméril & Bibron, 1835: 272); *E. cumberlandensis* (= *scripta troostii*) and *E. troostii* (= melanistic *scripta*) from the southern United States (Holbrook, 1836: 55); *E. elegans* (= *scripta elegans*) from the central United States (Wied-Neuwied, 1839: 213); *E. callirostris* from Colombia, *E. venusta* from Honduras, and *E. ventricosa* (= *venusta cataspila*) from Tamaulipus, Mexico (Gray, 1856b: 25); *E. grayi* from Guatemala (Bocourt, 1868: 121); *Chrysemys nebulosa* from Baja, Mexico (Van Denburgh, 1895: 84); *Pseudemys stejnegeri* from Puerto Rico (Schmidt, 1928: 147); *P. felis* (= *terrapen*) from Cat Island, Bahamas (Barbour, 1935); *P. malonei* (= *stejnegeri malonei*) from great Inagua, Bahamas (Barbour & Carr, 1938: 76); *P. decorata* from Haiti (Barbour & Carr, 1940: 409); and *P. granti* (= *decussata angusta*) from the Cayman Islands (Barbour & Carr, 1941). During the mid- to latter half of the twentieth century, most new forms of Sliders were described as subspecies of *scripta*: *Pseudemys scripta gaigeae* from southwestern Texas and adjacent Mexico (Hartweg, 1939: 1); *P. s. hiltoni* from Sonora and Sinaloa, Mexico (Carr, 1942: 1); *P. s. taylori* from Coahuila, Mexico (Legler, 1960: 75); *P. s. yaquia* from Sonora, Mexico (Legler & Webb, 1970: 157); *P. s. chichiriviche* from Venezuela (Pritchard & Trebbau, 1984: 191); *P. s. emolli* from Nicaragua and Costa Rica (Legler, 1990: 91); and *P. s. hartwegi* from Durango and Coahuila, Mexico (Legler, 1990: 89). An exception was Vanzolini's (1995: 111) description of the species *Trachemys adiutrix*, a new Slider in northern Brazil.

A number of Sliders have been described from presumptive distinctive features which have later proven unreliable. Labile taxonomic characters were used, including coloration and markings which in some cases were described from nonliving specimens. A particular source of confusion has been the extreme melanism which older males demonstrate. As males of many *Trachemys* species age, they lose their diagnostic color patterns and acquire dark mottled pigment on the shell and soft parts (Lovich et al., 1990; Tucker et al., 1995). Furthermore, *T. scripta* (and probably other species) has the capability to gradually change (presumably by endocrine control) the intensity of the melanin pattern in its shell from light to dark, or reverse, to match that of its aquatic substrate (Price et al., 2005; Rowe et al., 2006b, 2009). Shaw (1802: 28) described *Testudo rugosa* (= either *Trachemys terrapen* or *T. decussata*) in the West Indies based entirely on melanistic individuals. Holbrook (1836: 155) described *Emys troostii* from melanistic *T. scripta* in the southcentral United States, and Danforth (1925: 79) described *Pseudemys palustris* from melanistic males of *T. stejneg-*

eri in Puerto Rico. Viosca (1933: 210) concluded that *troostii* was based on melanistic male Sliders, but herpetologists were slow to adopt that interpretation (Carr, 1952). Williams (1956) noted that the most reliable diagnostic markings of Sliders are evident in juveniles (see Bour, 2003b: 8–9 for illustrations). He constructed a diagram (Fig. 62) to illustrate affinities among *Trachemys* based heavily on plastral patterns.

Over the last several decades, studies of nest conditions in emydid turtles have indicated an environmental influence on pigmentation (Ewert, 1979). Laboratory experiments by Etchberger et al. (1993) have indicated the labile nature of "diagnostic" markings. They altered temperature and oxygen and carbon dioxide concentrations during incubation, and discovered an effect on leg stripes, chin stripes, and plastron pattern in hatchling *T. scripta*. Increasing temperatures (22.5°C, 25°C, and 30°C) produced wider leg stripes and more concentric dark plastron spots, but resulted in a thinner medial chin stripe. Elevating carbon dioxide levels to 10% resulted in thinner leg and chin stripes at 29°C and 30°C. Curiously, the amount of plastron pigmentation (number and concentricity of spots) increased at 29°C, but decreased at 30°C. If such conditions vary naturally during incubation, reliance on hatchling plastron patterns to distinguish species/subspecies of *Trachemys* should be viewed with caution. In addition, body size and concomitant sexual maturity may not be a reliable taxonomic character, as it too may be plastic and influenced by microhabitat conditions. Probably the most important environmental factor in this regard is water temperature. Some species, such as *T. scripta*, have extensive geographic ranges and live under different water temperature regimes. A microhabitat with relatively warm water may promote increased growth of invertebrate and algae populations, resulting in greater sources of protein for turtles (Avery et al., 1993). Furthermore, faster and larger growth, accompanied by earlier sexual maturity, would be expected in tropical populations where feeding activity may occur all year (Christy et al., 1974; Gibbons et al., 1981). Somewhat surprising is that species longevity apparently is not influenced by climate. Temperate forms of *Trachemys* (which remain dormant during the cool season) apparently do not live to an older age than tropical populations which are active all year (Gibbons & Semlitsch, 1982; Seidel, 2003).

Additional problems in the identity of taxa of *Trachemys* have arisen from hybridization (Fritz, 1995a). Among the numerous examples of human introduction of Slider Turtles (especially *T. scripta elegans*), interbreeding with native forms of *Trachemys* and production of fertile offspring are common (Seidel & Adkins, 1987; Mitchell, 1994; Seidel et al., 1999; Stuart & Ernst, 2004; Tuberville et al., 2005; Aresco & Jackson, 2006; Stuart & Ward, 2009). This may not only obscure diagnostic characters, but also lead to the removal of mechanisms which maintain natural levels of reproductive isolation. Thus genetic "swamping" may occur and threaten species diversity (See "Comment" section of Seidel & Ernst, 2006: 15). A major aspect of taxonomic instability in Slider Turtles has been variable assignments to species or subspecies status. For many cladists who acknowledge no value in the subspecies concept, resolution of the problem is simple. However, for the majority of taxonomists who recognize subspecies, the issue in *Trachemys* is challenging. There appears to be no geographic locality where more than one form naturally occurs (i.e. absence of mico-sympatry). Therefore, the biological species concept (Mayr, 1963) cannot be applied. The extent of evolutionary divergence must be determined and regions of potential intergradation or parapatry identified. Insular forms, i.e. Antillean Sliders of the West Indies, provide a good example for testing such relationships.

Barbour & Carr (1940) presented a classical analysis of Antillean Sliders based mostly on color patterns and markings. They defined six species partitioned into two subgroups. Their subgoup "Terrapen" included *Pseudemys terrapen* on Jamaica (Lacépède, 1788: 129), *P. felis* Barbour, 1925: 205 restricted to Cat Island in the Bahamas, and the polytypic Cuban species *P. decussata* (Gray, 1931a: 11) (*P. d. decussata* (Gray, 1931a: 11), *P. d. angusta* Barbour & Carr, 1940: 402, *P. d. plana* Barbour & Carr, 1940: 405). Subgroup "Stejnegeri" included the bitypic species *P. stejnegeri* Schmidt, 1928: 147 (*P. s. stejnegeri* Schmidt, 1928: 147 on Puerto Rico and *P. s. vicina* Barbour & Carr, 1940: 408 in eastern Hispaniola), *P. decorata* Barbour & Carr, 1940: 409 in western Hispaniola, and *P. malonei* Barbour & Carr, 1938: 76 endemic to Great Inagua, Bahamas. A year later, Barbour & Carr (1941: 59) described a seventh species, *P. granti* (= *Trachemys decussata angusta*) from the Cayman Islands. They speculated this species had an affinity to Jamaican Sliders, and included it in the "Terrapen" subgroup. Barbour & Carr (1941) also presented a theory of relationships among West Indian *Trachemys* based on an original dispersal from Central America (Honduras) to Cuba (Fig. 63). Seidel & Adkins (1987) analyzed protein polymorphism by isoelectric focusing and corroborated the subgroup relationships of Barbour & Carr (1940, 1941). However, they found no biochemical difference between *Trachemys felis* (Barbour, 1935: 205) on Cat Island and *T. terrapen* (Lacépède, 1788: 129) from Jamaica. Therefore, Seidel & Adkins (1987) followed earlier suggestions of Williams (1956: 157) and Wermuth & Mertens (1961: 59) that *T. felis* be placed in the synonymy of *T. terrapen*. This was further supported by morphological analysis (Seidel, 1988a), which also included purported samples of *felis* from the Bahamian Islands of Eleuthra and Andros. Considering the geographic distance of these islands from Jamaica, the presence of *T. terrapen* in the northern Bahamas may be the result of introduction by British trade from Jamaica. However, fossil evidence suggests a natural origin of these turtles (Seidel, 1996). Olson et al. (1990) reported late Pleistocene skeletal remains from San Salvador (central Bahamas), including an emydid turtle which appears to be a *Trachemys*. In spite of the works of Barbour & Carr, the taxonomy of West Indian

Fig. 61a. Genus *Trachemys*. Row 1: Carapace of *Trachemys scripta scripta*, plastron of *Trachemys s. scripta*, carapace of *Trachemys adiutrix*, and plastron of *Trachemys adiutrix*. Photos of *Trachemys s. scripta* by Roger W. Barbour and Carl H. Ernst, and *Trachemys adiutrix* by Richard C. Vogt. Row 2: Carapace of *Trachemys callirostris chichiriviche*, plastron of *Trachemys c. chichiriviche*, carapace of *Trachemys decorata*, and plastron of *Trachemys decorata*. Photos of *Trachemys c. chichiriviche* by Carl H. Ernst and *Trachemys decorata* by Michael E. Seidel.

Row 3: Carapace of *Trachemys decussata angusta*, plastron of *Trachemys d. angusta*, carapace of *Trachemys dorbigni brasiliensis*, and plastron of *Trachemys d. brasiliensis*. Photos of *Trachemys d. angusta* by Michael E. Seidel and *Trachemys d. brasiliensis* by Carl H. Ernst. Row 4: Carapace of *Trachemys gaigeae gaigeae*, plastron of *Trachemys g. gaigeae*, carapace of juvenile *Trachemys grayi grayi*, and head of *Trachemys grayi emolli*. Photos of *Trachemys g. gaigeae* by Roger W. Barbour and Carl H. Ernst, *Trachemys grayi grayi* by Carl H. Ernst, and *Trachemys grayi emolli* by Dennis Uhrig.

Fig. 61b. Genus *Trachemys* (continued). Row 1: Carapace of *Trachemys grayi panamensis,* carapace of juvenile *Trachemys nebulosa nebulosa*, plastron of *Trachemys n. hiltoni*, and carapace of *Trachemys ornata*. Photos by Raul de Plecker (courtesy of Parque ReptiLandia), Lee Grismer, Cecil Schwalbe, and Paulino Ponce-Campos, respectively. Row 2: Plastron of *Trachemys ornata*, carapace of *Trachemys stejnegeri vicina*, plastron of *Trachemys s. stejnegeri*, and carapace of juvenile *Trachemys taylori*. Photos of *Trachemys ornata* by Paulino Ponce-Campos, *Trachemys stejnegeri* by Michael E. Seidel, and *Trachemys taylori* by Michael T. Jones.

Row 3: Plastron of juvenile *Trachemys taylori*, carapace of *Trachemys terrapen*, plastron of *Trachemys terrapen*, and carapace of *Trachemys venusta venusta*. Photos of *Trachemys taylori* and *Trachemys terrapen* by Michael E. Seidel, and *Trachemys venusta venusta* by Wayne Van Devender. Row 4: Plastron of *Trachemys v. cataspila*, plastron of *Trachemys v. uhrigi*, carapace of *Trachemys yaquia*, and plastron of *Trachemys yaquia.* Photos of *Trachemys v. cataspila* by John B. Iverson, *Trachemys v. uhrigi* by Dennis Uhrig, and *Trachemys yaquia* by Franck Bonin (courtesy of James R. Buskirk).

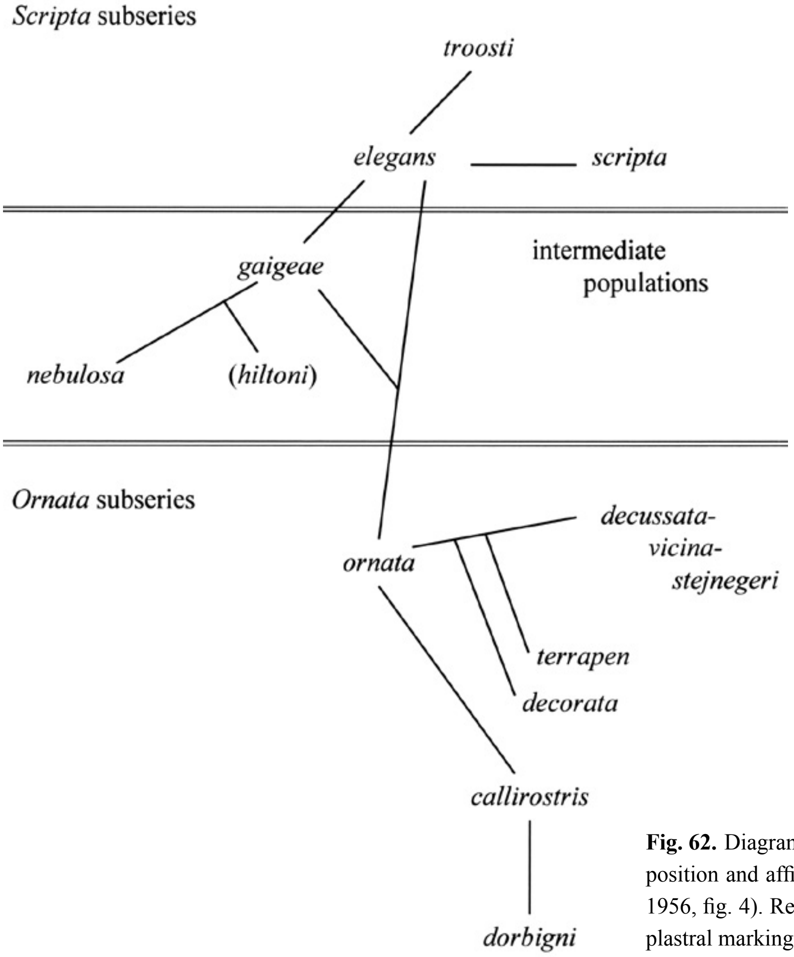


Fig. 62. Diagram to show groupings and approximate geographic position and affinities in the *scripta* [*Trachemys*] series (Williams 1956, fig. 4). Relationships are based primarily on comparisons of plastral markings.

Sliders remained unstable throughout the middle twentieth century. For instance, Grant (1948: 28) thought the evidence that Barbour & Carr (1940: 54) used to split *P. decussata* to create the subspecies *P. d. plana* was "insufficient" to establish *plana*, and that the other subspecies they established in their 1940 paper needed to be further studied to determine their legitimacy. Subsequent authors recognized as many as five species (Schwartz & Thomas, 1975; Henderson & Schwartz, 1984; Schwartz & Henderson, 1985, 1991) or as few as one (Wermuth & Mertens, 1961, 1977; Rivero, 1978; Obst, 1985).

Seidel (1988a) presented a comprehensive systematic review of West Indian *Trachemys* utilizing biochemical and morphological data. Species identity was tested by phenetic and phylogenetic analyses. Seidel found that Barbour & Carr's (1940: 405) subspecies from eastern Cuba, *T. decussata plana*, is not morphologically distinct from the nominate form *T. d. decussata* (Gray, 1831a: 11), and thus placed *plana* in its synonymy. Similarly, Seidel (1988a) found no morphological distinction between *T. granti* (Barbour & Carr, 1941: 59) from the Cayman Islands and *T. d. angusta* (Barbour & Carr, 1940: 402) on western Cuba, placing the former in synonymy of the latter. Seidel (1988a) proposed a phylogeny and biogeographic origin for the West Indian Sliders (Fig. 64). He concluded they are not collectively monophyletic and that they arose by multiple dispersals (invasions) from continental America. Using Cooters (genus *Pseudemys*) as an outgroup, Seidel identified a clade containing tropical continental *Trachemys* and *T. decussata* which formed the sister group to a clade of *T. stejnegeri* (Schmidt, 1928: 147) and *T. decorata* (Gray, 1831a: 11). These two clades collectively comprised a sister group to *T. terrapen* (Lacépède, 1788: 129). *Trachemys malonei* (Barbour & Carr, 1938: 76), which appeared morphologically distinct, formed an unresolved trichotomy with *T. stejnegeri vicina* (Barbour & Carr, 1940: 408) and *T. s. stejnegeri*. Therefore, Seidel (1988c: 2) relegated *malonei* to a subspecies of *T. stejnegeri*.

Modern phylogenetic analyses of West Indian *Trachemys* have supported Barbour & Carr's (1941) theory of single (monophyletic) origin from mainland America (e.g. Stephens & Wiens, 2003; Jackson et al., 2008; Parham et al., 2013). Some of these hypotheses are congruent with theories on the evolution of courtship and reproduction. Titillation courtship with long male foreclaws can be considered a primitive character state in *Trachemys* because it is widely represented in the subfamily Deirochelyinae. All Antillean Sliders utilize this stereotypical courtship ritual, also present in temperate *T. scripta* as well as in the genera *Chrysemys*, *Graptemys*, and *Pseudemys* (Ernst, 1974; Fritz, 1990a, 1990b, 1991; Seidel & Fritz, 1997). None of the continental Sliders in the Neotropics, from Mexico to Argentina, utilize this

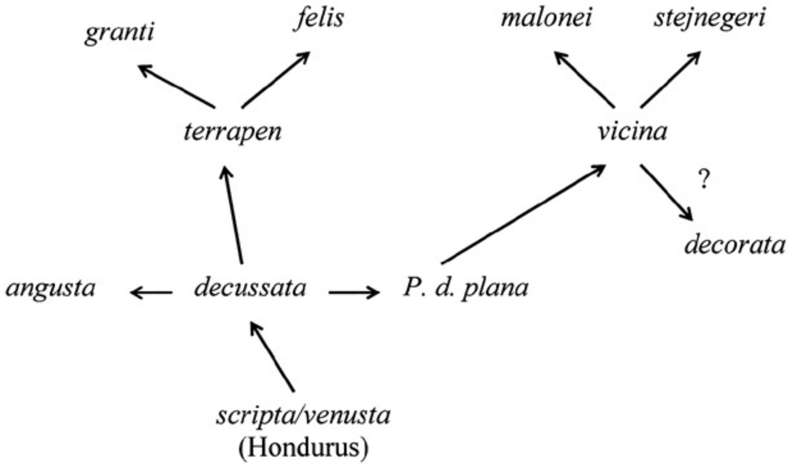


Fig. 63. A theory of evolutionary relationships among West Indian Sliders (*Trachemys*) based on geographic origin and morphology. Modified from Barbour and Carr (1941, Plate IX). Several of the taxa indicated (i.e. *granti*, *felis*, *plana*) are no longer recognized (sensu Seidel 1988a).

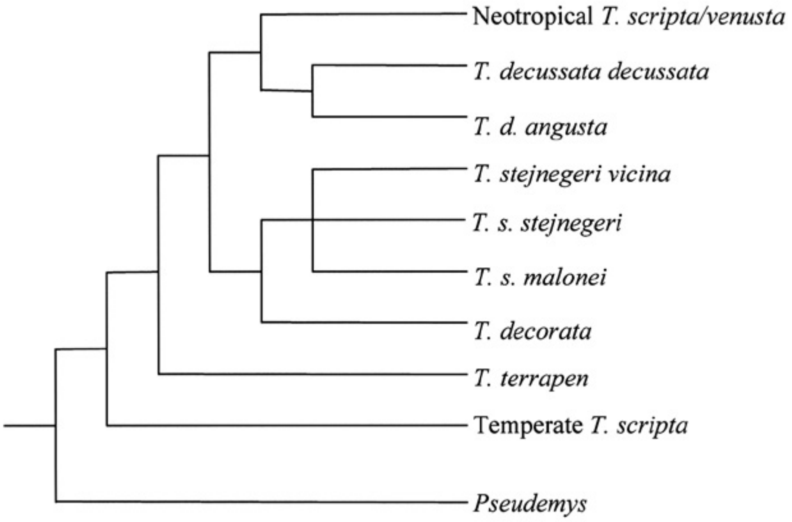


Fig. 64. Cladistic relationships among populations of West Indian *Trachemys* and *T. scripta* expressed by the PAUP algorithm based on binary coding of 32 morphological and biochemical characters. The tree is rooted with *Pseudemys* as an outgroup and the consistency index is 0.59. Modified from Seidel (1988a, fig. 4).

type of behavior (Legler, 1990; Fritz, 1991). If all West Indian *Trachemys* originated from an ancestral stock in Central or South America; it must have occurred early, before titillation behavior (a presumably plesiomorphic, primitive condition) became lost. Sliders in Meso- and South America have been described as recent invaders of the tropics (perhaps dating back only to the late Pleistocene) based on their temperate-adapted reproductive cycle (Moll & Moll, 1990). It could be assumed that their loss of titillation courtship (an acquired apomorphy?) was concordant with that tropical radiation. The most recent and comprehensive DNA analysis of *Trachemys* (Parham et al., 2015) indicates that the West Indian Sliders are the sister group to a large all-inclusive clade of Meso-South American *Trachemys.* Following this hypothesis, it is quite possible that loss of titillation behavior has been relatively "recent", occurring along the stem (lineage) leading to the origin of all *Trachemys* in the continental tropics and subtropics. Concomitantly, it could be theorized that West Indian Sliders are an earlier divergence from a *scripta*-like ancestor, from which they acquired and retained the primitive condition of titillation courtship. Perhaps noteworthy, analysis of variation in titillation courtship has proven useful for discerning relationships in other emydid genera (e.g. *Pseudemys*, Seidel & Fritz, 1997; *Graptemys*, Vogt, 1978).

Analysis of mitochondrial and cloned nuclear DNA by Parham et al. (2013) revealed some novel and important relationships within the West Indian clade. These authors proposed a phylogeny (Fig. 65) which places *T. decussata* (native to Cuba) as the sister group to a clade consisting of *T. terrapen* (Jamaica), *T. decorata* (Hispaniola), and *T. stejnegeri* (Puerto Rico and Hispaniola). They further reported that *T. stejnegeri* forms a sister group to *T. terrapen* plus *T. decorata.* Perhaps the most surprising find by Parham et al. was the presence of *P. decussata* in northwestern Jamaica. Previously, the only *Trachemys* known to inhabit Jamaica was *T. terrapen*. Tuberville et al. (2005) had reported that turtles in this region, unlike typical Jamaican *terrapen*, have distinct head stripes (including orange or reddish supratemporals) and plastral markings as seen in *T. decussata* or *T. stejnegeri*. Earlier, Seidel (1988a) had made similar observations for Sliders in western Jamaica, in the vicinity of Negril. Parham et

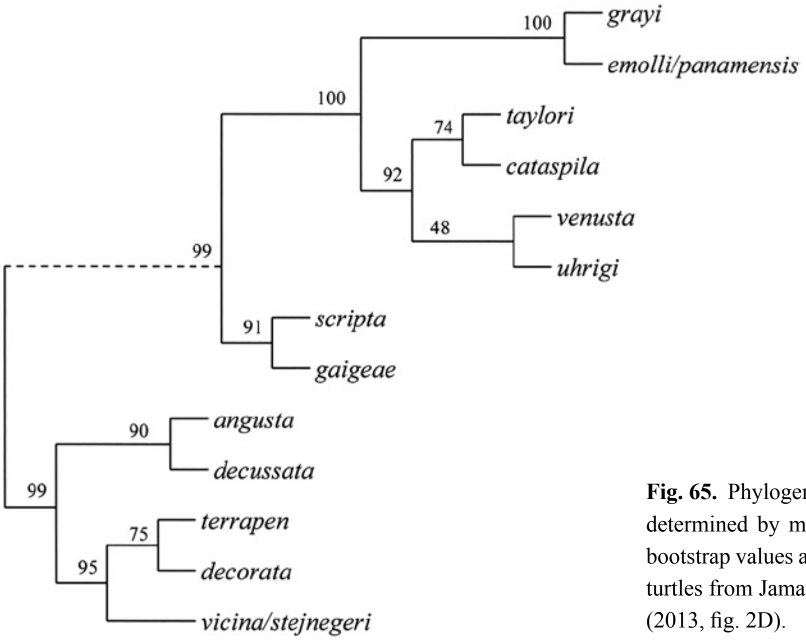


Fig. 65. Phylogenetic relationships among forms of *Trachemys*, determined by mitochondrial and nuclear DNA data. Likelihood bootstrap values appear at nodes. The sample of *decussata* includes turtles from Jamaica as well as Cuba. Modified from Parham et al. (2013, fig. 2D).

al. (2013) found that Sliders in northwestern Jamaica share a unique mitochondrial DNA haplotype with *T. d. decussata* on Cuba, thus confirming their identity. They also concluded that some hybridization (introgression) with *T. terrapen* is occurring in that region. Whether or not the presence of *T. decussata* on Jamaica represents a natural origin or human introduction remains undetermined.

Many authors, dating back to the nineteenth century, treated continental forms of Sliders as subspecies of *scripta* or *ornata* (e.g. Boulenger, 1889; Siebenrock, 1909; Carr, 1938b; Williams, 1956). For Sliders in the northern temperate regions, Carr (1952) recognized a large zone of intergradation between the Yellow-bellied Slider (*T. s. scripta*) in the southern Atlantic United States and the Red-eared Slider (*T. s. elegans*) in the south-central United States. Also, Ernst & Jett (1969) reported intergradation in Kentucky between *T. s. elegans* and *T. s. troostii.* Clearly these are typical and appropriate examples of subspecific relationships. Moll & Legler (1971) created the largest assemblage of *scripta* subspecies, 14 taxa ranging from northern temperate regions south into the tropics of Central and South America. A number of systematic studies have proposed that the more southern (Meso-South American) forms of *T. scripta* be partitioned into separate species. Based on morphological characters, Weaver & Rose (1967) divided continental Sliders into three species groups: *Chrysemys* (*Trachemys*) *scripta* (*C. s. scripta*, *C. s. elegans*, *C. s. troosti*), *C. gaigeae* (*C. g. gaigeae*, *C. g. hiltoni*, *C. g. taylori*), and a group comprised of *C. ornata*, *C. callirostris*, and tentatively *C. dorbigni* (see also Price & Hillis, 1989). An arrangement similar to this was published by Holman (1977) and Fritz (1990b), who also elevated *T. callirostris.* It is noteworthy that both Holman (1977) and Weaver & Rose (1967) constructed species groups which included a mixture of Sliders (*Trachemys*) and Cooters (*Pseudemys*). Wermuth & Mertens (1977) recognized four species of continental Sliders: *Pseudemys scripta* (including subspecies *scripta*, *elegans*, *troostii*, *gaigeae*, and *taylori*), *P. ornata* (including subspecies *ornata*, *callirostris*, *nebulosa*, and *yaquia*), *P. grayi*, and *P. dorbigni*. Quite surprisingly and without explanation, these authors had earlier (1961: *vii*) transferred the Mexican Slider, *Trachemys nebulosa hiltoni* (Carr, 1942: 1), to a subspecies of the River Cooter, *P. concinna*. The species *dorbigni*, native to southern South America, was partitioned into two subspecies (*T.* [*P.*] *dorbigni dorbigni*, p. 308 and *T.* [*P.*] *dorbigni brasiliensis*, p. 301) by Freiberg (1969). Barco & Larriera (1991) analyzed morphological variation between the two subspecies and concluded that the diagnostic character states are merely ontogenetic variants based on an insufficient (or skewed) sample size. *Trachemys dorbigni* was subsequently recognized by some authors as a monotypic species (e.g. Rogner, 1995; Turtle Taxonomy Working Group, 2007). Parenthetically, the type specimen of *T. dorbigni* (MNHN 9221, Dumérl & Bibron, 1835: 272) was originally designated from the type-locality "… Buenos-Ayers.", Argentina (Seidel, 1989: 1). However, Lescure et al. (2002: 529) corrected that location to "Rio Parana". Ward (1980a: 251, 1984: 46) proposed that Sliders (genus *Trachemys*) may consist of as many as 16 species, six being polytypic. Although apparently based on his observations of head and shell markings, it was not clear what species criterion Ward applied in making that decision.

In 1990, Legler (1990) presented a taxonomic and biogeographic analysis of Mesoamerican *Trachemys.* He described two new subspecies of *scripta*: *P.* (*T.*) *s. hartwegi* (p. 89) from the Rio Nazas of northcentral Mexico, and *P.* (*T.*) *s. emolli* (p. 91) from Nicaragua and Costa Rica (now also reported from El Salvador, Köhler et al., 2005 [2006], and southwestern Honduras, McCranie et al., 2013). Legler's (1990) descriptions of subspecies were based primarily on markings and pigmentation of the head, neck, carapace, and plastron. His conclusions regarding relationships among taxa were based on phenetic analysis of morphology and influenced strongly by geological history of river basins. In Mesoamerica, three groups were recognized: northern isolates in Mexico (*taylori*, *gaigeae*, *hartwegi*, *cataspila*, *venusta*), a Pacific coastal series (*hiltoni*, *nebulosa*, *yaquia*, *ornata*, *grayi*), and a Lake Nicaragua Pacific series (*emolli* and two undescribed forms in coastal Panama). Arrangement of a mega-polytypic *Trachemys* (*Pseudemys*) was retained by Legler (1990, sensu Moll & Legler, 1971). A major problem with that taxonomy is that it is now in conflict with modern phylogenetic analyses based on molecular data. Specifically, the West Indian species (sensu Barbour & Carr 1940, Seidel 1988; recognized by Legler and others) become nested within, or paraphyletic to, clades of continental *T. scripta* (see Jackson et al., 2008; Fritz et al., 2012; Parham et al., 2015). In the more recent text on Mexican turtles by Legler & Vogt (2013), the senior author continued to use a multi-polytypic *T. scripta.* However, these authors acknowledged that they "… regard each allopatric taxon [subspecies] as an incipient species." Inconsistent application of species/subspecies for continental Sliders persisted through the late twentieth century. Dixon (1987: 85), in his treatment of Texas turtles, recognized species rank for *T. gaigeae*, reverting back to Stejneger & Barbour's (1939: 165) assignment of that Slider. Elevation of *gaigeae* to species was discussed in depth by Ernst (1992) who concluded that its relationship to other Sliders required additional study. Seidel et al. (1999) compared distributional and morphological relationships among *T. s. gaigeae* (Hartweg, 1939: 397), *T. s. cataspila* [= *T. venusta cataspila* (Günther, 1885: 4)], and *T. s. elegans* (Wied-Neuweid, 1839: 213) in the lower Rio Grande Valley and northeastern Mexico where their ranges reach close proximity. They concluded that *gaigeae* and *cataspila* are distinct taxa at the species level. Subsequent analysis of mitochondrial and nuclear DNA further supported recognition of *T. gaigeae* as a species, although limited hybridization with *T. scripta elegans* has been detected (Stuart, 1995; Seidel et al., 1999; Forstner et al., 2009). Parenthetically, Farr et al. (2009) reported records of *T. s. cataspila* [= *T. venusta cataspila* (Günther, 1885: 4)] from northern Tamaulipas, Mexico; near or within the range of *T. s. elegans* in the Rio Grande drainage system; but observed no evidence of hybridization between them.

Seidel (2002a) addressed the confusion of species versus subspecies status of Slider Turtles with a comprehensive analysis (including all 26 currently recognized taxa) based mostly on morphological characters. His phylogenetic analysis did not resolve ancestral relationships among all taxa; but terminal clades were evident and interpreted as polytypic species (Fig. 66). The phylogeny-based taxonomy of Seidel (2002a, Table 2) received general acceptance (e.g. Iverson et al., 2007; Turtle Taxonomy Working Group, 2007, 2009; Bock et al., 2010; but not Wiens et al., 2010). Nevertheless, the taxonomic status of *T. venusta* (Gray, 1855b: 24) populations along the Pacific coast of Costa Rica and Panama remained uncertain (see Legler, 1990). J. T. Jackson et al. (2008) further analyzed phylogenetic relationships among species of *Trachemys* by examining mitochondrial DNA. Their results supported the taxonomy proposed by Seidel (2002a), which they considered "…the most reasonable for the genus." Similar to Seidel, Jackson et al. were unable to resolve variation in *T. venusta* (Fig. 67).

McCord et al. (2010) recognized additional geographic variants in *T. venusta* and described three new subspecies formerly included under *T. v. venusta* Gray, 1855b: 24 (sensu Seidel, 2002a). They defined the enigmatic Pacific coastal population (which Legler, 1990 called "Central American Pacific" population) as *T. v. panamensis* (= *T. grayi panamensis*) on p. 46. It is characterized by having a wide postorbital stripe in the area of the tympanum, the plastral pattern of juveniles that occupies 30–40% of the plastron, and the carapace is widest at the seam between the seventh and eighth marginals. It is more likely the GDULCE ("Golfo Dulce") morph of *Trachemys scripta* (Thunberg, *in* Schoepff, 1792: 16) described by Legler (1990). McCord et al. (2010) defined populations of *T. venusta* inhabiting Caribbean coastal regions of Honduras, Nicaragua, Costa Rica, and eastern Panama as *T. v. uhrigi* (p. 43). This subspecies is distinguished by a thin yellow postorbital stripe which contacts the orbit; pale orange or yellow ocelli markings on the carapace of the young, and a plastral figure which is greatly expanded (90% of plastral surface). The third new subspecies described by them is *T. v. iversoni* (p. 45). This Slider has a limited distribution in cenotes of northern Yucatan, Mexico. It is characterized by an anterior face which is blunt (short rostrum) in both males and females, a first vertebral scute which is longer than wide, and a greatly expanded plastral pattern. Unfortunately McCord et al. (2010) did not present a list of turtles examined and cited only two specimens (a holotype and paratype) upon which each of their descriptions were based. There is no statistical analysis of character variation described; thus, it is difficult to evaluate if the taxa they defined are clinal variants or discrete morphological (taxonomic) entities. Furthermore, if they relied on comparative material from the pet trade or live private collection (e.g. description of *Mauremys iversoni* by Pritchard & McCord, 1991), there are questions regarding locality data and possible hybrid origin (See Parham et al., 2001; Wink et al., 2001; Spinks et al., 2004; McCranie et al., 2013.). Molecular (DNA) evidence presented by Fritz et al. (2012) provided support for the recognition of *panamensis* (as a subspecies of *T. grayi*) but these authors did not resolve *uhrigi* as a recognizable taxon. Their analysis did not include *iversoni.* Recently, Parham et al. (2015) expressed doubt regarding validity of all three of the "new subspecies" described by McCord et al. (2010).

Mitochondrial and nuclear DNA evidence presented by Fritz et al. (2012) provided a case for species revision of Sliders in Central and South America (Fig. 68).

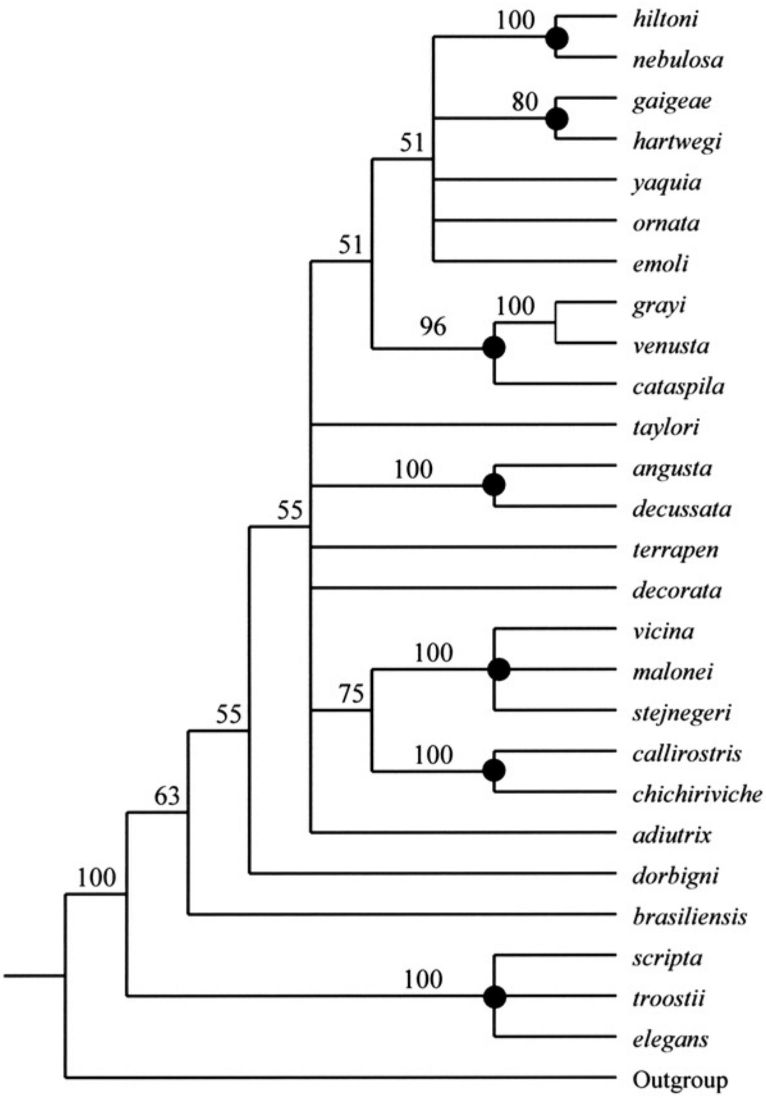


Fig. 66. Fifty percent majority-rule consensus tree (based on 23 morphological characters) indicating relationships among the forms of *Trachemys* (modified from Seidel 2002a, fig. 2). The tree is rooted with an outgroup of *Pseudemys* and *Graptemys*. The consistency index is 0.36, and numbers indicate percentages each branch occurred among all equally parsimonious trees.

These investigators found that the South American forms, *T. dorbigni* Duméril & Bibron, 1835: 272 and *T. adiutrix* Vanzolini, 1995: 111, form a sister pair which is strongly divergent from other tropical Sliders and should be treated as conspecific subspecies. This interpretation was followed by Alcalde et al. (2012) and further supported by McCranie et al. (2013). Nevertheless, the DNA data clearly indicate that each form is monophyletic, and the known ranges of these two taxa are broadly disjunct (separated by more than 2,000 km). Therefore, it seems that the more conservative approach would be to retain the two taxa as separate species (sensu Seidel, 2002a). Fritz et al. (2012) also concluded that *T. venusta* (sensu Seidel, 2002a) is a polyphyletic taxon. They found that *T. v. grayi* (Bocourt, 1868: 121) of southern Mexico and Guatemala, *T. emolli* (Legler, 1990: 91) of El Salvador, Nicaragua, Honduras, and Costa Rica, and *T. v. panamensis* McCord, Joseph-Ouni, Hagen & Blanck, 2010: 46 of Panama form a clade (Fig. 68) of Pacific Slope *Trachemys* which they defined as subspecies of *T. grayi* (sensu lato). This interpretation seems reasonable and is biogeographically supported by the proximal, but disjunct, ranges of these turtles along the Pacific coast of Central America. Similarly, the phylogenetic analysis of Parham et al. (2013) recovered a clade of these three taxa (Fig. 65), and those authors agreed with Fritz's re-elevation of *grayi* to species status. We also concur with that taxonomic change. Most recently, McCranie et al. (2013) expanded the range of *T. g. emolli* (based on morphological and mitochondrial DNA data) to include El Salvador and Honduras. From their analysis, they also substantiated the conclusions that *emolli* is best considered a subspecies of *T. grayi* and that *T. venusta uhrigi* is not a valid taxon. The phylogenies presented by McCranie et al. (2013), based on sequencing of mitochondrial genes (e.g. Fig. 69), generally support the results of Fritz et al. (2012).

Fritz et al. (2012) showed that *T. grayi* (sensu lato) forms the sister group to a clade of *T. callirostris* (Gray, 1855b: 25), *T. v. venusta* (including *uhrigi*), *T. ornata* (Gray, 1831a: 12), and *T. v. cataspila* (Günther, 1885: 4) which they assigned to a polytypic species *T. ornata* (Fig. 68). Within that clade, *T. callirostris* (Gray 1855b: 25) [consisting of *T. c. callirostris* and *T. c. chichiriviche* (Pritchard & Trebbau, 1984: 191) in northwestern South America] is supported as a monophyletic unit and conservatively should be treated as the bi-typic

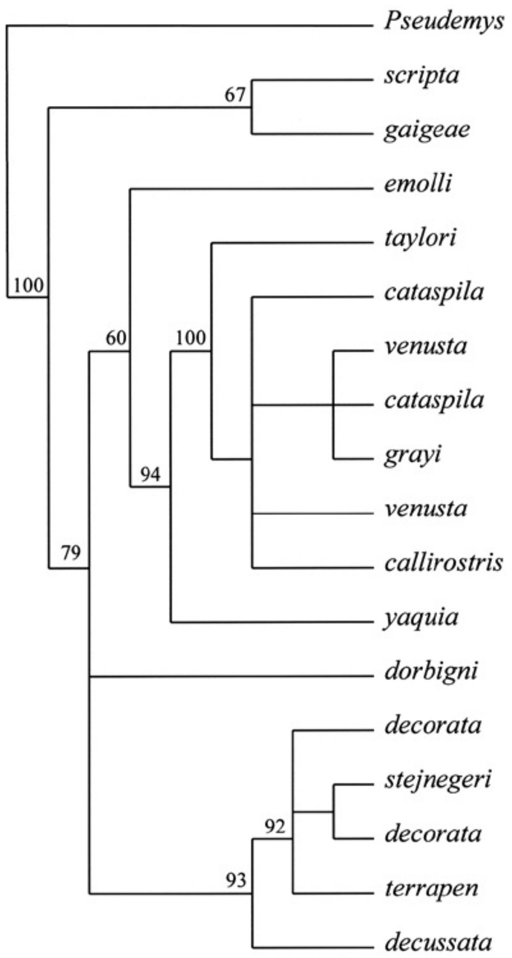


Fig. 67. Relationships among *Trachemys* turtles based on mitochondrial DNA sequencing and illustrated by bootstrap consensus of maximum parsimony analyses. Bootstrap values are shown at nodes. Modified from J.T. Jackson et al. (2008, fig. 1).

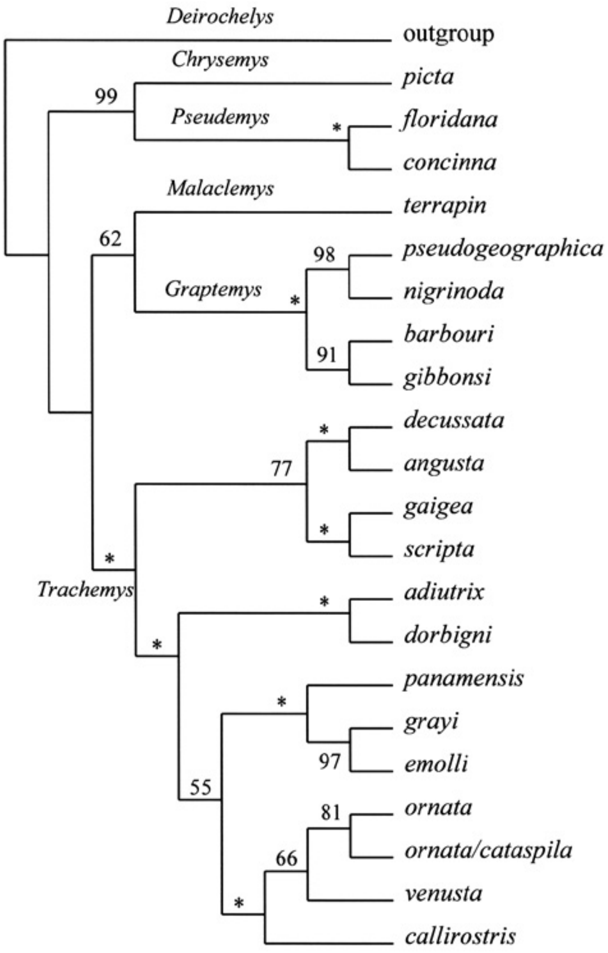


Fig. 68. Phylogeny of *Trachemys* and allied emydids, estimated by a maximum likelihood tree based on sequencing of four mitochondrial genes and five nuclear loci combined. Bootstrap values are shown at nodes and asterisks indicate maximum support. Modified from Fritz et al. (2012 [2011], fig. 3).

species *T. callirostris* (sensu Seidel, 2002a). On the other hand, the sister group to *T. callirostris*, i.e. *ornata*, *venusta*, and *cataspila*, is poorly resolved and not geographically cohesive. Identity of these three forms remains problematic. This is compounded by the questionable origin of an isolated population near Acapulco in the state of Guerrero, Mexico (Ernst & Seidel, 2008). These turtles had been sampled for molecular studies by previous authors (e.g. Fritz et al., 2012) and presumed to be *T. ornata.* In the 2011 checklist of the Turtle Taxonomy Working Group (TTWG), the authors state: “While Fritz et al. (2012) provide a useful set of hypotheses for future testing, we recognize that the taxonomy of *Trachemys* will remain dynamic and expect further changes when additional nuclear data, and deeper geographic sampling of field-verified specimens, are brought to bear on the problem. We therefore provide alternative taxonomies of Seidel (2002a) and Fritz et al. (2012) in this year’s checklist.”

Several recent phylogenetic studies have included DNA sequencing of the northern Mexico endemic Sliders. McCranie et al. (2013) found *T. yaquia* (Legler & Webb, 1970: 157) from northwestern Mexico to be monophyletic, thus supporting species status (sensu Seidel, 2002a). This had also been implicated in the preliminary genetic results of Herrmann & Rosen (2009). These investigators, after sequencing mitochondrial and nuclear DNA from field-sampled *T. yaquia* and *T. scripta elegans* (Wied-Neuweid, 1839: 213), stated that “… our result remains consistent with recognition of *T. yaquia* as a full species …” The molecular analysis by Jackson et al. (2008) also found strong support for *yaquia*. Most recently, Parham et al. (2015) demonstrated that *T. yaquia* (Sonora) and *T. ornata* (sampled from Sinaloa) form a sister group which is strongly divergent from other Sliders in Mexico (Fig. 70). These authors also confirmed (based on markings, coloration, and DNA sequencing), that Sliders in the Acapulco region are not *T. ornata*, but presumably represent an introduced colony of *T. venusta.* Another Slider from northwestern Mexico (Baja Peninsula), *T. nebulosa* (Van Denburgh, 1895: 84), was included in molecular phylogenetic analyses by Wiens et al. (2010) and Rödder et al. (2013). These investigators reported, with very low probabilities, an erroneous sister group relationship (based on mitochondrial DNA) between *T. nebulosa*

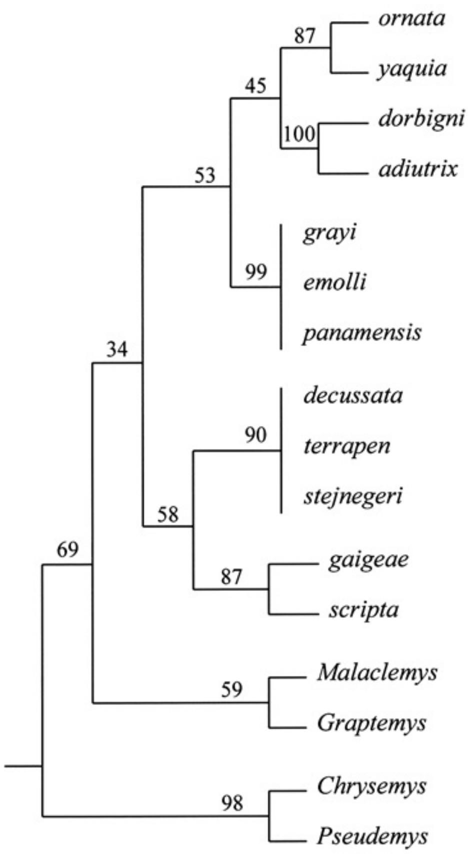


Fig. 69. Phylogeny of *Trachemys* illustrated by a maximum likelihood tree based on analysis of mitochondrial ND4 and tRNA-His genes. Modified from McCranie et al. (2013, fig. 3). Numbers on branches indicate nodal support by 500 bootstrap replicates. The taxon "*ornata*" here includes *callirostris*, *venusta*, *chichiriviche*, *uhrigi*, and *cataspila*; also included are two specimens of unknown origin, believed to be *emolli* and *taylori*. None of the relationships in the *ornata* branch were clearly resolved. Resolution of the three major (basal) clades is also weak, as indicated by bootstrap values 34, 53, 58.

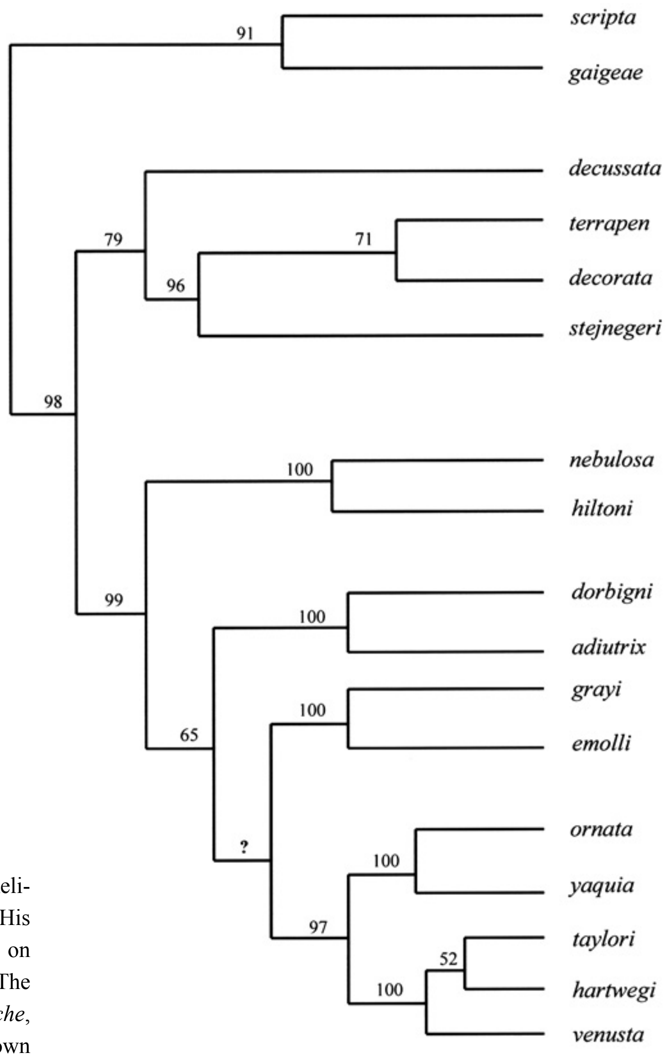


Fig. 70. Phylogenetic relationships among forms of *Trachemys*, determined by sequencing mitochondrial and nuclear DNA. Likelihood bootstrap values appear at nodes. Branch lengths are not drawn to scale, modified from Parham et al. (2015, fig. 2).

and *Malaclemys terrapin* Gray, 1844: 28. Parham et al. (2015) sampled *nebulosa* from Baja California and *hiltoni* from Sonora and Sinaloa. They found these two forms are closely allied sister taxa (Fig. 70), as reported by other authors and considered conspecific subspecies by Seidel (2002a). An endemic Slider from northcentral Mexico (Coahuila), *T. taylori* (Legler, 1960: 75), was examined in three molecular (DNA-based) analyses (Jackson et al., 2008; Spinks et al., 2009a; Parham et al., 2015). All of these studies found *taylori* to be monophyletic and quite distinct, despite reports of hybridization with *T. scripta elegans* (Legler, 1990; Legler and Vogt, 2013).

An additional taxonomic question regarding *Trachemys* in northern Mexico is the status of *hartwegi*. This Slider was described by Legler (1990) as *P.* (*T.*) *scripta hartwegi*. It is endemic to the Rio Nazas, an internal drainage system of Durango and Coahuila. Relying heavily on zoogeographic and geological evidence of stream piracy, Legler (1990) and Legler & Vogt (2013) believed that *hartwegi* is closely related to *gaigeae*. Based on phylogenetic analysis using morphological characters, Seidel (2002a) found support for that hypothesis and classified *hartwegi* as a subspecies of *T. gaigeae*. However, molecular evidence led Forstner et al. (2004) to question that relationship. The recent phylogeny presented by Parham et al. (2015) places *hartwegi* in a clade of MesoAmerican Sliders, broadly divergent from *T. gaigeae*. In this molecular phylogeny, *gaigeae* (somewhat surprisingly) is the sister taxon to *T. scripta* and is divergent from all other *Trachemys* with which it shares the apomorphic loss of titillation behavior (Fig. 70). Based on these results, an argument could be made for elevating *hartwegi* to species status. However, as cited earlier, there is considerable evidence that *gaigeae* and *scripta elegans* hybridize in the Rio Grande system bordering Mexico and the United States (Seidel et al., 1999; Forstner et al., 2004). This might explain their DNA-based phylogenetic affinity, and possibly offer a clue as to why *gaigeae* was not positioned as the sister taxon to *hartwegi* in the large clade of *Trachemys* species which lack titillation. Conservatively, we retain the designation *T. g. hartwegi* until this issue is further resolved.

Seidel and Ernst reviewed the genus *Trachemys* Agassiz, 1857: 252 in the Catalogue of American Amphibians and Reptiles, and presented a dichotomous key for 15 recognized species. Obst (1985), Bringsøe (2001a) and Bour (2003b) also published reviews of the genus. Bour (2003b) and McCord et al. (2010) illustrated excellent color figures of the plastron pattern in hatchlings of various species. Legler (1990) reviewed the Mesoamerican *Trachemys* (under the generic name *Pseudemys*). Accounts of *T. callirostris* (Bock et al., 2010) and *T. gaigeae* (Stuart & Ward, 2009) have been published in Conservation Biology of Freshwater Turtles and Tortoises. Comprehensive reviews of the species published in the Catalogue of American Amphibians and Reptiles include: *T. decorata* (Bickham, 1980), *T. decussata* (Seidel, 1988b), *T. stejnegeri* (Seidel, 1988c), *T. terrapen* (Seidel, 1988d), *T. dorbigni* (Seidel, 1989), *T. gaigeae* (Ernst, 1992; Stuart & Ernst, 2004), *T. taylori* (Seidel, 2002c), *T. callirostris* (Ernst, 2003a), *T. yaquia* (Ernst, 2003b), *T. venusta* (Ernst & Seidel, 2006), *T. scripta* (Seidel & Ernst, 2006), *T. emolli* (Ernst, 2008), *T. ornata* (Ernst & Seidel, 2008), *T. adiutrix* (Ernst et al., 2010), and *T. nebulosa* (Seidel, 2010a). Ernst (1990b), Bringsøe (2001b), and Thomas (2006) also published reviews of *T. scripta*; and Pritchard & Trebbau (1984) and Freiberg (1981) published reviews of *T. callirostris* and *T. dorbigni*, respectively. A comprehensive review of the identification and natural history of *Trachemys* species in Mexico is presented by Legler & Vogt (2013).

Epilogue

Taxonomists generally agree that development of a nomenclatural system should be natural, emphasize stability, represent phylogenetic relationships, and minimize unnecessary innovations of new taxa. In our review of emydid turtles, it is clear that many different phylogenies and classifications have been proposed. Nevertheless, it is our position that the bulk of current evidence supports a hypothesis for relationships among genera in the Emydidae Rafinesque, 1815: 75 (Fig. 71). As the current text was in final review, Spinks et al. (2016) published a comprehensive phylogenetic hypothesis for family Emydidae, based mostly on an expanded data set of nuclear DNA. Our hypothesis (Fig. 71) of generic relationships in the subfamily Deirochelyinae is congruent with theirs, but our illustration of relationships in the subfamily Emydinae is somewhat different. Clearly, there are aspects of the taxonomy of these turtles, especially at the species level, which remain controversial. Some of these will be resolved as theories and techniques become more refined. Nevertheless, there are persistent obstacles in the path to a "conclusive" classification.

As for all organisms, boundaries of the higher taxonomic categories (e.g. subfamilies and genera) are subjectively defined. They are hierarchical, monophyletic units, but there is no consensus regarding their measure of divergence. In contrast, it has been suggested that "species" is the most important level of classification, and is the only unit which has biological reality. However, there are multiple operational definitions for the species unit (e.g. phylogenetic, biological, evolutionary) and different views as to how they should be applied to our classification of emydid turtles. There are also various opinions regarding information content of higher taxa, especially genus level (Shaffer et al., 2007). For species which share an exclusive ancestor, assigning them to a single polytypic genus adds phylogenetic information to the binomial (e.g. *Emys*, sensu Parham & Feldman, 2002). Nevertheless, if this practice is overly inclusive, it can mask recognition of basal divergence and evolutionary distinctiveness (i.e. anagenesis, sensu Mayr & Bock, 2002). From a conservation perspective, it could be argued that threatened forms which are monotypic should receive first priority. Thus, some authors of emydid taxonomy favor recognition of select monotypic genera, emphasizing unique characters and extensive divergence (Iverson et al., 2012). As phylogenetic data accumulate at a rapid pace, it is not surprising that taxonomists are promoting innovative and often controversial solutions for classification (e.g. the Phylocode; de Queiroz & Gauthier, 1992, 1994).

Natural hybridization and introgression among turtles in the family Emydidae are well documented (Ernst & Lovich, 2009), and populations influenced by introgression can be difficult to classify. The problem is often exacerbated by human disturbance such as habitat alteration and geographic translocation of turtles (Seidel, 1988d; Adler, 2007; Buhlmann et al., 2008a, p. 149). Such activities may remove reproductive barriers by creating artificial microhabitats and unnatural sympatry. Our nomenclatural system for emydid turtles does not adequately accommodate classification of populations with frequent hybridization and high levels of admixture. We have noted that this condition probably contributes to the poorly resolved species taxonomy in genera such as *Graptemys*, *Pseudemys*, and *Trachemys*. If disruption of natural populations continues at its present rate, it will become increasingly difficult to obtain taxonomic consensus for many populations of emydid turtles.

Another challenge to the common goals of emydid systematists is how to assimilate conflicting data sets. We have noted examples of morphology-based phylogenies which are discordant with those based on molecular data (e.g. Stephens & Wiens, 2003; Seidel, 2002a and Fritz et al., 2012). Morphological phenotypes may be the result of environmental induction rather than genes, or parallel evolution yielding homoplasies. In some instances, suites of morphological characters may be the product of a single developmental gene mutation. Similar concerns involve determination of how many nucleotide-sequence variants are the products of a single evolutionary event.

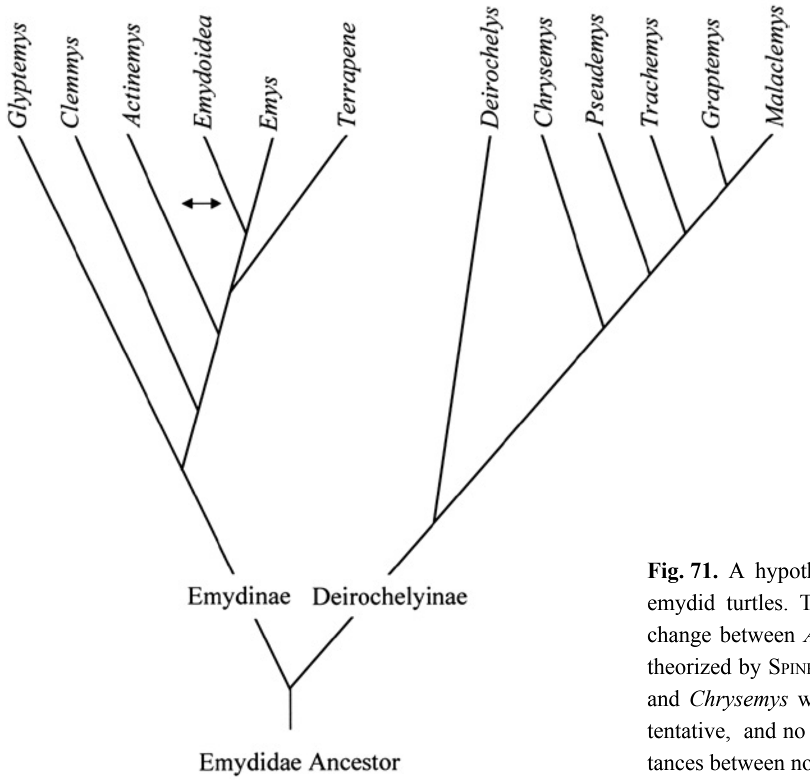


Fig. 71. A hypothesis of relationships among extant genera of emydid turtles. The arrow indicates probable ancient gene exchange between *Actinemys* and *Emydoidea* (see p. 27 in text) as theorized by Spinks & Shaffer (2009). The positions of *Clemmys* and *Chrysemys* within their respective subfamilies remain very tentative, and no significance is implied by branch lengths or distances between nodes.

Discordance between emydid phylogenies based on mitochondrial DNA and those based on nuclear DNA has also been well documented, and attributed to problems of introgression or lineage sorting (Spinks & Shaffer, 2009; Wiens et al., 2010). Currently, hypotheses based on nuclear DNA appear to be viewed as more reliable (Spinks et al., 2016). Compounding matters, selection of different subsets or single-exemplars of emydid samples can produce markedly different phylogenies (Spinks et al., 2013). Refinement of techniques and character selection, combined with broader population sampling, should help resolve some of these conflicts.

In conclusion, perhaps the most persistent obstacle to a flawless natural taxonomy for the Emydidae Rafinesque, 1815: 75 is the dynamic nature of the turtles themselves. Genetic studies over the last twenty years suggest that the complexity of emydid populations may exceed the potential to finitely categorize them. George Gaylord Simpson (1980) stated that classification is an artifice with no objective reality. It arises and exists only in the minds of its devisers, learners, and users. With these limitations, the discipline of systematics continues to provide us greater levels of accuracy, consensus, and stability for the taxonomy of emydid turtles.

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Table 1. Extant Taxa Assigned to the Family Emydidae

- Subfamily Emydinae Rafinesque, 1815: 75
  - *Emys* Duméril, 1805: 76
    - *Emys orbicularis* (Linneaus, 1758: 198) [Type species]
      - *E. o. orbicularis* (Linneaus, 1758: 198)
      - *E. o. eiselti* Fritz, Baran, Budak & Amthauer, 1998: 113
      - *E. o. galloitalica* Fritz, 1995b: 217
      - *E. o. hellenica* (Valenciennes, 1832: 61)
      - *E. o. ingauna* Jesu, Piombo, Salvidio, Lamagni, Ortale & Genta, 2004: 176
      - *E. o. occidentalis* Fritz, 1993: 131
      - *E. o. persica* Eichwald, 1831: 196
    - *Emys trinacris* Fritz, Fattizzo, Guicking, Tripepi, Pennisi, Lenk, Joger & Wink, 2005b: 364
  - *Actinemys* Agassiz, 1857: 252
    - *Actinemys marmorata* (Baird & Girard, 1852: 177) [Type species]
    - *Actinemys pallida* (Seeliger, 1945: 158)
  - *Clemmys* Ritgen, 1828: 270
    - *Clemmys guttata* (Schneider, 1792: 264) [Type species]
  - *Emydoidea* Gray, 1870: 19
    - *Emydoidea blandingii* (Holbrook, 1838: 35) [Type species]
  - *Glyptemys* Agassiz, 1857: 252
    - *Glyptemys muhlenbergii* (Schoepff, 1801: 132) [Type species]
    - *Glyptemys insculpta* (Le Conte, 1830: 112)
  - *Terrapene* Merrem, 1820: 27
    - *Terrapene carolina* (Linnaeus, 1758: 198) [Type species]
      - *T. c. carolina* (Linnaeus, 1758: 198)
      - *T. c. bauri* Taylor, 1895: 576
      - *T. c. major* (Agassiz, 1857: 445)
      - *T. c. mexicana* (Gray, 1849: 17) [further study may substantiate elevation to species status with *triunguis* and *yucatana* as subspecies, Martin et al., 2013]
      - *T. c. triunguis* (Agassiz, 1857: 279)
      - *T. c. yucatana* (Boulenger, 1895: 330)
    - *Terrapene coahuila* Schmidt & Owens, 1944: 101
    - *Terrapene nelsoni* Stejneger, 1925: 463
      - *T. n. nelsoni* Stejneger, 1925: 463
      - *T. n. klauberi* Bogert, 1943: 2
    - *Terrapene ornata* (Agassiz, 1857: 392)
      - *T. o. ornata* (Agassiz, 1857: 392)
      - *T. o. luteola* Smith & Ramsey, 1952: 45
- Subfamily Deirochelyinae Agassiz, 1857: 355
  - *Deirochelys* Agassiz, 1857: 252
    - *Deirochelys reticularia* (Latreille, *in* Sonnini & Latreille, 1802: 124) [Type species]
      - *D. r. reticularia* (Latreille, *in* Sonnini & Latreille, 1802: 124)
      - *D. r. chrysea* Schwartz, 1956: 467
      - *D. r. miaria* Schwartz, 1956: 467
  - *Chrysemys* Gray, 1844: 27
    - *Chrysemys picta* (Schneider, 1783: 348) [Type species]
      - *C. p. picta* (Schneider, 1783: 348)
      - *C. p. bellii* (Gray, 1831a: 12)
      - *C. p. dorsalis* Agassiz, 1857: 439
      - *C. p. marginata* Agassiz, 1857: 262
  - *Graptemys* Agassiz, 1857: 252
    - *Graptemys geographica* (Le Sueur, 1817: 86) [Type species]
    - *Graptemys barbouri* Carr & Marchand, 1942: 98
    - *Graptemys caglei* Haynes & McKown, 1974: 143
    - *Graptemys ernsti* Lovich & McCoy, 1992: 293
    - *Graptemys flavimaculata* Cagle, 1954: 167
    - *Graptemys gibbonsi* Lovich & McCoy, 1992: 293

  - *Graptemys nigrinoda* Cagle, 1954: 173
  - *Graptemys oculifera* (Baur, 1890: 262)
  - *Graptemys ouachitensis* Cagle, 1953a: 2
  - *Graptemys pearlensis* Ennen, Lovich, Kreiser, Selman & Qualls, 2010b: 104
  - *Graptemys pseudogeographica* (Gray, 1831b: 31)
    - *G. p. pseudogeographica* (Gray, 1831b: 31)
    - *G. p. kohnii* (Baur, 1890: 263)
  - *Graptemys pulchra* Baur, 1893b: 675
  - *Graptemys sabinensis* Cagle, 1953a: 2
  - *Graptemys versa* Stejneger, 1925: 463
- *Malaclemys* Gray, 1844: 28
  - *Malaclemys terrapin* (Schoepff, 1793: 64) [Type species]
    - *M. t. terrapin* (Schoepff, 1793: 64)
    - *M. t. centrata* (Latreille, *in* Sonnini & Latreille, 1802: 145)
    - *M. t. littoralis* Hay, 1904: 18
    - *M. t. macrospilota* Hay, 1904: 16
    - *M. t. pileata* (Wied-Neuwied, 1865: 17)
    - *M. t. rhizophorarum* Fowler, 1906: 112
    - *M. t. tequesta* Schwartz, 1955: 158
- *Pseudemys* Gray, 1856a: 197
  - *Pseudemys concinna* (Le Conte, 1830: 106) [Type species]
    - *P. c. concinna* (Le Conte, 1830: 106)
    - *P. c. floridana* (Le Conte, 1830: 100)
  - *Pseudemys alabamensis* Baur, 1893a: 224
  - *Pseudemys gorzugi* Ward, 1984: 29
  - *Pseudemys nelsoni* Carr, 1938c: 307
  - *Pseudemys peninsularis* Carr, 1938a: 105
  - *Pseudemys rubriventris* (Le Conte, 1830: 101)
  - *Pseudemys suwanniensis* Carr, 1937: 4
  - *Pseudemys texana* Baur, 1893a: 223
- *Trachemys* Agassiz, 1857: 252
  - *Trachemys scripta* (Thunberg, *in* Schoepff, 1792: 16) [Type species]
    - *T. s. scripta* (Thunberg, *in* Schoepff, 1792: 16)
    - *T. s. elegans* (Wied-Neuwied, 1839: 213)
    - *T. s. troostii* (Holbrook, 1836: 55)
  - *Trachemys adiutrix* Vanzolini, 1995: 111
  - *Trachemys callirostris* (Gray, 1855b: 25)
    - *T. c. callirostris* (Gray, 1855b: 25)
    - *T. c. chichiriviche* (Pritchard & Trebbau, 1984: 191)
  - *Trachemys decorata* (Barbour & Carr, 1940: 409)
  - *Trachemys decussata* (Gray, 1831a: 11)
    - *T. d. decussata* (Gray, 1831a: 11)
    - *T. d. angusta* (Barbour & Carr, 1940: 402)
  - *Trachemys dorbigni* (Duméril & Bibron, 1835: 272)
    - *T. d. brasiliensis* (Freiberg, 1969: 301)
    - *T. d. dorbigni* (Duméril & Bibron, 1835: 272)
  - *Trachemys gaigeae* (Hartweg, 1939: 1)
    - *T. g. gaigeae* (Hartweg, 1939: 1)
    - *T. g. hartwegi* (Legler, 1990: 89)
  - *Trachemys grayi* (Bocourt, 1868: 121) [Recognition of this polytypic species follows Fritz et al., 2012]
    - *T. g. grayi* (Bocourt, 1868: 121)
    - *T. g. emolli* (Legler, 1990: 91)
    - *T. g. panamensis* McCord, Joseph-Ouni, Hagen, & Blanck, 2010: 46
  - *Trachemys nebulosa* (Van Denburgh, 1895: 84)
    - *T. n. nebulosa* (Van Denburgh, 1895: 84)
    - *T. n. hiltoni* (Carr, 1942: 1)
  - *Trachemys ornata* (Gray, 1831a: 12)
  - *Trachemys stejnegeri* (Schmidt, 1928: 147)
    - *T. s. stejnegeri* (Schmidt, 1928: 147)

  T. s. malonei (Barbour & Carr, 1938: 76)
  T. s. vicina (Barbour & Carr, 1940: 408)
Trachemys taylori (Legler, 1960: 75)
Trachemys terrapen (Bonnaterre, 1789: 30)
Trachemys venusta (Gray, 1856b: 24) [Recognition of this species is tentative pending further study]
  T. v. venusta (Gray, 1856b: 24)
  T. v. cataspila (Günther, 1885: 4)
  T. v. iversoni McCord, Joseph-Ouni, Hagen & Blanck, 2010: 45
  T. v. uhrigi McCord, Joseph-Ouni, Hagen & Blanck, 2010: 43 [validity of this taxon is questionable; Fritz et al., 2012, McCranie et al., 2013]
Trachemys yaquia (Legler & Webb, 1970: 157)

Glossary of currently used scientific names for living turtles in the family Emydidae

Derivations of the names are those given by the original author of the taxon or are based on **Brown** (1956), **Jaeger** (1944), or accounts in the Catalog of American Amphibians and Reptiles.

Actinemys	ray or beam turtle; referring to the carapacial pattern
adiutrix	a feminine helper, referring to field assistant **Maria do Socorro**
alabamensis	belonging to, or from, Alabama
angusta	narrow, referring to the carapace which is normally less broad than in the nominate subspecies
barbouri	a proper name honoring Museum of Comparative Zoology herpetologist **Thomas Barbour**
bauri	a proper name honoring Bohemian [Czech Republic] born, Clark University professor, and early researcher of the genus *Terrapene*, **Georg H. C. L. Baur**
bellii	a proper name honoring British testudinologist **Thomas Bell**
blandingii	a proper name honoring Philadelphia naturalist **William Blanding**, who first observed the turtle
brasiliensis	belonging to, or from, Brazil
caglei	a proper name honoring Tulane University testudinologist **Fred R. Cagle**
callirostris	beautiful nose, referring to the orange rostral pattern
carolina	belonging to, or from, the Carolina region
cataspila	downward or inferior spot, referring to the position of the dark spot on the pleural scutes of the carapace
centrata	midpoint of a circle, point; referring to the configuration of growth annuli on each carapacial scute
chichiriviche	referring to the type locality, a hill in Edo, Falcon, Venezuela
chrysea	gold; referring to the color of the carapacial rim or plastron
Chrysemys	golden turtle; referring to the yellow head and shell markings
Clemmys	a tortoise
coahuila	belonging to, or from, Coahuila, Mexico
concinna	skillfully joined, neatly arranged; probably referring to the relatively smooth shell
decorata	elegantly marked, referring to the carapace pattern
decussata	beauty or splendor; probably referring to the markings of young individuals
Deirochelyinae	the subfamily of *Deirochelys*-like turtles
Deirochelys	hill, or hump, turtle, referring to the domed carapace of the female (*or* "apparently an allusion to the extremely long neck" **Zug & Schwartz**, 1971)
dorbigni	a proper name honoring French naturalist and paleontologist **Alcide C. V. D'Orbigny**
dorsalis	the back; referring to the prominent middorsal stripe on the carapace
eiselti	a proper name honoring the Austrian herpetologist **Josef Eiselt**, an authority on the herpetofauna of the Middle East
elegans	choice or elegant, referring to the refined markings on the skin and shell
emolli	a proper name honoring American testudinologist **Edward O. Moll**
Emydidae	the family of *Emys* [including *Deirochelys*] – like turtles
Emydinae	the subfamily of *Emys*-like turtles
Emydoidea	*Emys*-like; referring to the resemblance with the genus *Emys*
Emys	a tortoise
ernsti	a proper name honoring the American testudinologist **Carl H. Ernst**
flavimaculata	yellow-spotted, referring to the large yellow spots on the carapace
gaigeae	a proper name honoring University of Michigan herpetologist **Helen T. Gaige**
galloitalica	from Gaul, France, and Italrea, Italy; indicating the regional distribution of the taxon
geographica	geographic, map-like; referring to the carapacial pattern resembling contour lines on a map
gibbonsi	a proper name honoring University of Georgia turtle ecologist **J. Whitfield Gibbons**
Glyptemys	carved turtle; referring to the sculptured carapace
gorzugi	a proper name honoring Smithsonian Institution herpetologist **George R. Zug**
Graptemys	inscribed turtle; probably referring to the carapacial pattern
grayi	a proper name honoring **John E. Gray** of the British Museum of Natural History [The Natural History Museum], London
guttata	spotted, referring to the scattered yellow spots on the carapace
hartwegi	a proper name honoring University of Michigan herpetologist **Norman E. Hartweg**

hellenica	belonging to, or from, Greece; referring to the type-locality, central Messina, Peloponnese, Greece
hiltoni	a proper name honoring **John W. Hilton**, collector of the type-series
ingauna	a proper name honoring the Ingauni, an ancient Ligurian people, who once lived in the distributional region of the taxon
insculpta	engraved, sculptured; referring to the growth annuli on the carapacial scutes
iversoni	a proper name honoring American testudinologist **John B. Iverson**
klauberi	a proper name honoring the American herpetologist **Laurence M. Klauber**
kohnii	a proper name honoring the New Orleans turtle collector **Gustave Kohn**, who provided the type-specimen
littoralis	of the seashore; referring to the littoral zone habitat of the turtle
luteola	yellowish, referring to the turtle’s basic coloration
macrospilota	large spotted; referring to large yellow spot on each carapacial scute
major	larger, greater; referring to its greater carapace length
Malaclemys	soft tortoise, apparently referring to the “soft spongy skin” on its head
malonei	a proper name honoring **J. V. Malone**, one of the party that collected the type-specimen
marginata	margin, edge, border; referring to the scute border pattern on the carapace
marmorata	marbled; referring to the carapacial pattern
mexicana	belonging to, or from, Mexico
miaria	stained; referring to the dark plastral pattern
muhlenbergii	a proper name honoring the colonial Pennsylvania, pastor-naturalist, **Gotthilf H.E. Muhlenberg**
nebulosa	dark, cloudy, misty, indefinite; referring to the obscure dark ocelli-like markings on the pleural scutes of the carapace
nelsoni, (*Pseudemys*)	a proper name honoring **George Nelson**, chief preparator at the Museum of Comparative Zoology, Harvard
nelsoni, (*Terrapene*)	a proper name honoring **Edward W. Nelson**, former chief of the United States Biological Survey, a member of the team that collected the type-specimen
nigrinoda	black-knobbed, referring to the raised vertebral scutes
occidentalis	western or westerly; referring to the turtle’s range in northwestern Africa
oculifera	eye-bearing; referring to the pattern of light ocelli on the carapace
orbicularis	rounded, circular; referring to the rounded, flat carapace
ornata	ornate, decorated; referring to the carapace and plastron patterns
ouachitensis	belong to, or from, the Ouachita River, Louisiana
pallida	pale, referring to the turtle’s overall lighter color than the nominate subspecies
panamensis	belonging to, or from, Panama
pearlensis	belonging to, or from, the Pearl River, Mississippi
peninsularis	pertaining to a peninsula; referring the turtle’s restriction to peninsular Florida
persica	belong to, or from Persia (Iran)
picta	painted; referring to the colorful carapacial pattern
pileata	capped, covered with a cap; referring to the dark dorsal surface of the head
Pseudemys	false turtle, false *Emys*
pseudogeographica	not genuine map-like; referring to its resemblance of *Graptemys geographica*
pulchra	beautiful, referring to its markings
reticularia	netted; referring to the carapacial net-like pattern
rhizophorarum	named for the mangrove genus *Rhizophora*, referring to the mangrove habitat of the type-locality, Boca Grande Key, Lee County, Florida
rubriventris	red venter; referring to the reddish color of the plastron
sabinensis	belonging to, or from, the Sabine River, Louisiana
scripta	written; referring to the letter-like markings on the carapace
stejnegeri	a proper name honoring Smithsonian Institution herpetologist **Leonhard H. Stejneger**
suwanniensis	belong to, or from, the Suwannee River, Florida
taylori	a proper name honoring University of Kansas herpetologist **Edward H. Taylor**
tequesta	a proper name honoring the native American Tequesta tribe of eastern Florida
terrapen	a turtle
Terrapene	from the native American Algonquin name for a turtle
terrapin	a turtle
texana	belonging to, or from, Texas
Trachemys	rough turtle, referring to the roughened annuli on the carapace pleural scutes

trinacris	Trinacria, the Ancient Greek name for Sicily
triungius	three-clawed; referring to the three toes on each hind foot
troostii	a proper name honoring Tennessee naturalist **Gerard Troost**
uhrigi	a proper name honoring **Dennis Uhrig**, who (following **Legler**, 1990) recognized the uniqueness of the taxon
venusta	elegant, charming; referring to the ornate carapace and plastron patterns
versa	turned, changed; referring to the head pattern differing from that of *Graptemys pseudogeographica*
vicina	similar, close, or related to; presumably referring to the similarity between *Trachemys* turtles from Hispaniola and Puerto Rico
yaquia	a proper name referring to the indigenous native American tribe that formerly lived in the area of Sonora, Mexico, where the turtle is found.
yucatana	belonging to, or from, the Yucatan region of Mexico