

2. EVOLUTION

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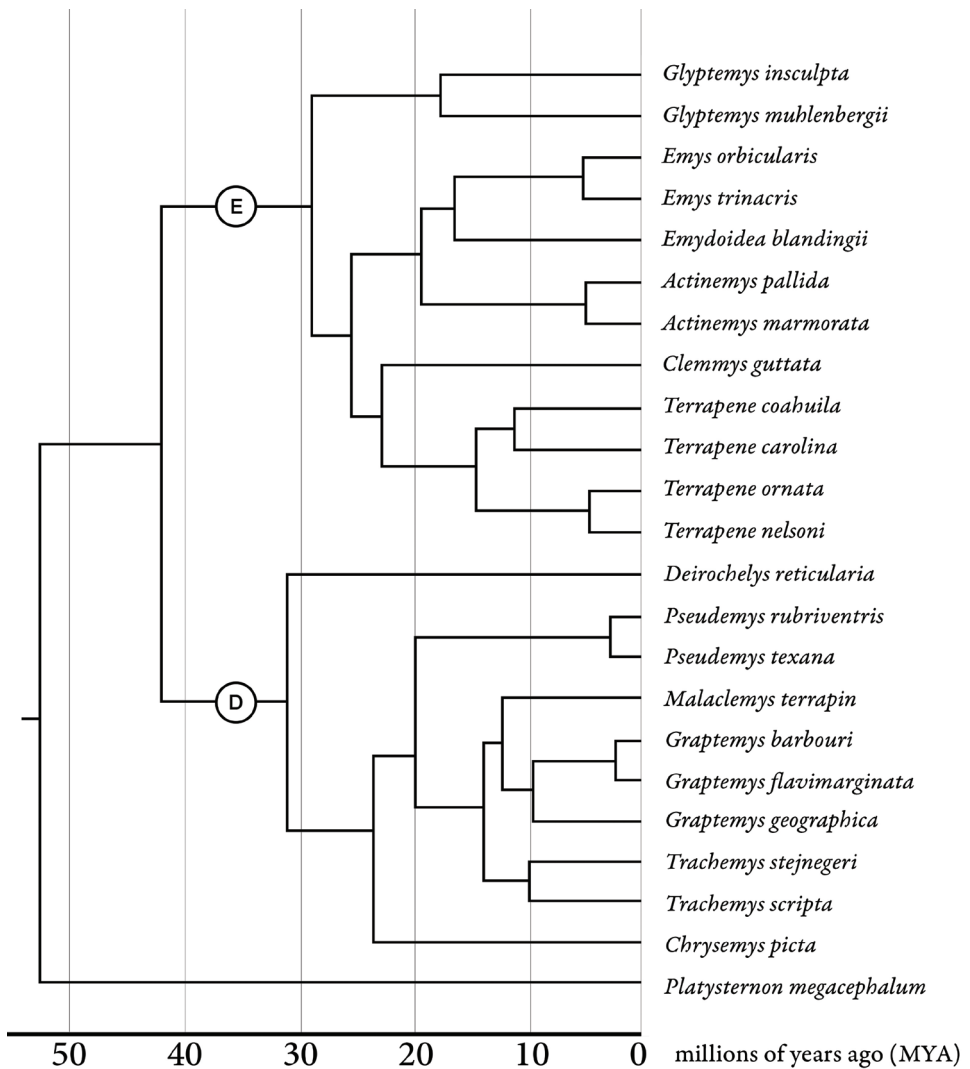
Juvenile Wood Turtle, Massachusetts. MIKE JONES

Introduction

The Wood Turtle, *Glyptemys insculpta*, has arrived at a turning point in its evolutionary history, having never previously encountered the suite of environmental challenges that it is currently experiencing. These anthropogenic challenges include: (1) rapid habitat destruction and fragmentation; (2) increased mesopredator abundance; (3) rapidly-changing precipitation and flooding patterns; and (4) decades of intense collection for the biological supply and pet trades. Natural selection—and millions of years of adaptation—have resulted in a species that requires large tracts of unfragmented, variable (yet specific) habitat with naturally low predator density, and high adult annual survivorship rates (Compton et al. 2002; Lapin et al. 2019). Within this adaptive context, the Wood Turtle has evolved a unique suite of survival adaptations. If we are to preserve the evolutionary potential of the Wood Turtle—or, at a pitiable minimum, prevent this species from joining the list of turtles that will disappear during the anthropogenic sixth mass extinction (Barnosky et al. 2011; Ceballos et al. 2015)—we must continue to investigate the species' evolutionary context, while reducing the negative influence of human activity on Wood Turtle populations across its range.

Despite evolving and surviving for millions of years in the presence of procyonines (raccoons), mustelids (e.g., weasels, skunks, otters), and other mesopredators, Wood Turtle populations have likely not encountered mesopredator densities of the current magnitude in the past (Zaveloff 2002; Harding 2008). The assortment of predator defenses that *G. insculpta* has evolved include: (1) morphological features (strong shell, thickened scales on the forelimbs); (2) behavioral responses (head retraction, strong home site fidelity, limited homing ability, responsiveness to river dynamics); and (3) environmental (cryptic basking in dense vegetative cover, hiding in forms and under flood debris in terrestrial habitats, utilizing aquatic habitats, and avoiding exposure to terrestrial predators when there is little thermal benefit to aerial exposure). These adaptations may not be as effective against narrow-snouted mesopredators—which can penetrate a hingeless shell—as they were against larger predators (e.g., canids) that formerly regulated mesopredator populations and kept their densities in check (Harding 2008). Perhaps more importantly, the Wood Turtle's unique evolutionary adaptations do not provide adequate protection from machinery (e.g., Saumure and Bider 1998; Saumure et al. 2007) and people (e.g., Garber and Burger 1995).

The earliest members of the genus *Glyptemys* evolved from an emydine ancestor during the Miocene Epoch (Holman and Fritz 2001; Montiel et al. 2016). Already by that point, the emydine lineage of Wood, Bog, Box, Blanding's, and Spotted Turtles had differentiated from its sister lineage, the Deirochelyinae. The Wood Turtle itself had differentiated well before the ice ages of the Pleistocene epoch, and during the post-glacial Holocene epoch, has maintained a distribution at middle latitudes in eastern North America (Ernst and Lovich 2009). This species has survived numerous climate cycles in its evolutionary past, ice ages and intervening warming periods, new assemblages of competitors and predators, and has responded to the changes associated with the advance and retreat of continental ice sheets by altering its range (Holman 1967; Parmalee and Klippel 1981; Tessier et al. 2005; Amato et al. 2007). The Wood Turtle, or its direct ancestors, evolved sex chromosomes during a prior period of global warming; thus, effectively decoupling changes in environmental temperature from population sex ratios (Valenzuela and Adams 2011; Montiel et al. 2016; Literman et al. 2017), differentiating this species from most other living turtles.



2.1—The freshwater turtle family Emydidae—the Pond Turtles—is comprised of two major lineages that likely diverged in the Eocene epoch and diversified throughout the Oligocene and Miocene epochs: subfamily Deirochelyinae, which includes the aquatic genera *Chrysemys*, *Pseudemys*, *Graptemys*, *Malaclemys*, *Trachemys*, and *Deirochelys*, and the subfamily Emydinae, which includes the semi-aquatic and terrestrial genera *Clemmys*, *Terrapene*, *Emydoidea*, *Emys*, *Actinemys*, and *Glyptemys*. The two subfamilies are denoted on the tree with a “D” and “E” symbol, respectively. Wood Turtles (*Glyptemys insculpta*) are placed within the subfamily Emydinae on the basis of morphological and molecular characters. According to the most current and most comprehensive evaluation (Spinks et al. 2016), the genus *Glyptemys* (Wood and Bog Turtles) probably diverged from other emydine genera in the Oligocene epoch, toward the end of the Paleogene Period. The placement of the Spotted Turtle (*Clemmys guttata*) remains unresolved, which may in part be caused by short internode lengths early in the emydine lineage. The genera *Emys*, *Actinemys*, and *Emydoidea* are grouped into a holarctic genus, *Emys*, by Spinks et al. (2016) and others. This tree is based on the divergence analysis provided by Spinks et al. (2016), with modifications based on Angielczyk et al. (2010). For more details and additional discussion, see Spinks et al. (2016).

Phylogeny

The Wood Turtle is placed within the genus *Glyptemys* with a single congener, the Bog Turtle (*G. mublenbergii*) of the central and southern Appalachian Mountains. The genus *Glyptemys* is placed within the subfamily Emydinae, which encompasses at least 11 North American and European species in the four major clades, roughly corresponding to the genera *Glyptemys*, *Emys* (including *Emys*, *Emydoidea*, and *Actinemys*), *Clemmys*, and *Terrapene* (2.1). The genus *Glyptemys* may be the sister taxon to a clade that includes the other emydine genera (Spinks et al. 2016). The Emydinae are the sister group to the Deirochelyinae, which includes the Sliders (*Trachemys*), Cooters (*Pseudemys*), Painted Turtles (*Chrysemys*), Map Turtles (*Graptemys*), Diamondback Terrapins (*Malaclemys*), and Chicken Turtles (*Deirochelys*). Together, these two subfamilies encompass the family Emydidae, which is mostly distributed in North America, with a few representatives in South America and Europe. The emydids are a remarkably diverse group of freshwater turtles, the result of a diversifying trend since the Oligocene (Vlachos 2018). The emydine species differ from the deirochelyines in that they are generally more terrestrial, longer-lived, later to reach maturity, and smaller.

The Wood Turtle was classified in the genus *Clemmys* (Ritgen 1828) for most of the 20th century (Strauch 1862; Babcock 1919). In the sense of McDowell (1964), *Clemmys* encompassed three North American species in addition to the Wood Turtle. These were the Spotted Turtle (*C. guttata*), Bog Turtle (*C. mublenbergii*), and Western (or Pacific) Pond Turtle (*C. marmorata*). Holman and Fritz (2001) note that McDowell's arrangement of *Clemmys* (in the broad sense) was based on plesiomorphic (basal) rather than synapomorphic (derived) traits, including an unhinged plastron, buttressed bony bridges connecting the plastron to the carapace, and the lack of a scapular suspensorium as described by Bramble (1974).

Beginning in the late 1980s, several authors critically re-evaluated the relationships within *Clemmys* (Gaffney and Meylan 1988; Lovich et al. 1991). Several authors subsequently provided evidence that the traditional genus *Clemmys* was made paraphyletic¹ by not including the sister genera *Emys* and *Emydoidea* (which are more closely related to *Actinemys* [formerly *Clemmys*] *marmorata* than to either *G. insculpta* or *G. mublenbergii*) and possibly also the Box Turtles, *Terrapene* (Bickham et al. 1996; Burke et al. 1996; Lenk et al. 1999; Holman and Fritz 2001; Ernst 2001a; Feldman and Parham 2002; Seidel and Wood 2002; Stephens and Wiens 2003; Wiens et al. 2010; Fritz et al. 2011; see Crother 2017). Burke et al. (1996) speculated on possible reconfigurations of the emydine taxa to resolve the clear paraphyly of *Clemmys*, as broadly defined. Their recommendations included combining most species (except *G. insculpta* and *G. mublenbergii*) into *Emys*; although, this would have obscured clearly monophyletic lineages and distinct genera groups. Holman and Fritz (2001) reassigned the Wood Turtle from *Clemmys* to *Glyptemys* (Agassiz 1857) and Feldman and Parham (2002) reassigned the Wood Turtle from *Clemmys* to *Calemys* (Agassiz 1857) without reference to Holman and Fritz. *Glyptemys* and *Calemys* occur on the same page for Wood Turtle and Bog Turtle, respectively, in the original publication by Agassiz (1857, Vol. 1). Although *Calemys* is listed first in Agassiz (1857), *Glyptemys* was selected by Holman and Fritz (2001) based mostly on preference, using the principle of the first reviser.

1 Paraphyly is an evolutionary concept that describes a taxonomic group of animals (e.g., Class Reptilia) containing a common ancestor and only some (e.g., turtles, lepidosaurs, and crocodylians) of the living descendants. In the case of Reptiles, the group has excluded birds, which are more closely related to crocodylians than either are related to lizards, snakes, Rhychocephalians, or turtles. If a group is paraphyletic, it means that some members of the related group have been placed into another group.



2.2—Wood Turtles have hybridized with Blanding’s Turtles (*Emydoidea blandingii*) under rare conditions in captivity. Hybrids appear intermediate between the two species. JAMES HARDING



2.3—Bog Turtles (*Glyptemys mublenbergii*) are the Wood Turtle’s closest living relative and the only other living species in the genus *Glyptemys*. The two species likely diverged in the Miocene epoch of the Neogene Period. The two, living *Glyptemys* species historically occurred in close proximity in the northern part of the Bog Turtle’s range from Massachusetts to Maryland. *Top left*: an adult female Bog Turtle from North Carolina (MIKE KNOERR). *Top right*: adult male Bog Turtle from New Jersey (MIKE JONES). *Bottom right*: hatchling Bog Turtle from North Carolina (MIKE KNOERR). *Bottom left*: plastron of an adult male Bog Turtle from Massachusetts (MIKE JONES).

The current taxonomy of the Emydinae remains unresolved. Most areas of concern pertain primarily to the final status of the genera *Actinemys*, *Emydoidea*, and *Emys*, or to the species-level divisions within the Eastern Box Turtle clade (*Terrapene carolina* sensu lato). All authors agree that the Wood and Bog Turtles form a living monophyletic clade within the subfamily Emydinae (Bickham et al. 1996; Burke et al. 1996; Lenk et al. 1999; Holman and Fritz 2001; Feldman and Parham 2002). Hybridization between a female Wood Turtle and at least one male Blanding's Turtle has been reported by Harding and Davis (1999) (2.2).

Subfamily Emydinae

Genus *Glyptemys*

The genus *Glyptemys* (Agassiz 1857) contains two living species, *G. insculpta* and *G. mublenbergii*. Wood Turtles being the focus of this entire book, will not be further discussed here. The Wood Turtle's congener and sister taxon, the Bog Turtle (*G. mublenbergii*) is a much smaller turtle that rarely exceeds 100 mm in carapace length (Ernst and Lovich 2009) (2.3). Bog Turtles have a disjunct distribution, with one primary area of occurrence extending from Massachusetts to Maryland and another extending from Virginia to northern Georgia. Outlying populations occur on the Lake Ontario plain, and formerly in the vicinity of Lake George, New York. Bog Turtles are a species of open, graminoid-dominated bogs and fens, often with a hydrology characterized by groundwater seepages, rills, and springheads (Ernst and Lovich 2009).

Genus *Emys*

The genus *Emys* (Duméril 1806) contains three well-defined lineages generally referred to the individual genera *Emys*, *Emydoidea*, and *Actinemys* (2.4). In this strict sense, *Emys* contains a species complex that includes the European Pond Turtles (*Emys orbicularis*), which extend from the Iberian Peninsula to the Caspian shore of Iran (Fritz et al. 2009), including many of the Mediterranean, Adriatic, and Aegean islands. Throughout this enormous region, *E. orbicularis* may be found in clear-flowing rivers, ephemeral wetlands, ponds and reservoirs, marshes, agricultural ditches, and coastal lagoons. The genus *Emydoidea* contains a single species, Blanding's Turtle (*E. blandingii*), which ranges from Nebraska to Ontario, with outlying populations in the Hudson Valley of New York, east-Central New England, and the Kejimikujik region of southern Nova Scotia (Compton 2007). Blanding's Turtles occur occasionally in large rivers, but are primarily a species of large and deep marshes, shrub swamps, and ephemeral pools. Finally, the genus *Actinemys* contains two recognized species, the Western Pond Turtles (*A. marmorata* and *A. pallida*). These species historically ranged continuously from the Coast Ranges of Oregon to the Sierra Juarez of Baja California, with outlying occurrences near Puget Sound, Washington (Fisher 2018); the Mojave River, California (Lovich and Meyer 2002); and the Sierra San Pedro Mártir of Baja California (Grismer 2002). Recently, an extreme southern outlier was discovered in a palm oasis of the Vizcaino Desert of central Baja California (Valdez-Villavicencio et al. 2016), perhaps the most disjunct and isolated of any North American emydine occurrence. More than its congeners, the Western Pond Turtles are often associated with flowing streams.

Genus *Clemmys*

The genus *Clemmys* (Ritgen 1828) contains a single living species, the Spotted Turtle (*C. guttata*), which ranges along the Atlantic Coastal Plain and adjacent piedmont from southern Maine to north-central Florida, and from western Pennsylvania to Indiana and Illinois (2.5). Within this area, Spotted Turtles occur in a wide range of shallow and ephemeral wetlands, including interdunal swales, vernal pools, and forested swamps dominated by Sweetgum



2.4—The clade *Emys* includes at least two species on the Pacific coast of North America from Washington to Baja California, a single species in east-central North America from Nebraska to Nova Scotia, and a species complex in southern Europe and northern Africa. Three distinct clades within this group are usually referred to the genera *Actinemys*, *Emydoidea*, and *Emys*. *Top left*: Western Pond Turtle (*Actinemys pallida*). *Top right*: Western Pond Turtle (*Actinemys marmorata*). *Bottom right*: adult female Blanding's Turtle (*Emydoidea blandingii*). MIKE JONES. *Bottom left*: adult European Pond Turtle (*Emys orbicularis*). ALEXANDRE ROUX



2.5— The genus *Clemmys* includes a single species, the Spotted Turtle (*Clemmys guttata*), which co-occurs with the Wood Turtle in southern New England, New York, New Jersey, Pennsylvania, and western Michigan. An adult female from Massachusetts is pictured. MIKE JONES

(*Liquidambar styraciflua*), tupelo (*Nyssa* spp.), Baldcypress (*Taxodium distichum*), Red Maple (*Acer rubrum*), or Tamarack (*Larix laricina*). Spotted Turtles occur on many offshore and barrier islands from Massachusetts to North Carolina; southern populations are generally found further inland (Ernst and Lovich 2009).

Genus *Terrapene*

The genus *Terrapene* includes 4–8 species of North American Box Turtle (2.6). Well-resolved species include: (1) the Spotted Box Turtle (*Terrapene nelsoni*), which ranges the crest of Mexico's Sierra Madre Occidental (Buskirk and Ponce-Campos 2011); (2) the Ornate Box Turtle (*Terrapene ornata*), a grassland species found from the Sonoran and Chihuahuan grasslands of Arizona, New Mexico, Texas, and Sonora (Legler and Vogt 2013) to a series of isolated relictual occurrences in Wisconsin and Illinois; and (3) the Coahuila Box Turtle (*T. coahuila*), which is known only from marl-pools and springs in the Chihuahuan Desert of Cuatrocienegas, Coahuila, Mexico (Howeth and Brown 2011). Finally, there is a group of about five species that historically grouped within the superspecies *T. carolina* (Dodd 2001). These include: (1) the Florida Box Turtle (*T. bauri*); (2) the Yucatán Box Turtle (*T. yucatanana*); (3) the Mexican Box Turtle (*T. c. mexicana*); (4) the Three-toed Box Turtle (*T. c. triunguis*), and (5) Eastern or Woodland Box Turtle (*T. c. carolina*). A very large and mysterious form known as the Gulf Coast Box Turtle (*T. c. major*) occurs in the large river basins near the Gulf of Mexico coast; this may actually be an introgressed form of the Pleistocene Giant Box Turtle (*T. putnami*) (Butler et al. 2011; Martin et al. 2013; Kiester and Willey 2015; Martin et al. 2020).

Fossil Record

Miocene

The genus *Glyptemys* appears first in the middle to Late Barstovian (Middle Miocene) of the Niobrara River Valley of northern Nebraska (ca. 14.5–11.5 million ybp, Holman and Fritz 2001; Ernst and Lovich 2009).² The species found in this area has been assigned to *Glyptemys valentinensis* (Holman and Fritz 2001), which may have given rise to *G. insculpta* in the Middle Miocene between the Late Barstovian and Late Hemphillian times (11.5–5.5 million ybp). *Glyptemys valentinensis* differs from *G. insculpta* primarily in its average body size, which is smaller than the modern species, although not as small as the 1850s adult *G. insculpta* measured by Jones et al. (2019). In addition, *G. valentinensis* had a less prominently serrate posterior carapace margin. The holotype for this species, UNSM 76564, is a remarkably complete carapace that was originally identified as Painted Turtle (*Chrysemys picta*) by Holman and Sullivan (1981) (2.7).

Pleistocene

Pleistocene-age fossils suggest that Wood Turtles occupied portions of their contemporary range during interglacial events. Late Pleistocene remains generally support the prevailing hypothesis of a large refugium around the southern terminus of the Appalachian Mountains, from Mississippi to Georgia.

Frankstown Cave.— Early to Middle Pleistocene (Irvingtonian 1.9 million to 250,000 ybp) Wood Turtle remains were recovered from the Frankstown Cave, Blair County, Pennsylvania

2 *Glyptemys* specimens were obtained from the Sand Lizard Quarry, Knox County; Crookston Bridge, Nenzel, Stewart, and Valentine Railway Quarries of Cherry County; Norden Bridge Quarry of Brown County; and the Forked Hills of Hayden in Boyd County (Holman and Fritz 2001).



2.6—The genus *Terrapene*, the North American Box Turtles, includes several distinct lineages with species-level confusion caused by high levels of introgression in the southeastern United States. *Top left*: the Coahuila Box Turtle (*Terrapene coahuila*) occurs only in the desert springs of Cuatro Ciénegas, Coahuila, Mexico. *Middle*: the Florida Box Turtle (*Terrapene bauri*) and Yucatán Box Turtle (*Terrapene yucatana*) are southern-latitude representatives of the Eastern Box Turtle (*Terrapene carolina*) species complex that is distributed from New England to the Yucatán Peninsula. An adult male from Yucatán is pictured at middle right, and an adult male from Florida is pictured at middle left. *Bottom*: the Ornate Box Turtles (*Terrapene ornata*) occur throughout the prairies and warm deserts of the western USA and Mexico. An adult female is pictured at bottom right, and an adult male is pictured at bottom left. MIKE JONES



2.7—During the Miocene epoch, a smaller relative of the Wood Turtle, described as *Glyptemys valentinensis*, inhabited the Niobrara River valley of northern Nebraska. Fossils have been recovered from at least eight distinct localities. The holotype specimen, UNSM 76564, is pictured. ROSS SECORD (NEBRASKA STATE MUSEUM)

(Peterson 1926). The Pennsylvania reports provide additional evidence that Wood Turtles occupied at least part of their contemporary range during an interglacial event of the Late Pleistocene (Hay 1923; Parris and Daeschler 1995).

Port Kennedy Cave.—Wood Turtle remains from the Port Kennedy Cave, a limestone solution feature in Montgomery County, Pennsylvania, were dated to the Late Irvingtonian or Middle Pleistocene (850,000–250,000 ybp) (2.8). Here, skeletal remains of *G. insculpta* were found in association with Box Turtles (*Terrapene carolina*), Blanding’s Turtle (*Emydoidea blandingii*), and a species of *Hesperotestudo* tortoise (Parris and Daeschler 1995). Noteworthy mammalian associates reported by these authors included Mastodon, Wheatley’s Ground Sloth (*Megalonyx wheatleyi*), Lesser Short-faced Bear (*Arctodus pristinus*), Long-nosed Peccary (*Mylohyus nasutus*), Hay’s or Giant Tapir (*Tapirus haysii*), skunk (*Brachyprotoma obtusata*), and Eastern Cottontail (*Sylvilagus floridanus*). Plant remains included hickory (*Carya* sp.), beech (*Fagus* sp.), and Pitch Pine (*Pinus rigida*). The remarkable assemblages from Port Kennedy were studied by Cope (1899) and Hay (1908), both of whom noted the



2.8.—During the last interglacial period of the Pleistocene epoch, Wood Turtles occupied at least a portion of their current range. Fossils are known from Nova Scotia and Pennsylvania. Pictured: ASNP 151, fragmentary remains from the Port Kennedy Cave, Pennsylvania, USA, which were studied by Edward Drinker Cope (1899). PHOTO: NED GILMORE (ACADEMY OF NATURAL SCIENCES OF DREXEL UNIVERSITY/ASNPN).

presence of Wood Turtles. According to Phillips (2006), Cope (1899) noted that Port Kennedy Wood Turtles exhibited a thicker, more enlarged gular surface of the anterior plastral lobe than found in contemporary specimens.

East Milford Mastodon Site.—Wood Turtle remains were recovered from the East Milford mastodon site near the current Shubenacadie River in Halifax County, Nova Scotia (Holman and Clouthier 1995). The Wood Turtle remains were found preserved in a layer of dark, organic clay deposited in a gypsum sinkhole in association with Mastodon (*Mammut americanum*), Painted Turtle, and Northern Leopard Frog (*Lithobates pipiens*). The East Milford remains are particularly noteworthy, because they represent a rare interglacial occurrence of Wood Turtles from an area where they must have subsequently been displaced by advancing Wisconsinan Ice Sheets. The East Milford remains were dated by Holman and Clouthier (1995) to roughly 70,000 to 80,000 ybp.

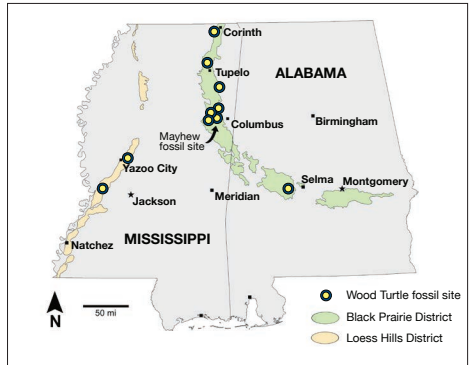
Last Glacial Maximum

During the last glacial advance or last glacial maximum (i.e., Wisconsinan glaciation) of the Pleistocene epoch—and immediately thereafter—Wood Turtles occurred well south of the ice margin around the margin of the southern Appalachian Mountains. Molecular studies have hypothesized at least one southern Pleistocene refugium for *G. insculpta* (Amato 2006; see Phylogeography discussion later in this chapter), and supporting fossil evidence has been recovered from sites in Tennessee, Georgia, Alabama, and Mississippi (Phillips 2006).

Cheek Bend Cave.—Wood Turtle remains (a partial carapace) from Cheek Bend Cave along the Duck River, Maury County, central Tennessee (Parmalee and Klippel 1981; Klippel et al. 1982) were estimated to have originated in the Late Pleistocene (Rancholabrean, 12,000–16,000 ybp). Wood Turtles from Cheek Bend



2.9.—During the last glacial advance of the Pleistocene epoch, Wood Turtles occurred at the margin of the southern Appalachian Mountains. Fossils from the last glacial maximum have been recovered from Mississippi, Tennessee, and a site near Ladds, Bartow County, Georgia (the stream nearest the quarry is pictured). MIKE JONES



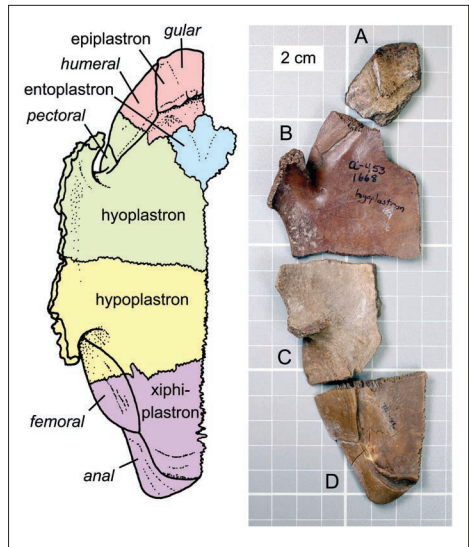
2.10.—Map of Pleistocene Wood Turtle localities in the Deep South. The Black Prairie District is generally more fossiliferous than the Loess Hills, but the former has also been sampled more purposefully. MAP: GEORGE PHILLIPS (MISSISSIPPI MUSEUM OF NATURAL SCIENCES).

were associated with Arctic Shrew (*Sorex palustris*), Yellow-Cheeked Vole (*Microtus xanthognathus*), American Marten (*Martes americana*), and Beautiful Armadillo (*Dasybus bellus*), apparently representing a juxtaposition of boreal and subtropical mammals, as noted by Phillips (2006).

Ladds Quarry.—Wood Turtle remains—consisting of a partial plastron and pleural bones—from Ladds Quarry, Bartow County, Georgia were Late Pleistocene (Rancholabrean) in age (Holman 1967; 1985a; 1985b). These remains provide additional clarity and detail to the geographic extent of the southern refugium occupied by *G. insculpta* during the Late Pleistocene (2.9)

Black Prairie.—Dozens of dissociated Wood Turtle shell elements have been recovered from Late Pleistocene alluvial deposits in the Black Prairie (or Black Belt, Barone 2005) of Mississippi and Alabama, as well as the Loess Hills (or Loess Bluffs/Bluff Hills, Krinitzky and Turnbull 1967) district of western Mississippi (Phillips 2006) (2.10). These physiographic districts exhibit botanical and faunal formations originating in previous Pleistocene interglacials, representing survivorship and reorganization through multiple glacial phases and megafaunal extinction (e.g., Williams et al. 2001). Of the two districts, the most productive single fossil locality lies in the Black Prairie near Mayhew, Mississippi (2.11), where the Wood Turtle represents over 10% of the identified chelonian remains in a rather diverse assemblage (Phillips 2006) (2.12). Blanding’s Turtle (*Emydoidea blandingii*) is also present in the Mayhew samples. Thus, both extant cool temperate chelonians—Wood and Blanding’s—inhabited the Deep South in the Late Pleistocene (Jackson and Kaye 1974; Phillips 2006). Otherwise, Wood Turtle remains at Mayhew co-occur primarily with chelonian taxa that are extant in the Black Prairie (eight of 13 species, 61.5%),³ as discussed further below.

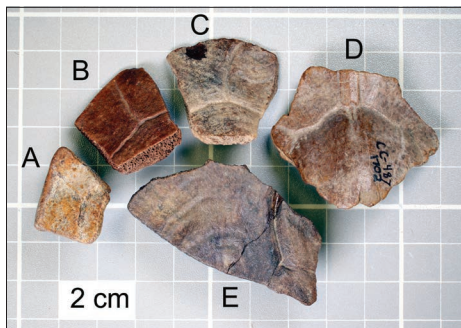
Among the deirochelyines, the genus *Pseudemys* (cooters) is well-represented in the fossil assemblage at Mayhew. Some of these specimens are probably attributable to River Cooter (*Pseudemys concinna*), a modern resident; however, a thick-shelled Red-bellied Cooter (*Pseudemys cf. rubriventris*)—which no longer inhabits the area—is well-represented (Kaye 1974b; Phillips 2006). Elements of Slider (*Trachemys scripta*), Painted Turtle (*Chrysemys picta*), and Alabama Map Turtle (*Graptemys cf. pulchra*) were each less common than Red-bellied Cooter (Phillips 2006).



2.11.—Top: Wood Turtle plastral elements (left side, dorsal aspect) from the Late Pleistocene of the Mississippi Loess Hills (A) and Black Prairie (B–D). (A) epiplastron (MMNS VP-7982); (B) incomplete hyoplastron (MMNS VP-1668); (C) partial hypoplastron (MMNS VP-1795); and (D) xiphoplastron (MMNS VP-7477). Specimens collected in Warren (A), Lowndes (B, C), and Lee (D) counties and curated at the Mississippi Museum of Natural Science, Jackson, Mississippi. Plastral schematic adapted from Holman and Fritz (2001), with kind permission. Individual bony elements are colored; dorsal presentation of named scutes in *italics*. PHOTOS: GEORGE PHILLIPS (MISSISSIPPI MUSEUM OF NATURAL SCIENCES).

3 The form of Box Turtle present at Mayhew was the larger subspecies *T. putnami* or *T. c. major* and not the currently resident *T. c. triunguis* (Jackson and Kaye 1974a).

Kinosternid remains were also recovered from the Mayhew deposits. In addition to Common Musk Turtle, the now extralimital Razorback Musk Turtle (*Sternotherus carinatus*) was also present, although the modern resident Stripe-necked Musk Turtle (*Sternotherus minor peltifer*) was absent (Phillips 2006). A single specimen of Gopher Tortoise (*Gopherus polyphemus*) was recovered from the Mayhew site; this is the northern- and inland-most record of this taxon (Franz and Quitmeyer 2005). Spiny Softshell (*Apalone spinifer*) was present, but the Smooth Softshell (*A. mutica*) was not (Kaye 1974b; Phillips 2006). Kaye (1974b) recorded both lineages of extant chelydrids (*Macrochelys*, *Chelydra*), although they were not common (Phillips 2006). The extinct Giant Nearctic Tortoise (*Hesperotestudo crassiscutata*) rounds out the Mayhew assemblage (Kaye 1974b; Jackson and Kaye 1975; Phillips 2006). The absence of Stripe-necked Musk Turtle and Smooth Softshell, species of riverine habitats, is probably environmental. The totality (turtles, other vertebrates, and sedimentology) of the Black Prairie assemblage suggests smaller, occasionally impounded streams and associated riparian habitat.



2.12. Wood Turtle carapacial elements (left side, dorsal aspect) from the Late Pleistocene of the Mississippi Black Prairie (see 2.10). (A) third peripheral (MMNS VP-1707); (B) second peripheral (MMNS VP-1881); (C) first peripheral (MMNS VP-4281); (D) incomplete nuchal (MMNS VP-1702); and (E) first costal (MMNS VP-4123). Specimens collected in Lowndes (A–D) and Monroe (E) counties and curated at the Mississippi Museum of Natural Science, Jackson, Mississippi. PHOTOS: GEORGE PHILLIPS (MISSISSIPPI MUSEUM OF NATURAL SCIENCES).

In addition to the chelonian component, the Black Prairie paleofauna included a similarly disharmonious suite of mammals and other vertebrates. Caribou (*Rangifer tarandus*), Meadow Vole (*Microtus pennsylvanicus*), and Southern Bog Lemming (*Synaptomys cooperi*)—all currently higher latitude, cool temperate taxa—are intermixed with Beautiful Armadillo (*Dasyurus bellus*), Northern Pamphater (*Holmesina septentrionalis*), and Indigo Snake (*Drymarchon corais*)—species with pre-Pleistocene roots in subtropical and more southern biomes (Kaye 1974b; Frazier 1985; Dobie et al. 1996; McDonald et al. 1996).

Collectively, the composition (diversity, relative abundance, and presence/absence) of Late Pleistocene chelonians at Mayhew suggests an ecosystem of small, sylvan, occasionally impounded, perennial streams with at least seasonally dry, sandy riparian habitat. This is in contrast to an upland Black Prairie fossil assemblage of low chelonian diversity, low aquatic species diversity, and, along with a complementary sedimentology, generally suggestive of intermittent prairie streams with clayey alluvium and lightly wooded riparian habitat (Phillips 2006). The relative abundance of Wood Turtle at lowland sites, like Mayhew, may suggest small glades or openings associated with the riparian habitats.

The co-occurrence of ecologically incongruous chelonian (and other) taxa (at least based on modern distributions) such as the aquatic, cool temperate Blanding's Turtle and terrestrial, subtropical Gopher Tortoise, is suggestive of either a disharmonious fauna (Lundelius 1989) or a time-averaged assemblage (e.g., Behrensmeyer 1982). The components of fluvial deposits are frequently reworked, in which case older fossils may be reincorporated into younger deposits (with younger fossils), but the extent of this attritional reworking, and thus time-averaging, can sometimes be confined to reasonably narrow intervals. Phillips (2006) summarized the cumulative



2.13.—Wood Turtle remains from the West Nishnabotna River near the city of Malvern, Mills County, Iowa, radiocarbon dated to the Late Pleistocene ($10,220 \pm 30$ B.P., 12,095-11,803 cal B.P.). PHOTOS: MATT HILL (IOWA STATE UNIVERSITY).

evidence for confinement of the Black Prairie assemblage to the Rancholabrean Land Mammal Age, and thus to the Late Pleistocene. However, mixing of previous interglacial (Sangamon) fossils with those of the last glacial phase (Wisconsinan) cannot be completely ruled out.

Nishnabotna River.—The partial shell of a wood turtle (*Glyptemys insculpta*) was collected from the West Nishnabotna River near Malvern, Mills County, southwestern Iowa by Matt Hill of Iowa State University (2.13) (Hill, in prep). This specimen was radiocarbon dated to the Late Pleistocene ($10,220 \pm 30$ B.P.; 12,095–11,803 cal B.P.).

Wood Turtle remains are prominently absent from the Late Pleistocene (roughly 18,530 to 18,940 ybp) Ardis local fauna reported from the Giant Cement Quarry near Harleyville, Dorchester County, South Carolina, USA, by Bentley and Knight (1998). Here, excavations of clay deposits among limestone solution chambers revealed Eastern Mud Turtle (*Kinosternon subrubrum*), Common Musk Turtle (*Sternotherus odoratus*), Snapping Turtle (*Chelydra serpentina*), Alligator Snapping Turtle (*Macrochelys temminckii*), Painted Turtle (*Chrysemys picta*), Chicken Turtle (*Deirochelys reticularia*), Common Slider (*Trachemys scripta*), Cooters (*Pseudemys* sp.), Spotted Turtle (*Clemmys guttata*), Bog Turtle, Blanding's Turtle, Giant Box Turtle (*Terrapene carolina putnami* or *T. c. major*), Giant Tortoise (*Hesperotestudo crassiscutata*), and softshells (*Apalone* spp). The authors suggest that the Ardis turtle fauna represents a “disharmonious” fauna with no modern analog.

The report of a Wood Turtle nuchal bone from Quarternary deposits at McFaddin Beach, Texas (Russell 1975) is undoubtedly in error. As pointed out by Phillips (2006), the description matches exactly that of Diamondback Terrapin (*Malaclemys terrapin*), which is known to inhabit the area today.

Recent Prehistory

Wood Turtle remains and subfossils have been reported from numerous mid- to late-Holocene archaeological sites throughout the United States and Canada.

In Ontario, Wood Turtle remains were recovered from the Roebuck Native American site, Leeds and Grenville United Counties, Ontario (Bleakney 1958a). Adler (1968) reported Wood Turtle remains from the Raddatz Rockshelter, Sauk County, Wisconsin, and the Juntunen site on Bois Blanc Island in the Mackinac Strait, Mackinac County, Michigan. Evidence of a single Wood Turtle was recovered from the Little Ossipee North site in Oxford County, Maine, dating from approximately 1,000 ybp (Sobolik and Will 2000). Wood Turtle fragments accounted for

33% of turtle remains in a midden at the Olsen Site near Cushing, Knox County, Maine—a coastal site, with no currently confirmed populations within 30 km (Downs 1987 in Rhodin 1995; Maine Department of Inland Fisheries and Wildlife, unpubl. data). In southern New Hampshire, Wood Turtle remains accounted for 61% of all turtle remains in shell middens at Sewall's Falls, Merrimack County, New Hampshire (Howe 1988 in Rhodin 1995). By contrast, Wood Turtle remains accounted for only 11% of the large sample from the Concord Shell Heap on the bank of the Sudbury River, Concord, Middlesex County, Massachusetts (Rhodin 1995). Wood Turtle remains are even more rare in the turtle bone fauna at Flag Swamp, Middlesex County, Massachusetts (Huntington and Shaw 1982) and the Cedar Swamp, Westborough, Worcester County, Massachusetts (Rhodin 1986; 1992).

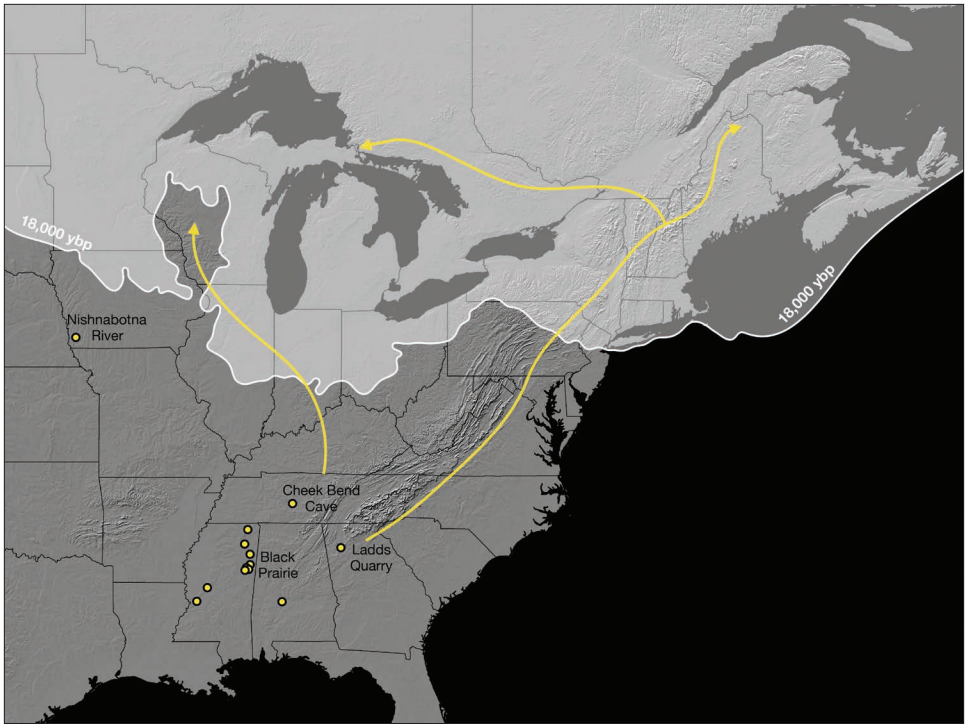
Chromosomal Evolution

Recent genetic and chromosomal studies indicate that the genus *Glyptemys* derived genotypic sex determination (GSD) ~20 million ybp from the ancestral environmental sex determining system (temperature-dependent; TSD) present in a common ancestor that *Glyptemys* spp. shared with other emydid turtles (Montiel et al. 2016, Literman et al. 2017). Molecular data suggest that the two congeners of the genus, *G. insculpta* and *G. mühlenbergii*, split between 8 and 18 million ybp (Montiel et al. 2016), a date that is consistent with the few fossil remains of the genus. *Glyptemys insculpta* possesses a diploid count of 50 chromosomes, distributed as 13 pairs of macrochromosomes and 12 pairs of microchromosomes (Bickham 1975; Montiel 2016). Both *G. insculpta* and *G. mühlenbergii* possess slightly heteromorphic, macrochromosomal XX/XY sex chromosomes that are homologous with chromosome four of *Chrysemys picta*. In *G. insculpta*, the fourth largest pair macrochromosomes in males is characterized by a submetacentric chromosome and a slightly larger submetacentric chromosome; the fourth pair in females is submetacentric and homomorphic. Although an earlier cytogenetic study (Bickham 1975) could not differentiate sex chromosomes in *G. insculpta*, Montiel et al. (2016) determined that the XX/XY chromosomes of the Wood Turtle were the result of at least two inversions between the X and Y chromosomes and subsequent intrachromosomal rearrangements of genes that co-localize with the male-specific region of the Y chromosome.

Genotypic sex determining mechanisms have evolved independently in several lineages of turtles, but the ~20 million ybp derived XX/XY system of the genus *Glyptemys* is apparently the youngest known chelonian example, a group characterized by a low rate of chromosomal changes (Bickham 1981; Olmo 2008). This date corresponds to a period of global warming before the Miocene Epoch Ice Age; thus, increasing environmental temperatures may have influenced selective forces that favored a shift from TSD to a GSD system to counter-balance potential female-biased sex ratios (Valenzuela and Adams 2011; Montiel et al. 2016). In this scenario, masculinizing mutations and the associated inversions identified by Montiel et al. (2016) may have limited recombination and increased the divergence of sex chromosomes in members of this genus.

Phylogeography

The most current phylogeographic hypothesis for the modern distribution of the Wood Turtle comes from Amato et al. (2008) and Rödder et al. (2013). Amato et al. (2008) examined variation in a 750 bp segment of the mitochondrial control region in 117 individuals from 29 locations across the range. They identified 21 haplotypes with little genetic variation among



2.14.—Following the Last Glacial Maximum (shown as a white line) at the end of the Wisconsin phase of the Pleistocene ice ages, Wood Turtles probably colonized their current range from a refugium in the southern Appalachians of Tennessee, Mississippi, Alabama, and Georgia (yellow dots demarcating Late Pleistocene collection sites). The post-Pleistocene colonization hypothesis of Amato et al. (2008) is illustrated by yellow arrows, showing movement into New England and eastern Canada, with continued migration from eastern Canada into the Great Lakes region, as well as direct migration from the southern refugium into the Great Lakes region. BASE DEM CREATED BY EMMY WHISTLER / ANTIOCH UNIVERSITY NEW ENGLAND.

them; the highest pairwise difference was 2%. They suggest that the low level of observed genetic variation can be explained by a severe bottleneck as well as selective sweep when the Wood Turtle was isolated in its southern refugium during the last Pleistocene glacial maximum, from 90,000 to 18,000 years ago. Amato et al. (2008) interpret the presence of fossil Wood Turtles in northwestern Georgia (Holman 1967) and south-central Tennessee (Parmalee and Klippel 1981), about 240 km apart, dating to the Late Pleistocene-Early Holocene as evidence of a refugium in the southern Appalachian region.

Amato et al. (2008) conclude that the Wood Turtle likely exhibited a rapid northward expansion along two major routes from its southern refugium as the Laurentide ice sheet retreated (2.14). In particular, they infer from their analyses that the Wood Turtle experienced rapid population growth beginning approximately 12,000 years ago, which corresponds well with the most recent glacial retreat. They found a significant association of genetic variability and geographical distribution among the haplotypes, as revealed by nested clade analysis. They also found that a large number of intermediate haplotypes were missing, suggesting that they were not sampled or that some were lost to a population bottleneck following glaciation. From this, they inferred that the first route of rapid expansion via long distance dispersal occurred along the Atlantic coast of North America from Virginia to Nova Scotia, with a secondary westward expansion across the

top of the Great Lakes region that was characterized primarily by contiguous dispersal, but also some long-distance dispersal and restricted gene flow. The second route, a westward infiltration, occurred from the Georgia-Alabama refugium to western localities south of the Great Lakes in Michigan, Wisconsin, and Minnesota, and was characterized by long-distance dispersal and restricted gene flow, as populations of the Wood Turtle are not found along this Midwestern route. Amato et al. (2008) and the paleophylogeographic models presented by Rödder et al. (2013) suggest that a second refugium, west of the Appalachian Mountains, cannot be discounted as the source of this westward infiltration. Phillips (2006) and the supplementary fossil evidence presented above, which were unknown to Amato et al. (2008) and Rödder et al. (2013), support these models. Based on the paleobotanical and alluvial valley evolution (Delcourt and Delcourt 1996), the Mississippi River Valley and/or adjoining Blufflands is a logical corridor for dispersal of Wood Turtles to and from the Loess Hills. Based on hypothesized alternate paths of the lower Tennessee River (Shaw 1918; Kaye 1974a), a dispersal route between the upper Tombigbee River, which drains the Black Prairie, and the Ohio River may have been available for movement of Wood Turtles during glacial fluctuations. However, considering the Cheek Bend Cave occurrence in Maury County, Tennessee (Klippel et al. 1982), the full extent of the Interior Low Plateaus, bordered by the Tennessee River to the west (and south), would have made for a larger dispersal corridor, at least to the edge of the Gulf Coastal Plain to the southeast (Black Prairie paleofauna, Tombigbee River) and the Appalachian foothills to the southwest (Ladds Quarry paleofauna, Georgia).

A secondary westward expansion north of the Great Lakes is inferred first because some animals from clades that are located along the eastern seaboard of North America are also found in eastern Ontario, Michigan (including the Upper Peninsula) and Minnesota, suggesting a westward infiltration by contiguous range expansion. It is also inferred, again by contiguous westward range expansion, because animals from that same eastern clade, around Lake Ontario, are also found along the northern shore of Lake Huron. Phylogenetic structuring also suggests the presence of at least three more clades that expanded contiguously north of the Great Lakes. Finally, movement southward across the Great Lakes region by long distance dispersal and restricted gene flow is evidenced by the presence of a clade that includes haplotypes from central and southern Ontario as well as southern Minnesota. Amato et al. (2008) conclude that although there is solid evidence of phylogenetic structuring by geography, no clades are distinct enough to warrant conservation status reassessment. However, at the same time, they caution the assignment of conservation units when using neutral genetic markers. In addition, they interpret this to have both positive and negative consequences: (1) loss of location populations may not have severe consequences to species persistence; and (2) the species gene pool may not contain sufficient variation for future adaptation.

Population Genetics

There is currently limited information on variation and structuring within and among populations of the Wood Turtle across its range. Information on patterns of population structure at relatively small spatial scales (i.e., 12, 25, 43.3, 120, and ca. 100–450 km), either within or across major basins, are limited to studies in Québec (Tessier et al. 2005), Pennsylvania (Castellano et al. 2009), Iowa and West Virginia (Spradling et al. 2010), Ontario (Fridgen et al. 2013) and Michigan (Willoughby et al. 2013). Each of these studies has used varying numbers of nuclear microsatellite loci (5–9) to examine intra- and interpopulation genetic variation in the Wood Turtle at the local-to-regional scale. More recently, some studies (e.g. Bouchard et al. 2019, Weigel

and Whiteley *in* Jones et al. 2018) have also used microsatellite loci (9 and 16, respectively) to examine genetic variation within and among populations at even larger scales (i.e., watershed basins in eastern Ontario, Québec, and New Brunswick, a ca. 770 km maximum straight line distance and 1,340 km maximum river distance, Bouchard et al. 2019; by state and basin in the northeastern United States from Virginia to Maine over ca. 1,230 km minimum straight line distance). In this section, we present a synthesis of these papers from the regional to the local scale (i.e. from the largest to smallest scale of population clustering and differentiation).

Across the Northeast, from northern Virginia to Northern Maine, Weigel and Whiteley (*in* Jones et al. 2018) suggest that populations of the Wood Turtle cluster into four major population groups based upon a sample of 1,244 individuals from 62 sites. These clusters correspond to population groups in northern Maine, coastal Massachusetts and Rhode Island, New York and New Jersey, and the Potomac Basin. They found that populations from New Hampshire and Pennsylvania were admixed with adjacent population clusters. They also found that sites in the Connecticut, Merrimac and Kennebec River basins indicate mixed ancestry between the coastal Massachusetts and the northern Maine sites should be considered a genetically similar group. Therefore, they suggest five evolutionarily significant units (ESUs) made up of the four distinct clusters and the three-river basin mixed ancestry group. They further suggest that the admixed populations in New Hampshire, New York and Pennsylvania should be grouped with their adjacent clusters. Population genetic structure is best described by an island stepping-stone model where sites are exchanging individuals with neighboring sites creating a gradation of genetic structure over the Northeast. Further, their isolation by distance tests within the major clusters suggested that gene flow among nearest neighbors, with and across watershed boundaries, occurs both by water course, as expected, and also overland, with overland movement being more important for some groups, such as Potomac, but less important others, such as Northern Maine. For example, their full-sibling family tests indicate a maximum distance of 50 km between closely related turtles. Ninety-one percent of pairwise comparisons among sample sites were significant after correction for multiple tests. Not surprisingly then, the northern and southern states were the most distinct with populations from Virginia being among the most divergent in the entire sample. Among populations across the Northeast, genetic diversity as measured by allelic richness, private alleles and heterozygosity was within the range of other Wood Turtle genetic studies (e.g., Tessier et al. 2005; Castellano et al. 2009; Spradling et al. 2010; Fridgen et al. 2013; Willoughby et al. 2013), and did not indicate a loss of diversity. However, due to the very long generation time, relatively low dispersal rates, and low population abundances of the Wood Turtle, current population genetic data may reflect conditions several generations ago, possibly as long as ca. 100 years. Therefore, the effects of anthropogenic population fragmentation may not be detected for some time.

In eastern Canada, across a similar distance from eastern Ontario to northwestern New Brunswick, Bouchard et al. (2019) found that the population structure of 331 turtles from 24 locations in 12 watersheds was optimized at only two clusters, one north and one south of the St. Lawrence River. To test their hypothesis of clustering by watershed further, they found that additional clustering runs revealed five clusters on the North Shore that corresponded directly to their watersheds. On the South Shore, the situation was not as clear, with some clusters containing more than one watershed and others containing only one sample site within a watershed. In all cases, genetic diversity within watersheds was similar and observed heterozygosity was relatively high. These findings are similar to Tessier et al. (2005) who examined genetic diversity in two isolated populations on the North Shore of the St. Lawrence and four relatively proximal populations on the south shore in Québec. They found that all loci were extremely polymorphic

and populations were highly variable, and that north and south shore sites were distinct, suggesting independent colonization, but southern sites were not distinct from each other. In fact, Tessier et al.'s (2005) findings on the differences in allelic distribution and genetic variability among their two sampled north shore sites suggested that there were two distinct northern colonization events; with isolation and random drift playing a major role in differentiation. Bouchard et al. (2019) interpret the clear distinction among the North Shore and South Shore sites as arising from an ancient dispersal barrier rather than post-glacial colonization. Yet, surprisingly they conclude that since certain individuals from North Shore sites contain an ancestral genetic signature similar to South Shore individuals, despite the St. Lawrence barrier, anthropogenic movement must be the cause. Overall, similar to Tessier et al. (2005), they found that despite anthropogenic pressures being more severe and population declines occurring on the South Shore, there were no significant different differences in genetic diversity between watersheds on opposite shores of the St. Lawrence. However, contrary to Tessier et al. (2005), they found lower levels of genetic diversity in more isolated watersheds and explain that by founder effect of post-glacial colonization. Despite that, Bouchard et al. (2019) suggest that each site, including the sites in Tessier et al. (2005), should be its own conservation management unit.

In terms of spatial scale, Spradling et al. (2010) is the next largest, with comparison of genetic diversity within and among sites in Iowa, as the extreme western edge of the species' range and West Virginia, some 1,235 km apart. They examined individuals from two localities, 12 km apart in Iowa, and from seven localities with a maximum distance of 25 km between samples in West Virginia. Not surprisingly, they found no structure in either sampling group, suggesting that both the Iowa sample and the West Virginia sample form one group each. However, they did find that genetic diversity was lower in Iowa than West Virginia, with expected heterozygosity being significantly lower. Nevertheless, they did not find evidence for a population bottleneck or inbreeding in Iowa or West Virginia, despite apparent severe population declines in Iowa. Again, this observation may be because of the long generation time of the Wood Turtle coupled with the close proximity of sites leading to gene flow in Iowa. They conclude that fixation indices and private alleles found in Iowa suggest that Iowa is a peripheral isolate that may represent a significant contribution to the genetic diversity of the species, and that both sites may be considered their own conservation management units. Next, in terms of distance between sites is Fridgen et al. (2013), who compared 79 turtles across four populations in three regions some ca. 340 km apart in eastern, southern and central Ontario. They found that the central Ontario population should be its own conservation management unit because it separated from the eastern and southern populations, which were undifferentiated by structure analysis and principal components analysis. Expected heterozygosity was relatively high among the four populations and genetic diversity did not vary much among the populations; however, there was higher heterozygosity and lower evidence of inbreeding in the central and eastern populations compared to the anthropogenically impacted southern population. In fact, despite the observation that heterozygosity in Ontario was generally similar to Québec and Iowa, the southern population, which underwent drastic population declines, had the lowest heterozygosity of any reported population. This observation appears contrary to the suggestion that the signature of anthropogenic disturbance as a loss of genetic diversity is slow to build up because of the long generation time of the Wood Turtle, or it may suggest a long history of population decline in southern Ontario.

Nearby in northern Michigan, Willoughby et al. (2013) examined 68 samples from roughly 20 km on three rivers in the Lower Peninsula, each approximately 120 km from another. They found that clustering identified two distinct populations; a northern cluster comprising the northeastern and northwestern sampling locations and a southern cluster. They do not comment

on conservation management units, but considering that measures of genetic diversity were comparable with other studies, it is reasonable to conclude that the northern and southern clusters could be separate conservation management units. Not surprisingly, since the two northern populations clustered, structure analysis also revealed admixed individuals from both groups, suggesting some common ancestry between the northern and southern clusters. Nonetheless, fixation indices indicated that the northern and southern clusters were more isolated than the two northern populations. Overall, genetic diversity was high, but heterozygosity was higher in the northern population. There too, coalescent theory population size models indicated that there had been a demographic decline in both the northern and southern populations; however, loss of genetic diversity was not detected using bottleneck and inbreeding measures. They suggest that genetic diversity may be maintained in these declining populations by the relatively high migration rate between the two clusters. They further infer that the result of two clusters, rather than three, indicates that the historic pattern of urbanization and agriculture may not be sufficient to isolate populations by measurable genetic differentiation. Finally, they speculate that Amato et al.'s (2008) phylogeographic hypothesis may explain the difference between the northern and southern population clusters with the southern population arising from the westward infiltration across the Midwest and the northern population having ancestry in the secondary westward expansion across the top of the Great Lakes.

The smallest spatial scale comparison of population aggregations comes from two studies in the Northeast, Castellano et al. (2009) and Robillard et al. (2019). Castellano et al. (2009) measured genetic diversity among four aggregations in the Delaware Water Gap of Pennsylvania, with a maximum distance of 43.3 km apart. They found very high genetic diversity, among the highest reported heterozygosity values, and no evidence of structure among the aggregations, concluding that the four aggregations are one conservation management unit. This was explained by their high estimates of gene flow among a large overall population size. Indeed, they report that their data suggest that the population has undergone a recent and rapid expansion. Robillard et al. (2019) examined the effect of population segregation due to the development of a large highway that bisected historically inhabited creeks in the Susquehanna drainage of south-central New York. Using 38 historic samples collected from 1958–1968 and 26 current samples from 2015–2016 in a study area with sites 15–50 km apart, they examined genetic diversity north and south of the highway with six microsatellite loci. As expected, they found that the historic samples clustered into one population but that current samples clustered into a northern and southern sample, with three additional compelling findings. First, aggregations of turtles from their sampling sites had become more genetically differentiated over the nearly 60-year period, with fixation values dropping from 0.081 to 0.166. Second there had been a marked loss of heterozygosity in the northern population compared to historic values, and third, in a possibly related phenomenon, migration over the study period appeared to be oriented southward, coming from the northern sites to the southern sites. Overall they concluded that there had been the development of genetic fragmentation among the sample sites in the north and the south as a result of the highway, noting that among historic sites the genetic differentiation was similar to those of Tessier et al. (2005) that had comparable distances among (15–50 km), but that contemporary differentiation was comparable to Tessier et al.'s (2005) sites that were much farther apart (>60 km).

Summary

From its origins in the Miocene, the genus *Glyptemys* radiated to encompass two living forms, *G. insculpta* and *G. muhlenbergii*, the only emyde taxa known to exhibit chromosomal sex

determination. Although the extinct form *G. valentinensis* is well-represented from Miocene deposits in Nebraska, most of the fossil record of *G. insculpta* dates to the Pleistocene and later. Considerable fossil evidence indicates two noteworthy patterns in the paleodistribution of the Wood Turtle, namely, that Wood Turtles were present in portions of their current range during previous interglacial periods, and that Wood Turtles weathered part of the last glacial advance near the southern terminus of the Appalachian Mountains in Mississippi, Alabama, Tennessee, and Georgia, with an enigmatic fossil occurrence from extreme southwestern Iowa.

To date, genetic studies provide a somewhat ambiguous interpretation. Some studies demonstrate little effect of modern fragmentation on genetic diversity and differentiation, while others clearly do. In conclusion, clearly more studies are needed under more circumstances to understand how the population size and demographic structure, underlying genetic diversity, and degree and temporal and spatial scale affect genetic fragmentation and depauperation in the Wood Turtle.

BIOLOGY & CONSERVATION
of the **WOOD TURTLE**

Michael T. Jones
Lisabeth L. Willey

Editors

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