The Canadian Field-Naturalist

Note

A late Pleistocene Wood Turtle (*Glyptemys insculpta*) from Iowa, USA: response of the taxon to glaciation and formation of the current range

Matthew G. Hill

Department of World Languages and Cultures, 3102 Pearson Hall, Iowa State University, Ames, Iowa 50011-1050 USA; email: mghill@iastate.edu

Hill, M.G. 2022. A late Pleistocene Wood Turtle (*Glyptemys insculpta*) from Iowa, USA: response of the taxon to glaciation and formation of the current range. Canadian Field-Naturalist 136(3): 206–212. https://doi.org/10.22621/cfn.v136i3.2705

Abstract

The partial shell of a Wood Turtle (*Glyptemys insculpta*) was collected from the West Branch of the East Nishnabotna River in southwestern Iowa, near Malvern. By direct accelerator mass spectrometry, it radiocarbon dates to the late Pleistocene (10 220 ± 30 years before present [BP], 11 975–11 813 calibrated years [cal] BP). Other subfossil evidence indicates that Wood Turtles moved far south of their current range, into the southeastern United States, in response to late Pleistocene glaciation. The specimen suggests that the species also moved south and west, into a previously undocumented western range, where favourable habitat and, in particular, somewhat cooler summer temperatures prevailed until ~10 200 cal BP. My assessment of the Holocene subfossil record suggests that establishment of the western portion of the current range may have occurred within the past 1000 years. Phylogenetic analysis and direct radiometric dating of subfossil specimens are needed to determine additional details about the late Pleistocene dispersal of Wood Turtle and the postglacial formation of their current range.

Key words: Range formation; paleozoology; reptile; paleoclimate; herpetofauna

Résumé

La carapace partielle d'une Tortue des bois (*Glyptemys insculpta*) a été collectée du bras ouest de la Rivière Est Nishnabotna (East Nishnabotna River) au sud-ouest de l'Iowa, près de Malvern. Sa datation radiocarbone par spectrométrie de masse par accélérateur remonte au Pléistocène tardif (10 220 ± 30 avant le présent [AP], 11 975–11 813 calibré [cal] AP). Une autre évidence subfossile montre que les Tortues des bois se sont déplacées loin au sud de leur aire de répartition actuelle, au sud-est des Etats-Unis, suite à la période glaciaire du Pléistocène tardif. Le spécimen montre que les espèces se sont aussi déplacées au sud et à l'ouest, dans une aire de répartition occidentale non documentée auparavant, où un habitat favorable et, en particulier, des températures estivales un peu plus fraîches prédominaient jusqu'à ~10 200 cal AP. Mon évaluation du registre subfossile de l'Holocène suggère que l'établissement de la partie ouest de l'aire de répartition actuelle s'est peut-être produit au cours des 1000 dernières années. L'analyse phylogénétique et la datation radiométrique directe des spécimens subfossiles sont nécessaires pour déterminer des détails supplémentaires sur la dispersion de la Tortue des bois pendant le Pléistocène tardif et la formation postglaciaire de leur aire de répartition actuelle.

Mots-clés : habitat, paléozoologie, reptile, paléoclimat, herpétofaune

Quaternary temporal and geographic distributions of extant and extinct fauna are routinely used to reconstruct environment and community architecture as well as to profile how biota differentially respond to climate change (Holman 1992; Bell *et al.* 2010; Williams *et al.* 2018). The recovery of the partial shell of a Wood Turtle (*Glyptemys insculpta*; formerly *Clemmys insculpta*) from southwest Iowa in 2019 (Figure 1), directly radiocarbon dated to ~12 000 calibrated years (cal) before present (BP), provides the opportunity to examine response of the taxon to climate change, the character of the regional late Pleistocene environment, and the establishment of the species' current range.

Wood Turtle is a medium-sized, semi-terrestrial turtle that currently ranges across the northern Great Lakes, northeastern United States, and southeastern Canada (Ernst and Lovich 2009; Jones *et al.* 2021;

A contribution towards the cost of this publication has been provided by the Thomas Manning Memorial Fund of the Ottawa Field-Naturalists' Club.

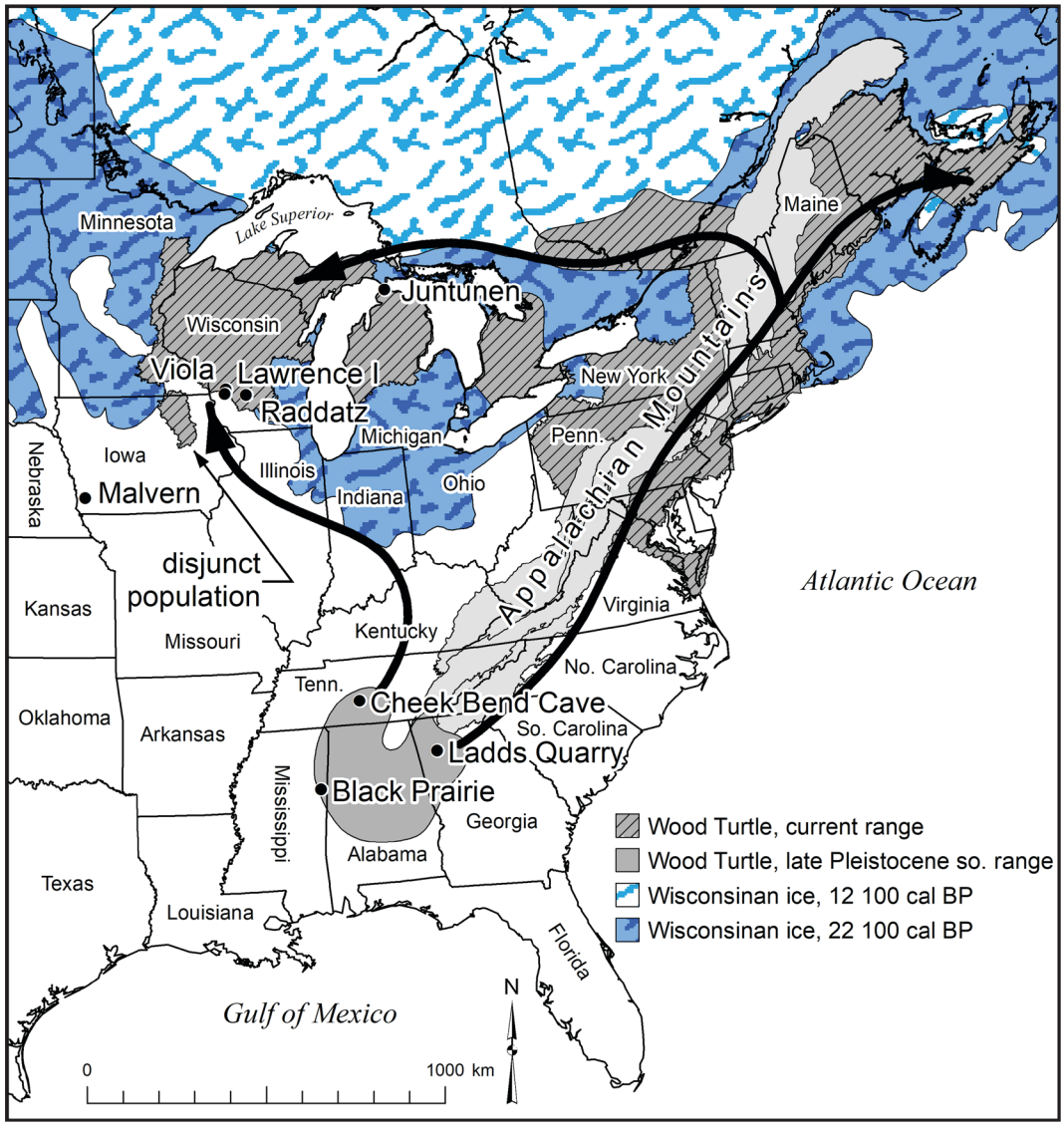

FIGURE 1. Current range of Wood Turtle (*Glyptemys insculpta*) in the contiguous United States and Canada (Ernst and Lovich 2009: 251; USGS 2018), including the location of extra-limital records, relative to the position of the ice margin during the last glacial maximum (22 100 calibrated years before present [cal BP]) and at 12 100 cal BP (Dalton *et al*. 2020), when the taxon was present in southwest Iowa. Also included are the proposed recolonization routes from the late Pleistocene southern range from Jones *et al.* (2021) as originally proposed by Amato *et al.* (2008).

Figure 1). A small, disjunct, and genetically isolated population occurs in the Cedar River basin in northeastern Iowa and crosses the state border into southeastern Minnesota (Spradling *et al.* 2010; Lapin *et al.* 2019). In general, Wood Turtle is found north of the 29°C (85°F) isotherm for normal daily maximum July temperature (Parmalee and Klippel 1981). It is a habitat generalist that occurs in hard-bottomed (e.g., sand, gravel, or cobble substrates) rivers and streams adjacent to forested riparian areas that contain foraging and nesting habitat (Lapin *et al.* 2019). Wood Turtles hibernate in fast-flowing water with high levels of dissolved oxygen, and lotic water sources are central to individual home ranges (Otten 2017). Although some individuals become more terrestrial during summer, in Iowa, they are usually not found farther than 300 m from lotic habitat (Tamplin 2016, 2019). Wood Turtles are opportunistic omnivores; earthworms,

snails, slugs, and plant material are primary foods (Ernst and Lovich 2009).

Previously found late Pleistocene remains from Black Prairie, Mississippi (Phillips 2006), Ladds Quarry, Georgia (Holman 1967, 1985), and Cheek Bend Cave, Tennessee (Parmalee and Klippel 1981; Klippel and Parmalee 1982; Figure 1) indicate that the taxon survived late Wisconsinian glaciation by dispersing southward ~1000 km south of the present range. Concomitant with retreat of the Laurentide ice sheet, genetic profiles of modern specimens show that the turtle rapidly recolonized the area that ultimately resulted in its current range by taking two routes northward (Amato *et al.* 2008). One population dispersed from Alabama–Georgia, moving northward along the eastern seaboard into New Brunswick and Nova Scotia (Figure 1), with a tentacle then moving west across the Great Lakes region, possibly as far west as northern Wisconsin. The Ladds Quarry material appears to support this interpretation of the genetic evidence. Another population originated somewhat south and west of the Appalachian Mountains and recolonized Wisconsin, Minnesota, and lower Michigan (Figure 1). The remains from Cheek Bend Cave and Black Prairie support this route.

The subfossil turtle shell described here (Figure 2) was collected in July 2019 from a sand-and-gravel bar on the west branch of the East Nishnabotna River, near the city of Malvern, Mills County, Iowa (41.005403°N, 95.529881°W). It is now curated in the Paleontological Repository, Department of Earth and Environmental Sciences, University of Iowa (cat no. SUI – 148451). The specimen consists of about 50% of the anterior carapace and plastron (fused), including all of the left plastral bones. The left half of the plastron, which is complete, is 20 cm in maximum length. Except for subtle geological rounding of recent fracture edges, natural margins, and topographic highs, the physical condition of the specimen is excellent. The carapace is keeled and heavily sculpted, while the plastron is deeply concave and smooth. These features indicate it was an adult male Wood Turtle ≥25 years old when it died (Ernst and Lovich 2009; J.W. Tamplin pers. comm. 19 February 2020). A sample of plastron submitted for radiocarbon dating produced a median age of 11 889 cal BP (Table 1) and indicates the specimen is very late Pleistocene in age, hovering over the Pleistocene–Holocene boundary (Rasmussen *et al.* 2014).

The shell is somewhat similar to that of several turtles that share a modern range with Wood Turtles: Blanding's Turtle (*Emydoidea blandingii*), Common Map Turtle (*Graptemys geographica*), and False Map Turtle (*Graptemys pseudogeographica*). Although distinguishing these taxa can be difficult when only isolated pieces are available (Holman and Clouthier 1995), the identity of the Malvern shell is unquestionable and based on hands-on comparison with modern turtle material in my personal collection, published descriptions of Wood Turtle shell morphology, and feedback from specialists who examined digital images of the specimen (see Acknowledgements).

The Malvern record extends the late Pleistocene range of Wood Turtle several hundred kilometres south and west of the modern range (Figure 1) and suggests that somewhat cooler summer temperatures prevailed in southwest Iowa and adjacent areas of northwest Missouri, northeast Kansas, and eastern Nebraska until at least ~12 000 cal BP. Unfortunately, there are no vegetation or pollen studies from this area from that period to corroborate my assumption. Marshes, bogs and oxbow lakes, and wet meadows flanking rivers and streams, common landscape features today, were also abundant at the end of the Pleistocene. By 10 200 cal BP, summers were probably too warm and the environment too dry (Baker *et al.* 2000) to support Wood Turtles.

The specimen also suggests the existence of a previously undocumented, late Pleistocene western range for Wood Turtle. Although the extent of this range is unknown, it probably stretched into adjacent states. The potential for other subfossil specimens from these areas is high. Alternatively, the specimen may provide support for two rapid reinfiltration routes from the southern range. One population of turtles moved along the eastern seaboard, while another—involving the Malvern turtle—moved through the interior highlands, interior plateau, and central lowlands into the southern and western Great Lakes states. Assuming favourable preservation of ancient DNA, phylogenetic analysis of the Malvern specimen—ideally in conjunction with analyses of specimens from the southeast—could address these possibilities as well as determine additional details about the taxon's late Wisconsinan dispersal and the formation of its current range.

The current range of Wood Turtle covers the Upper Peninsula of Michigan, northern lower Michigan, most of Wisconsin, and parts of southeast Minnesota and northeast Iowa. Holocene subfossils in these areas—loosely, the western range—are absent or rare. To date, there are no Holocene records west of the Mississippi River (border between Illinois and Iowa) and only one from Michigan and three from Wisconsin, all from archaeological contexts (Figure 1). (I exclude a late Holocene record in western Wisconsin [Penman and Yerkes 1992] cited in the Neotoma database [Williams *et al.* 2018], because the three specimens were assigned to a different taxon in the final faunal report [Styles and White 1994].) The Juntunen,

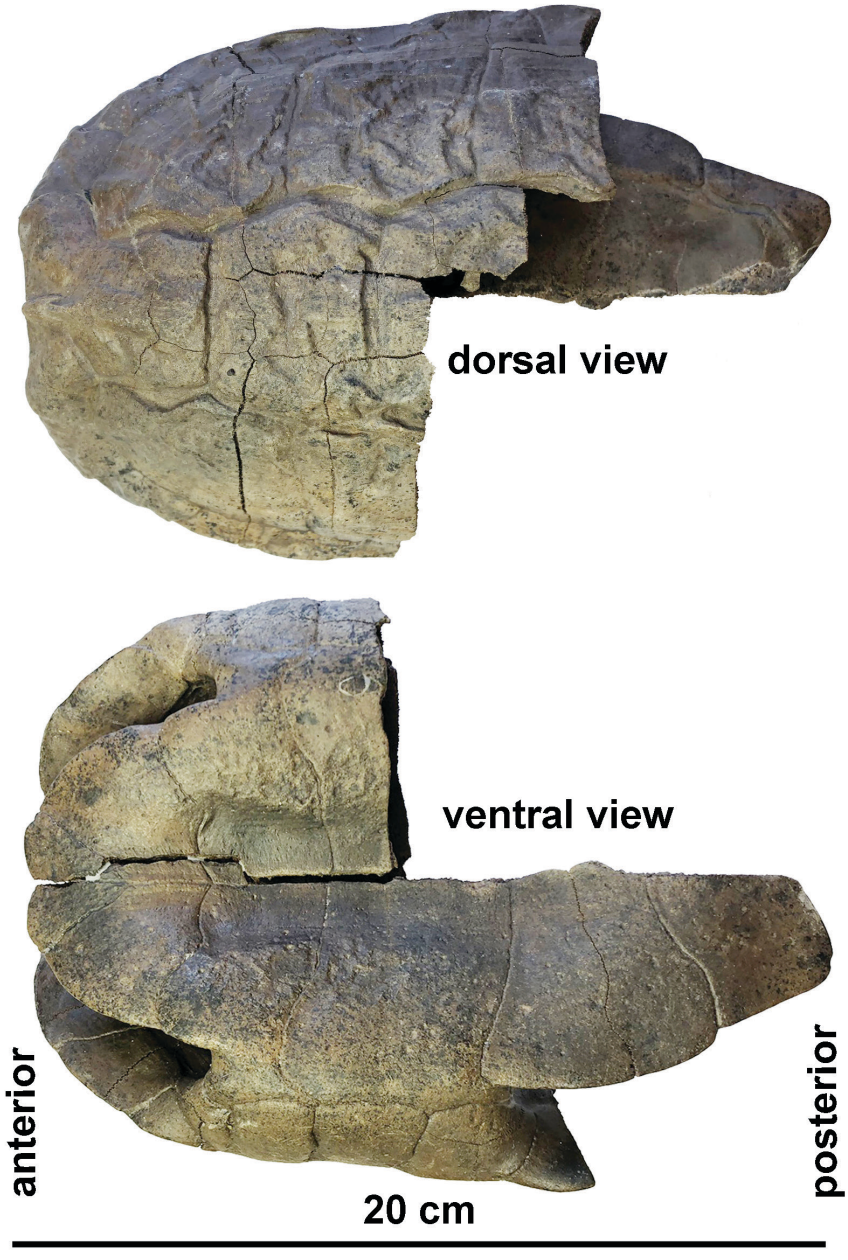

FIGURE 2. Subfossil Wood Turtle (*Glyptemys insculpta*) shell from near Malvern, Mills County, Iowa (cat no. SUI – 148451). Photo: Matthew G. Hill.

Michigan, record is very late Holocene (about ≤1000 cal BP; Cleland 1966); the skeletal basis of identification is not specified (Adler 1968). Two of the Wisconsin records are also late Holocene. The first is a nuchal (the most anterior carapace element), from the Middle Woodland component (1810 ± 80 years BP, 1890–1535 cal BP) at Viola rock shelter (Theler 1989; Steventon and Kutzbach 1990; J.L. Theler pers. comm. 21 August 2020). It is possible that this record is much older or much younger than the indirect date derived from dating the associated charcoal; rock shelter deposits are notoriously complex and direct

Table 1. Accelerator mass spectrometry (AMS) radiometric and isotopic results for the subfossil Wood Turtle (*Glyptemys insculpta*) shell from near Malvern, Mills County, Iowa, as determined by the Keck-Carbon Cycle AMS Facility, University of California, Irvine, USA.

Laboratory no. 231586	
Age ^{14}C years BP ± 1 sigma	10 220 ± 30
Calibrated age, ^{14}C years BP, cal BP, 2 sigma range (median)*	11 975–11 813 (11 889)
Fraction modern	0.2802 ± 0.0010
δ^{13}C‰ (PBD)	−21.3
δ^{15}N‰ (PBD)	6.8

* BP = before present, PBD = Pee Dee Belemnite. OxCal 4.4 (Bronk Ramsey and Lee 2016) and IntCal20 (Reimer *et al.* 2020) were used to calibrate the measured radiocarbon age.

dating is required to resolve this issue.

The second record consists of two carapace elements (a peripheral no. 7 and a proneural) from the late Middle Woodland–Late Woodland component at Lawrence I rock shelter (Berwick 1975). The taxonomic identification of these specimens requires verification because, as noted above, isolated carapace pieces from several taxa that co-occur in the region can be difficult to distinguish. Unfortunately, they could not be relocated in the collections at the Wisconsin Historical Society (WHS).

The third record is a complete nuchal from Raddatz rock shelter (Adler 1968), which I verified using digital images provided by WHS personnel. Parmalee (1959: Table 2) and Cleland (1966: Table 7) do not list the specimen in their enumerations of the site fauna; it is possibly tallied in the sample of indistinguishable Painted Turtle (*Chrysemys picta*), Blanding's Turtle, and/or map turtle (*Graptemys* spp.) remains. However, in part, because of the long, complicated history of custody and use of the collection (Speth *et al.* 2017), exact provenance has been lost, which muddles where the specimen falls in time. Summary data provided by Cleland (1966: Table 7), combined with his (opaque) discussion of the stratigraphy (1966: 104–105), indicates it was recovered from deposits dating to either the early-late Holocene (level 3, ~3500 cal BP) or the middle Holocene (level 11, ~7500–5000 cal BP). Regionally, these were the two warmest and driest intervals of time since deglaciation (Maher 1982; Winkler *et al.* 1986; Keen and Shane 1990), conditions that stand in contrast to current Wood Turtle range, which is well to the north, suggesting that Wood Turtle prefer much cooler habitats. Direct accelerator mass spectrometry dating of the specimen will be required to resolve this seeming discrepancy.

If Wood Turtles were present in the western half of the current range during the Holocene, then it is unusual that their remains have not been recovered more often at archaeological sites, as is the case with other turtle taxa (Theler 2000: Table 5). Faunal preservation at open human habitations and in rock shelters across the region is generally excellent, and many large faunal samples with high taxonomic diversity have been reported (Parmalee 1959, 1960, 1963; Cleland 1966, 1970; Styles and White 1993, 1994, 1995; Theler 1993, 2000; Kuehn 1998; Baker and Theler 2005; Kuehn and Clark 2012). The geographic locations of the known records and the lack of Wood Turtles at other archeological sites suggests that the formation of the western range occurred relatively recently, perhaps within the past 1000 years. In this scenario, the western Wisconsin rock shelter records represent a now-extinct, Holocene population that may be more closely related to those animals that recolonized the region from the south following deglaciation, with the caveat that the Lawrence I record requires checking (assuming the material is relocated) and that the Raddatz rock shelter record requires direct dating. Direct dating of the Viola and Lawrence I records would also shed light on this supposition. Furthermore, the current western range may have been shaped by a very late Holocene population that spread across the northern Great Lakes and into Wisconsin, Minnesota, and possibly, Iowa.

In conclusion, Wood Turtles inhabited some areas of the southeast and eastern Central Plains at the end of the Pleistocene, presumably migrating to these locations from a more northern, ancestral range that had become inhospitable due to advancing Laurentide ice. A general, northward movement of these populations attended subsequent deglaciation and environmental amelioration. Formation of the current range, particularly that which stretches across the northern Great Lakes region into northern and southwestern Wisconsin, may have occurred during the very late Holocene. The extant population in northeast Iowa, and possibly that which also inhabits southwest Wisconsin, may be most closely related to the aforementioned Central Plains population.

Acknowledgements

Special thanks to Jim McClarnon, discoverer of the Malvern specimen, and the other members of the McClarnon family for their enthusiastic support and interest in this research. Rachel Harvieux and Marlin Hawley attempted to locate the specimens from the Lawrence I rock shelter in the collections at the Wisconsin Historical Society. John Lambert scanned the shell. Conversations with Jim Theler (University of Wisconsin—LaCrosse), Tom La Duke, and, particularly, Wood Turtle scholars Jeff Tamplin (University of Northern Iowa) and Mike Jones were

especially helpful. Ron Brooks, R. Lee Lyman, and an anonymous reviewer provided constructive comments. Jean-Pierre Taoutel translated the abstract into French.

Literature Cited

Adler, K. 1968. Turtles from archeological sites in the Great Lakes region. Michigan Archaeologist 14: 147–163.

Amato, M.L., R.J. Brooks, and J. Fu. 2008. A phylogeographic analysis of populations of the wood turtle (*Glyptemys insculpta*) throughout its range. Molecular Ecology 17: 570–581. https://doi.org/10.1111/j.1365-294x.2007.03580.x

Baker, J.D., and J.L. Theler. 2005. Animal remains from the Midway Site (21BL37), Beltrami County, Minnesota. Minnesota Archaeologist 64: 105–144.

Baker, R.G., G.G. Fredlund, R.D. Mandel, and E.A. Bettis, III. 2000. Holocene environments of the central Great Plains: multi-proxy evidence from alluvial sequences, southeastern Nebraska. Quaternary International 67: 75–88. https://doi.org/10.1016/s1040-6182(00)00010-0

Bell, C.J., J.A. Gauthier, and G.S. Bever. 2010. Covert biases, circularity, and apomorphies: a critical look at the North American Quaternary herpetofaunal stability hypothesis. Quaternary International 217: 30–36. https://doi.org/10.1016/j.quaint.2009.08.009

Berwick, D.E. 1975. Analysis of the vertebrate fauna of Lawrence I rockshelter (Ve-154), Vernon County, Wisconsin. M.A. thesis, University of Wisconsin, Madison, Wisconsin, USA.

Bronk Ramsey, C., and S. Lee. 2016. Recent and planned developments of the program OxCal. Radiocarbon 55: 720–730. https://doi.org/10.1017/S0033822200057878

Cleland, C.E. 1966. The prehistoric animal ecology and ethnozoology of the upper Great Lakes region. Anthropological papers 29. Museum of Anthropology, University of Michigan, Ann Arbor, Michigan, USA. https://doi.org/10.3998/mpub.11396632

Cleland, C.E. 1970. Comparison of the faunal remains from French and British refuse pits at Fort Michilimackinac: a study in changing subsistence patterns. Occasional papers in archaeology and history 3. National Historic Sites Service, Department of Indian Affairs and Northern Development, Ottawa, Ontario, Canada.

Dalton, A.S., M. Margold, C.R. Stokes, L. Tarasov, A.S. Dyke, R.S. Adams, S. Allard, H.E. Arends, N. Atkinson, J.W. Attig, P.J. Barnett, R.L. Barnett, M. Batterson, P. Bernatchez, H.W. Borns, Jr., A. Breckenridge, J.P. Briner, E. Brouard, J.E. Campbell, A.E. Carlson, J.J. Clague, B.B. Curry, R.A. Daigneault, H. Dubé-Loubert, D.J. Easterbrook, D.A. Franzi, H.G. Friedrich, S. Funder, M.S. Gauthier, A.S. Gowan, K.L. Harris, B. Hétu, T.S. Hooyer, C.E. Jennings, M.D. Johnson, A.E. Kehew, S.E. Kelley, D. Kerr, E.L. King, K.K. Kjeldsen, A.R. Knaeble, P. Lajeunesse, T.R. Lakeman, M. Lamothe, P. Larson, M. Lavoie, H.M. Loope, T.V. Lowell, B.A. Lusardi, L. Manz, I. McMartin, F.C. Nixon, S. Occhietti, M.A. Parkhill, D.J.W. Piper, A.G. Pronk, P.J.H. Richard, J.C. Ridge, M. Ross, M. Roy, A. Seaman, J. Shaw, R.R. Stea, J.T. Teller, W.B. Thompson, L.H. Thorleifson, D.J. Utting, J.J. Veillette, B.C. Ward, T.K. Weddle, and H.E. Wright, Jr. 2020. An updated radiocarbon-based ice margin chronology for the last deglaciation of the North American ice sheet complex. Quaternary Science Reviews 234: 106223. https://doi.org/10.1016/j.quascirev.2020.106223

Ernst, C.H., and J.E. Lovich. 2009. Turtles of the United States and Canada. Second Edition. Johns Hopkins University Press, Baltimore, Maryland, USA.

Holman, J.A. 1967. A Pleistocene herpetofauna from Ladds, Georgia. Bulletin of the Georgia Academy of Science 25: 154–166.

Holman, J.A. 1985. Herpetofauna of Ladds Quarry. National Geographic Research 1: 423–436.

Holman, J.A. 1992. Late Quaternary herpetofauna of the central Great Lakes region, USA: zoogeographical and paleoecological implications. Quaternary Science Reviews 11: 345–351. https://doi.org/10.1016/0277-3791(92)90005-s

Holman, J.A., and S.G. Clouthier. 1995. Pleistocene herpetofaunal remains from the East Milford mastodon site (ca. 70,000–80,000 BP), Halifax County, Nova Scotia. Canadian Journal of Earth Sciences 32: 210–215. https://doi.org/10.1139/e95-017

Jones, M.T., J.W. Tamplin, T.S.B. Akre, L.L. Willey, and R. Saumure. 2021. Evolution. Pages 21–43 *in* Biology and Conservation of the Wood Turtle. *Edited by* M.T. Jones and L.L. Willey. Northeast Association of Fish and Wildlife Agencies, Petersburg, New York, USA.

Keen, K.L., and L.C.K. Shane. 1990. A continuous record of Holocene eolian activity and vegetation change at Lake Ann, east-central Minnesota. Geological Society of America Bulletin 102: 1646–1657. https://doi.org/10.1130/0016-7606(1990)102<1646:acrohe>2.3.co;2

Klippel, W.E., and P.W. Parmalee. 1982. Paleontology of Cheek Bend Cave, Maury County, Tennessee. Tennessee Valley Authority, Knoxville, Tennessee, USA.

Kuehn, S.R. 1998. New evidence for late Paleoindian–early Archaic subsistence behavior in the western Great Lakes. American Antiquity 63: 457–476. https://doi.org/10.2307/2694630

Kuehn, S.R., and J.A. Clark, Jr. 2012. Analysis of faunal remains from three late Paleoindian (Lake Poygan phase) sites in east-central Wisconsin. Illinois Archaeology 24: 123–158.

Lapin, C.N., J.W. Tamplin, M.M. Cochrane, J.E. Woodford, D.J. Brown, and R.A. Moen. 2019. A regional analysis of *Glyptemys insculpta* (wood turtle) survival in the upper midwest of the USA. Herpetological Conservation and Biology 14: 668–679.

Maher, L.J., Jr. 1982. The palynology of Devils Lake, Sauk County, Wisconsin. Pages 119–135 *in* Quaternary History of the Driftless Area. *Edited by* J.C. Knox. Field Trip Guide Book no. 5. Geological and Natural History Survey, University of Wisconsin Extension, Madison, Wisconsin, USA.

Otten, J.G. 2017. Factors influencing wood turtle (*Glyptemys insculpta*) home range size in Iowa: a comparison between suburban and rural populations. M.Sc. thesis,

University of Northern Iowa, Cedar Falls, Iowa, USA.

Parmalee, P.W. 1959. Animal remains from the Raddatz rockshelter, Sk5, Wisconsin. Wisconsin Archeologist 40: 83–90.

Parmalee, P.W. 1960. Animal remains from the Durst rockshelter, Sauk County, Wisconsin. Wisconsin Archeologist 41: 11–17.

Parmalee, P.W. 1963. Vertebrate remains from the Bell site, Winnebago County, Wisconsin. Wisconsin Archeologist 44: 58–69.

Parmalee, P.W., and W.E. Klippel. 1981. Remains of the wood turtle *Clemmys insculpta* (Le Conte) from a late Pleistocene deposit in middle Tennessee. American Midland Naturalist 105: 413–416. https://doi.org/10.2307/2424767

Penman, J.T., and R.W. Yerkes. 1992. Vertebrate remains from the Filler site, a late prehistoric occupation in La Crosse County, Wisconsin. Wisconsin Archeologist 73: 199–236.

Phillips, G.E. 2006. Paleofaunistics of nonmammalian vertebrates from the late Pleistocene of the Mississippi–Alabama Black Prairie. M.Sc. thesis, North Carolina State University, Raleigh, North Carolina, USA.

Rasmussen, S.O., M. Bigler, S.P. Blockley, T. Blunier, S.L. Buchardt, H.B. Clausen, I. Cvijanovic, D. Dahl-Jensen, S.J. Johnsen, H. Fischer, V. Gkinis, M. Guillevic, W.Z. Hoek, J.J. Lowe, J.B. Pedro, T. Popp, I.K. Seierstad, J.P. Steffensen, A.M. Svensson, P. Vallelonga, B.M. Vinther, M.J.C. Walker, J.J. Wheatley, and M. Winstrup. 2014. A stratigraphic framework for abrupt climatic changes during the last glacial period based on three synchronized Greenland ice-core records: refining and extending the INTIMATE event stratigraphy. Quaternary Science Reviews 106: 14–28. https://doi.org/10.1016/j.quascirev.2014.09.007

Reimer, P.J., W.E.N. Austin, E. Bard, A. Bayliss, P.G. Blackwell, C. Bronk Ramsey, M. Butzin, H. Cheng, R.L. Edwards, M. Friedrich, P.M. Grootes, T.P. Guilderson, I. Hajdas, T.J. Heaton, A.G. Hogg, K.A. Hughen, B. Kromer, S.W. Manning, R. Muscheler, J.G. Palmer, C. Pearson, J. van der Plicht, R.W. Reimer, D.A. Richards, E.M. Scott, J.R. Southon, C.S.M. Turney, L. Wacker, F. Adolphi, U. Büntgen, M. Capano, S.M. Fahrni, A. Fogtmann-Schulz, R. Friedrich, P. Köhler, S. Kudsk, F. Miyake, J. Olsen, F. Reinig, M. Sakamoto, A. Sookdeo, and S. Talamo. 2020. The IntCal20 northern hemisphere radiocarbon age calibration curve (0–55 cal kBP). Radiocarbon 62: 725–757. https://doi.org/10.1017/rdc.2020.41

Speth, J.M., M.F. Hawley, and T.J. Martin. 2017. Paul W. Parmalee's original notes on the Raddatz rockshelter (47SK5) fauna. Wisconsin Archeologist 98: 75–99.

Spradling, T.A., J.W. Tamplin, S.S. Dow, and K.J. Meyer. 2010. Conservation genetics of a peripherally isolated population of the wood turtle (*Glyptemys insculpta*) in Iowa. Conservation Genetics 11: 1667–1677. https://doi.org/10.1007/s10592-010-0059-y

Steventon, R.L., and J.E. Kutzbach. 1990. University of Wisconsin radiocarbon dates XXVI. Radiocarbon 32: 209–228. https://doi.org/10.1017/s0033822200040182

Styles, B.W., and K. White. 1993. Analysis of faunal remains. Pages 99–115 *in* The Tremaine Site Complex: Oneota Occupation in the La Crosse Locality, Wisconsin, Volume 1. The OT Site (47Lc-262). Archaeological research series 1. *Edited by* J. O'Gorman. State Historical Society of Wisconsin, Madison, Wisconsin, USA.

Styles, B.W., and K. White. 1994. Analysis of faunal remains. Pages 91–104 *in* The Tremaine Site Complex: Oneota Occupation in the La Crosse Locality, Wisconsin, Volume 2. The Filler Site (47Lc-149). Archaeological research series 2. *Edited by* J. O'Gorman. State Historical Society of Wisconsin, Madison, Wisconsin, USA.

Styles, B.W., and K. White. 1995. Analysis of faunal remains. Pages 197–223 *in* The Tremaine Site Complex: Oneota Occupation in the La Crosse Locality, Wisconsin, Volume 3. The Tremaine Site (47Lc-95). Archaeological research series 3. *Edited by* J. O'Gorman. State Historical Society of Wisconsin, Madison, Wisconsin, USA.

Tamplin, J.W. 2016. Upper Midwest turtle habitat improvement. Final report. United States Fish and Wildlife Service, Des Moines, Iowa, USA.

Tamplin, J.W. 2019. Upper Midwest turtle conservation. Final report. United States Fish and Wildlife Service, Des Moines, Iowa, USA.

Theler, J.L. 1989. Inventory of faunal remains from Viola rockshelter, Vernon County, Wisconsin. Mississippi Valley Archaeology Center, La Crosse, Wisconsin, USA.

Theler, J.L. 1993. Faunal remains. Pages 416–428 *in* Further Archaeological Investigations in the Wisconsin Headwaters: the Results of the 1992 Field Season. Reports of investigation 159. *Edited by* C.R. Moffat, C.M. Arzigian, and J.L. Theler. Mississippi Valley Archaeology Center, La Crosse, Wisconsin, USA.

Theler, J.L. 2000. Animal remains for Native American archaeological sites in western Wisconsin. Transactions of the Wisconsin Academy of Sciences, Arts and Letters 88: 121–142.

USGS (United States Geological Survey). 2018. U.S. Geological Survey – gap analysis project species range maps CONUS_2001. USGS, Department of the Interior, Washington, DC, USA. https://doi.org/10.5066/f7q81b3r

Williams, J.W., E.C. Grimm, J.L. Blois, D.F. Charles, E.B. Davis, S.J. Goring, R.W. Graham, A.J. Smith, M. Anderson, J. Arroyo-Cabrales, A.C. Ashworth, J.L. Betancourt, B.W. Bills, R.K. Booth, P.I. Buckland, B.B. Curry, T. Giesecke, S.T. Jackson, C. Latorre, J. Nichols, T. Purdum, R.E. Roth, M. Stryker, and H. Takahara. 2018. The Neotoma Paleoecology Database, a multiproxy, international, community-curated data resource. Quaternary Research 89: 156–177. https://doi.org/10.1017/qua.2017.105

Winkler, M.G., A.M. Swain, and J.E. Kutzbach. 1986. Middle Holocene dry period in the northern midwestern United States: lake levels and pollen stratigraphy. Quaternary Research 25: 235–250. https://doi.org/10.1016/0033-5894(86)90060-8

Received 11 January 2021
Accepted 21 December 2022
Associate Editor: R.J. Brooks