Editorial Comment. – This section has been established as a forum for the exchange of ideas, opinions, position statements, policy recommendations, and other reviews regarding turtle-related matters. Commentaries and points of view represent the personal opinions of the authors, and are peer-reviewed only to the extent necessary to help authors avoid clear errors or obvious misrepresentations or to improve the clarity of their submission, while allowing them the freedom to express opinions or conclusions that may be at significant variance with those of other authorities. We hope that controversial opinions expressed in this section will be counterbalanced by responsible replies from other specialists, and we encourage a productive dialogue in print between the interested parties. Shorter position statements, policy recommendations, book reviews, obituaries, and other reports are reviewed only by the editorial staff. The editors reserve the right to reject any submissions that do not meet clear standards of scientific professionalism.

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An Overview of the North American Turtle Genus *Clemmys* Ritgen, 1828

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The genus *Clemmys* Ritgen, 1828, encompasses a group of four small to medium-sized, semiaquatic, extant turtles (Fig. 1) confined to the United States, Canada, and Baja California, Mexico: the spotted turtle, *C. guttata*; wood turtle, *C. insculpta*; bog turtle, *C. muhlenbergii*; and Pacific pond turtle, *C. marmorata* (with two poorly defined subspecies; Seeliger, 1945; Holland, 1994; Gray, 1995; Janzen et al., 1997). Below, I present a general overview of the genus, pointing out various questions or controversies that need to be researched, and provide a prognosis for survival of the four species.

Distinguishing Characteristics. — Usually considered one of the oldest genera in the family Emydidae, the genus *Clemmys* is best characterized by its hingeless, weakly buttressed plastron; keeled or smooth carapace; short neck; upper jaw lacking a prominent notch or cusps; smooth, narrow crushing surfaces on the maxilla which lack involvement from the palatine or pterygoid; no contact between the pterygoid and basioccipital; contact between the angular bone and Meckel's cartilage; the jugal tapered ventrally, but not contacting the pterygoid; the frontal bone contributing to the orbit; and webbed toes. Other characters are discussed by Bramble (1974), Bury and Ernst (1977), Ernst and Barbour (1989), and Ernst et al. (1994).

Fossil Record. — The oldest fossils possibly assignable to Clemmys are those of the questionable Cretaceous (Maestrictian) species C. backmani Russell, 1934, from Pretty Butte, Slope County, North Dakota (Quammen, 1992), and also known from the Paleocene Ravenscrag formation of Big Muddy Valley, Saskatchewan (Russell, 1934). Other fossils assignable to Clemmys are: C. morrisiae Hay, 1908, from the Bridger Eocene of Grizzly Buttes in southwestern Wyoming; C. saxea Hay, 1903, from the Upper Miocene Mascall beds on Beaver Creek near Crooked River, Oregon; *C. percrassa* Cope, 1899, a questionable species from Pleistocene deposits of Port Kennedy Cave, Montgomery County, Pennsylvania; and *C. owyheensis* Brattstrom and Sturn, 1959, from Pliocene (Hemphillian) deposits of Dry Creek, a tributary of Crooked Creek, Malhuer County, Oregon, and Upper Pliocene deposits in Twin Falls County, Idaho (Zug, 1969). Several unanswered questions exist about these fossil species. Are they truly members of the genus *Clemmys*? If so, what are the relationships between the various fossil species, and between them and the four living species? These are interesting questions that hopefully someday soon will be answered.

Of the living species, C. guttata is reported from the Pleistocene (Rancholabrean) of Dorchester County, South Carolina (Bentley and Knight, 1993); C. insculpta from Pleistocene (Irvingtonian) deposits in Pennsylvania (Hay, 1923) and Pleistocene (Rancholabrean) sites in northwestern Georgia (Holman, 1967), Pennsylvania (Richmond, 1964), and Tennessee (Parmalee and Klippel, 1981). Early Pleistocene (Blancan) skeletal material assigned to C. muhlenbergii has been found in western Maryland (Holman, 1977), and fossils of C. marmorata date from the Pliocene (Blancan) of California and Oregon and the Pleistocene (Irvingtonian, Rancholabrean) of California (Brattstrom, 1953, 1955; Brattstrom and Sturn, 1959; Miller, 1971; Gustafason, 1978; Dundas et al., 1996). This is not surprising, because the modern emydid fauna of North America in general dates from the Pliocene/Pleistocene.

Intergeneric Relationships. — The four living species of Clemmys are members of the family Emydidae (sensu Gaffney and Meylan, 1988) and, along with the North American species Emydoidea blandingii and the four species of Terrapene plus the Old World species Emys orbicularis, form the "Clemmys complex" (all other members of the family Emydidae belong to the "Chrysemys complex"; Ernst and Barbour, 1989; Ernst et al., 1994). This grouping (the "Clemmys complex") was first proposed by McDowell (1964) under the name "Emys complex" based on skull, jaw, vertebrae, and shell osteology, and has been supported by the studies of Milstead (1969), Bramble (1974), Bickham (1975, 1976), Merkle (1975), Bickham and Baker (1979), Gaffney and Meylan (1988), Seidel and Adkins (1989), Bickham et al. (1996), and Burke et al. (1996).

The relationship of the four genera within the *Clemmys* complex has been debated. The plastron of *Clemmys* is



Figure 1. Upper left: Spotted turtle, *Clemmys guttata* (photo by CHE). Upper right: Wood turtle, *Clemmys insculpta* (photo by James H. Harding). Lower left: Pacific pond turtle, *Clemmys marmorata* (photo by CHE). Lower right: Bog turtle, *Clemmys muhlenbergii* (photo by Roger W. Barbour).

hingeless and almost rigid (some movement, correlated with the feeble plastron buttresses, is possible at the bridge), that of the other three genera hinged and movable. Clemmys is thought to be ancestral to the hinged genera of which Emys is considered primitive, Emydoidea intermediate, and Terrapene most derived (Bramble, 1974). All four genera share an isoelectric focused myoglobin band not found in the Chrysemys complex. On the basis of this distinct myoglobin pattern, Seidel and Adkins (1989) suggested dividing the Emydidae into two subfamilies, of which the Clemmys complex would form the subfamily Emydinae, and all other living emydid species would be assigned to the subfamily Deirochelyinae, an arrangement first suggested by Gaffney and Meylan (1988) on morphological grounds. This partition has been further supported by mitochondrial ribosomal RNA gene studies of Bickham et al. (1996).

Intrageneric Relationships. — Relationships within the genus Clemmys are confusing and controversial. Bickham (1975) found no apparent intrageneric karyotypic differences, but Merkle (1975), in an electrophoretic study of 17 different protein bands (apparently using the same specimens) considered C. guttata and C. muhlenbergii most similar, with C. muhlenbergii next most similar to C. marmorata, and C. insculpta the most primitive member, sharing the least number of protein bands with the other three species. This arrangement is supported by the case of hybridization between wild C. guttata and C. muhlenbergii reported by Ernst (1983). However, some aspects of my observations of carapace morphology (shape, presence or

absence of a dorsal keel, presence or absence of serrations on the posterior rim, shape and dimensions of the neural bones, and shape and dimensions of various scutes) indicate that *C. marmorata* is more similar to *C. guttata* and *C. insculpta* than to *C. muhlenbergii*, and that *C. insculpta* and *C. muhlenbergii* are very similar. This arrangement is supported by a study of mitochondrial DNA variation by Amato et al. (1997). However, analysis of the plastral scute formulae suggests *C. muhlenbergii* forms a separate group from the other three species, and that *C. insculpta* is most similar to *C. marmorata* (Lovich et al., 1991).

The two most discordant studies are those of mitochondrial ribosomal RNA genes by Bickham et al. (1996), and the research by Burke et al. (1996) which included behavioral, life history, morphological, and ribosomal DNA data. Both sets of authors considered the genus *Clemmys* to be paraphyletic.

Bickham et al. (1996) found the genus to be composed of three separate clades, necessitating a new generic arrangement. They found *C. insculpta* and *C. muhlenbergii* closely related and sharing a common ancestor. These two species formed a sister clade to one containing *C. marmorata*, *Emydoidea blandingii* and *Emys orbicularis*. *Clemmys* guttata, however, was yet another monospecific clade. Their data supported name changes within the present genus *Clemmys* that would result in the generic name being only conserved for *C. guttata*, the type species of the genus. The species *C. insculpta* and *C. muhlenbergii* would be assigned to either the genus *Calemys* Agassiz, 1857, or *Glyptemys* Agassiz, 1857, depending on the first revisor, and *C. marmorata* and *Emydoidea blandingii* would be synonymized with the genus *Emys* Duméril, 1806, by priority. This is not surprising to anyone who is familiar with *Clemmys marmorata* and with certain populations of *Emys orbicularis*, as these two turtles, except for the presence or absence of a weak plastral hinge, can be superficially almost identical.

The research of Burke et al. (1996) indicated that C. *insculpta and C. muhlenbergii* formed a single clade, but that C. guttata and C. marmorata, although more closely related to each other than to the other species of Clemmys, were positioned in two monotypic clades. This arrangement would require a new name for C. marmorata; the name Actinemys Agassiz, 1857, is available.

Confusion reigns! Pick new suites of characters and a different arrangement of species results.

Life History Strategies. — Although others may disagree, I believe the major differences in life history strategies among the four species of *Clemmys* may be summarized under three broad concepts: habitat selection, fecundity, and sex determination. Microhabitat differences between the four species can be best defined by water depth, terrestriality, and thermal ecology, and are most critical in eastern North America where three species may live in close proximity.

Clemmys muhlenbergii lives in soft muck substrates with water depths usually only to 1–3 (1–18) cm, and its scant terrestrial activity occurs normally within 1–4 m of water (Lovich and Herman, 1992). Its activity temperature range is 16.2–31.0°C (Ernst, 1977).

Clemmys insculpta mainly uses moving water for hibernation, mating, and movements between semiterrestrial habitats (although aquatic tendencies vary between populations; Harding and Bloomer, 1979), and normally can be found in waters 10–130 cm deep (Harding, 1991; Tuttle, 1996; Tuttle and Carroll, 1997; Niederberger and Seidel, 1999; Ernst, 2001). Terrestrial activity, usually in riparian woodlands to about 100 m from the nearest water, occurs mostly during the summer. Its thermal activity range is 3.4-32.0°C (Ernst, 1986; Farrell and Graham, 1991; Tuttle, 1996).

Clemmys guttata is the most aquatic of the eastern species, usually spending most of its short annual activity period in waters of 5–15 (1–45) cm. Terrestrial activity is most associated with nesting in June or with occasional overland migrations to adjacent waterbodies, but at some localities terrestrial estivation occurs during the summer (Graham, 1995; Lewis and Faulhaber, 1999; Perillo, 1997; pers. obs.). Clemmys guttata can withstand very cold temperatures, and has been found active with cloacal temperatures of 3–32°C (Ernst, 1982; Lewis and Ritzenthaler, 1997).

Clemmys marmorata is much like the wood turtle in its riparian habitat requirements (Rathbun et al., 1992; Holland, 1994). Much time is spent ashore adjacent to its predominately stream habitat. It is active from February to November, but mostly from May to October at cloacal temperatures of 9–34°C (Brattstrom, 1965; Bury, 1972; Goodman and Stewart, 2000). Normally, the spotted turtle is only active from February or March (depending on latitude) to June, with some limited activity in the autumn. Bog and wood turtles are normally active from March to October or November, with some individuals estivating in the summer.

Fecundity is generally low in the genus Clemmys when compared to that of other emydid species. The bog turtle probably lays only one clutch of 1-6 eggs per year, with a limited number of hatchlings overwintering in the nest in the Mid-Atlantic region (Bloomer and Bloomer, 1973; Ernst et al., 1994). Most eggs are deposited in sedge tussocks, as normally no nest cavity is dug. The wood turtle lays only one clutch of 4-18 eggs (Harding, 1991) with no overwintering of hatchlings. The nest is excavated in soil, and the site may be a considerable distance from water (to 700 m, pers. obs.). The spotted turtle is capable of laying two clutches of 1-8 eggs per year (Ernst, 1970; Wilson, 1989; Ernst and Zug, 1994; Litzgus and Brooks, 1998), with some hatchlings overwintering in the nest in the Mid-Atlantic region. Most nest cavities are dug in the bank within 3 m of water, but some use sedge tussocks much as do bog turtles. The western pond turtle probably lays two clutches per year of 1-13 eggs, and some hatchlings overwinter in the nest (Buskirk, 1991; Holland, 1994; Goodman, 1997). The nest site is usually close to water (Rathbun et al., 1992).

There is a dichotomy in the method of sex determination within the genus (which supports division of the genus). The spotted turtle and western pond turtle have temperature dependent sex determination (TSD), while the wood turtle has genetic sex determination (GSD) (Ewert and Nelson, 1991). The sex determining method of the bog turtle remains unknown.

Conservation Problems. — The four species of Clemmys share the problem of discrete and isolated small populations (Ernst, 1976, 1977; Farrell and Graham, 1991; Holland, 1994; Tuttle, 1996), which makes them vulnerable to environmental change, and several factors have adversely affected their populations in the past several decades.

Habitat destruction and alteration are the most serious problems facing the various species of Clemmys. The most serious forms of this are outright destruction or mass alteration of primary habitat (Brattstrom, 1988; Holland, 1994). Along wooded streams, habitat destruction has resulted from clear cutting, commercial and residential development, and highway construction. In agricultural areas the plowing of old fields and draining of wet meadows and bogs has had the same effect, and the flooding of lowlands, while impounding streams, has eliminated the shallow wetlands necessary for bog and spotted turtles. Pollution with pesticides or domestic, commercial, and industrial runoff have poisoned some Clemmys habitats. In addition, some chemicals now entering the environment are known to affect the endocrinology of reptiles by altering concentrations of sex-steroid and thyroid hormones, and lowering the reproductive capability of males by causing feminization (Crain et al., 1998).

Particularly hard hit by habitat alteration is the bog turtle, which by its stringent habitat selection has an intrinsic

vulnerability. It inhabits shallow, boggy seepage areas, usually in pastures or along flood plains of streams in woodlands. Such habitats are naturally the last stages of ecological succession as a waterway dries and changes to land. The species is rendered more vulnerable by its generally small colony size (usually less than 50 individuals, pers. obs.) coupled with low reproductive output (1-6 eggs per clutch, usually 2-3, and one clutch per year; Ernst et al., 1994). Living in such a precarious habitat may not have presented a problem in the past when other such habitats were nearby and bog turtles could migrate to them as their habitat dried. However, over the last several decades, many such habitats have been destroyed or altered. One Pennsylvania population that had about 150 bog turtles in 1965 was reduced to only 5 individuals by 1985 when the habitat was purposely drained to create more pasture for dairy cattle. Similar problems have been noted with the habitats of both spotted turtles and wood turtles, and in the Pacific states, several formerly good stream habitats of the western pond turtle have been virtually destroyed. In Canada agriculture practices have resulted in reduced growth and recruitment, and adult injury, mutilation, and death (Saumure and Bider, 1998).

Commercial trade in the species of Clemmys has increased over the past quarter century. Most of the collected individuals are shipped to Europe or Japan, where they are in great demand for the pet trade and command high prices. The bog turtle, wood turtle and spotted turtle have been particularly hard hit, but the western pond turtle has not escaped the ravages of pet trade collectors. Unfortunately, since hatchlings and juveniles of the four species are secretive and very difficult to collect, and occur naturally in low numbers in many colonies, it is the breeding adults that are usually taken, thus lowering the capacity of the population to recover over time. Commercial trade in C. muhlenbergii is now illegal as the species is protected as endangered or threatened in most of the states in which it resides, and it is federally listed as threatened. The bog turtle was added to Appendix I of the Convention on International Trade in Endangered Species (CITES) in 1992. The wood turtle, C. insculpta, is also protected at least from commercial exploitation practically range-wide, and was added to Appendix II of CITES in 1992. Unfortunately, the spotted turtle and western pond turtle do not have full protection over their range, and this must be addressed in the near future if they are to survive in some states.

Levell (2000) has suggested that the propagation of wood turtles by turtle hobbyist should be encouraged and legally permitted to provide individuals to meet the demands of the pet trade. He believed that regulation of commercial trade in legitimate captive-produced wood turtles and other species under 4 inches would remove stress on wild populations. While this sounds reasonable, it has several drawbacks. Young turtles sold in the pet trade come from eggs laid by adults which have been removed from wild populations, thus lowering the fitness of those populations. Also, a lag period of several years would occur before propagated hatchlings could mature and reach a size desirable for sales, encouraging the collection of wild turtles during this period. If trade in wood turtles opens up, it will probably spur an increase in poaching, not slow it. It takes several years of growth before wood turtles become mature, so, at present, if adult or large subadult wood turtles are offered in the pet trade, very few have been raised in captivity. Levell suggests there is relatively little commerce in adult wood turtles. In my opinion, this is incorrect. I have served as an expert witness for the U.S. Fish and Wildlife Service in the trial of a reptile dealer in Manhattan from whom a large number of adult C. insculpta (both sexes), supposedly from Illinois, were confiscated. Although the species was once included in a checklist of turtles from the Fox River, the wood turtle is considered non-indigenous by the Illinois Department of Natural Resources. I have also been frequently asked to identify wood turtles confiscated from reptile collectors in Virginia, where the species is protected as threatened. If we allow commercial trade in wood turtles, more of these illegal situations will arise.

Another potential problem with captive turtles is the introduction of diseased individuals of any species into the habitats of susceptible populations of healthy *Clemmys*. This has occurred twice when sick captive turtles of other species were released into the habitat of healthy *Clemmys marmorata* (Holland, 1994). It is a well documented occurrence in desert tortoise (*Gopherus agassizii*) populations, and could occur in any North American turtle.

Populations of *Clemmys* may not be able to withstand continued interference by new associations with humans. Garber and Burger (1995) reported that two isolated and protected southern New England wood turtle populations declined and were extirpated in the 10 years following their habitats being opened for hiking and fishing activities. *Clemmys* habitats must be protected as refuges with no, or extremely little, interference from humans if breeding populations are to survive.

Finally, the problem of global warming must be considered. If the climates of North America are undergoing a longterm warming trend, this will adversely affect the species of *Clemmys* in two ways. First, since *C. guttata* and *C. marmorata* have TSD, future clutches incubating at warmer temperatures, at least in northern populations, may produce a preponderance of females at the expense of males, and possibly later all female clutches. This not only would skew the sex ratio away from the normal 1:1, but eventually would provide no replacements for males. Second, the three eastern species and the highland populations of *C. marmorata* are adapted to cool habitats. Warming of these habitats could cause significant ecological effects, and reduce these populations, many of which are already stressed by other factors.

The four species of *Clemmys* are the most threatened turtles in North America, and, if we do not change our ways, they will probably disappear. However, their plight is not hopeless, and with good conservation practices, they will survive. We need new more strict laws protecting them and their habitats in every state within their respective ranges. Not only should such regulations be on the books, but they must be stringently enforced. Habitat regulation is particularly important as the Clemmys are rather specific, particularly the bog turtle, in their habitat requirements. Land must be purchased for creation of natural preserves, such as the Nature Conservancy's bog turtle sanctuary in northeastern Lancaster County, Pennsylvania. Additional funded life history studies are needed — there are too many critical aspects of their biology that are poorly known. Commercial exploitation should be carefully regulated, and offenders severely punished under the law. Finally, we need to inform the public of their plight and the necessary role turtles play in natural communities. Education of the public may be the key to the future of Clemmys and other North American turtles. If the above concerns are addressed, there is no reason why the four Clemmys cannot survive through this new century.

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LITERATURE CITED

- AGASSIZ, L. 1857. Contributions to the natural history of the United States. Vols. 1-2. Little, Brown and Co., Boston, 643 pp.
- AMATO, G.D., BEHLER, J.L., TRYON, B.W., AND HERMAN, D.W. 1997.
 Molecular variation in the bog turtle, *Clemmys muhlenbergii*. In: Van Abbema, J. (Ed.). Proceedings: Conservation, Restoration, and Management of Tortoises and Turtles – An International Conference. N.Y. Turtle and Tortoise Society, pp. 259-262.
- BENTLEY, C.C. AND KNIGHT, J.L. 1993. The oldest spotted turtle: *Clemmys guttata* (Testudines: Emydidae) from the Late Pleistocene (Rancholabrean) Ardis Local Fauna, Dorchester County, South Carolina. South Carolina Geology 36:59-63.
- BICKHAM, J.W. 1975. A cytosystematic study of turtles in the genera *Clemmys, Mauremys* and *Sacalia*. Herpetologica 31:198-204.
- BICKHAM, J.W. 1976. A meiotic analysis of four species of turtles. Genetica 46:193-198.
- BICKHAM, J.W. AND BAKER, R.J. 1979. Canalization model of chromosomal evolution. Bull. Carnegie Mus. Nat. Hist. 13:70-84.
- BICKHAM, J.W., LAMB, T., MINX, P., AND PATTON, J.C. 1996. Molecular systematics of the genus *Clemmys* and the intergeneric relationships of emydid turtles. Herpetologica 52:89-97.
- BLOOMER, T.J. AND BLOOMER, D.M. 1973. New Jersey's bog turtle: destined to extinction? HERP, Bull. New York Herpetol. Soc. 9(3-4):8-12.
- Bramble, D.M. 1974. Emydid shell kinesis: biomechanics and evolution. Copeia 19.74:707-727.
- BRATTSTROM, B.H. 1953. The amphibians and reptiles from Rancho La Brea. Trans. San Diego Soc. Nat. Hist. 11:365-392.
- BRATTSTROM, B.H. 1955. Small herpetofauna from the Pleistocene of Carpinteria, California. Copeia 1955:138-139.
- BRATTSTROM, B.H. 1965. Body temperatures of reptiles. Amer. Midl. Nat. 73:376-422.
- BRATTSTROM, B.H. 1988. Habitat destruction in California with special reference to *Clemmys marmorata*: a perspective. In: DeLisle, H.F., Brown, P.R., Kaufman, B., and McGurty, B.M.

- (Eds.). Proceedings of the Conference on California Herpetology, Southwest. Herpetol. Soc., pp. 13-24.
- BRATTSTROM, B.H. AND STURN, A. 1959. A new species of fossil turtle from the Pliocene of Oregon, with notes on other fossil *Clemmys* from western North America. Bull. So. California Acad. Sci. 58:65-71.
- BURKE, R.L., LEUTERITZ, T.E., AND WOLF, A.J. 1996. Phylogenetic relationships of emydine turtles. Herpetologica 52:572-584.
- BURY, R.B. 1972. Habits and home range of the Pacific pond turtle, *Clemmys marmorata*, in a stream community. Ph.D. Thesis, University of California, Berkeley.
- BURY, R.B. AND ERNST, C.H. 1977. *Clemmys*. Catalog. Amer. Amphib. Rept. 202:1-2.
- BUSKIRK, J.R. 1991. An overview of the western pond turtle, *Clemmys marmorata*. In: Beaman, K.R., Caporaso, F., McKeown, S., and Graff, M.D. (Eds.). Proceedings of the First International Symposium on Turtles and Tortoises: Conservation and Captive Husbandry. Chapman Univ., Orange, California, pp. 16-23.
- COPE, E.D. 1899. Vertebrate remains from Port Kennedy bone deposit. J. Acad. Nat. Sci. Philadelphia Ser. (2)9:193-267.
- CRAIN, D.A., GUILLETTE, L.J., JR., PICKFORD, D.B., PERCIVAL, H.F., AND WOODWARD, A.R. 1998. Sex-steroid and thyroid hormone concentrations in juvenile alligators (*Alligator mississippiensis*) from contaminated and reference lakes in Florida, USA. Environ. Toxicol. Chem. 17:446-452.
- DUNDAS, R.G., SMITH, R.B., AND VEROSUB, K.L. 1996. The Farmed Landfill Locality (Pleistocene, Irvingtonian), Madera County, California: preliminary report and significance. Paleobios 17:50-58.
- DUMÉRIL, A.M.C. 1806. Zoologie analytique, ou methode naturelle de classification des animaux, rendue plus facil a l'aide de tableaux synoptiques. Allais, Paris, 344 pp.
- ERNST, C.H. 1970. Reproduction in *Clemmys guttata*. Herpetologica 26:228-232.
- ERNST, C.H. 1976. Ecology of the spotted turtle, *Clemmys guttata* (Reptilia, Testudines, Testudinidae), in southeastern Pennsylvania. J. Herpetol. 10:25-33.
- ERNST, C.H. 1977. Biological notes on the bog turtle, *Clemmys muhlenbergii*. Herpetologica 33:241-246.
- ERNST, C.H. 1982. Environmental temperatures and activities in wild spotted turtles, *Clemmys guttata*. J. Herpetol. 16:112-120.
- ERNST, C.H. 1983. Clemmys guttata (spotted turtle) x Clemmys muhlenbergii (bog turtle). Natural hybrid. Herpetol. Rev. 14:75.
- ERNST, C.H. 1986. Environmental temperatures and activities in the wood turtle, *Clemmys insculpta*. J. Herpetol. 20:222-229.
- ERNST, C.H. 2001. Some ecological parameters of the wood turtle, *Clemmys insculpta*, in southeastern Pennsylvania. Chelonian Conservation and Biology 4:xxx-xxx.
- ERNST, C.H. AND BARBOUR, R.W. 1989. Turtles of the World. Smithsonian Inst. Press, Washington, D.C., 313 pp.
- ERNST, C.H. AND ZUG, G.R. 1994. Observations on the reproductive biology of the spotted turtle, *Clemmys guttata*, in southeastern Pennsylvania. J. Herpetol. 28:99-102.
- ERNST, C.H., LOVICH, J.E., AND BARBOUR, R.W. 1994. Turtles of the United States and Canada. Smithsonian Inst. Press, Washington, D.C., 682 pp.
- EWERT, M.A. AND NELSON, C.E. 1991. Sex determination in turtles: diverse patterns and some possible adaptive values. Copeia 1991:50-69.
- FARRELL, R.F. AND GRAHAM, T.E. 1991. Ecological notes on the turtle *Clemmys insculpta* in northwestern New Jersey. J. Herpetol. 25:1-9.
- GARBER, S.D. AND BURGER, J. 1995. A 20-year study documenting

the relationship between turtle decline and human recreation. Ecol. Appl. 5:1151-1162.

- GAFFNEY, E.S. AND MEYLAN, P.A. 1988. A phylogeny of turtles. In: Benton, M.J. (Ed.). The Phylogeny and Classification of the Tetrapods, Volume I: Amphibians, Reptiles, Birds. Syst. Assoc. Spec. Vol 35A:157-219.
- GOODMAN, R.H., JR. 1997. Occurrence of double clutching in the southwestern pond turtle, *Clemmys marmorata pallida*, in the Los Angeles basin. Chelonian Conservation and Biology 2:419-420.
- GOODMAN, R.H., JR. AND STEWART, G.R. 2000. Aquatic home ranges of female western pond turtles, *Clemmys marmorata*, at two sites in southern California. Chelonian Conservation and Biology 3:743-745.
- GRAHAM, T.E. 1995. Habitat use and population parameters of the spotted turtle, *Clemmys guttata*, a Species of Special Concern in Massachusetts. Chelonian Conservation and Biology 1:207-214.
- GRAY, E.M. 1995. DNA fingerprinting reveals lack of genetic variation in northern populations of the western pond turtle (*Clemmys marmorata*). Conservation Biology. 9:1244-1254.
- GUSTAFSON, E.P. 1978. The vertebrate faunas of the Pliocene Ringold Formation, south-central Washington. Bull. Mus. Nat. Hist. Univ. Oregon 23:1-62.
- HARDING, J.H. 1991. A twenty year wood turtle study in Michigan: implications for conservation. In: Beaman, K.R., Caporaso, F., McKeown, S., and Graff, M.D. (Eds.). Proceedings of the First International Symposium on Turtles and Tortoises: Conservation and Captive Husbandry. Chapman Univ., Orange, California, pp. 31-35.
- HARDING, J.H. AND BLOOMER, T.J. 1979. The wood turtle, *Clemmys* insculpta...a natural history. HERP, Bull. New York Herpetol. Soc. 15(1):9-26.
- HAY, O.P. 1903. Two new species of turtles from Oregon. Bull. Geol. Dept. Univ. California 3:237-241.
- HAY, O.P. 1908. The fossil turtles of North America. Carnegie Inst. Washington Publ. 75:1-568.
- HAY, O.P. 1923. The Pleistocene of North America and its vertebrated animals from the states east of the Mississippi River and from the Canadian provinces east of longitude 95°. Carnegie Inst. Washington Publ. 322A:1-385.
- HOLLAND, D.C. 1994. The western pond turtle: habitat and history. Report U.S. Dept. Energy Contract No. DE-B179-92BP62137.
- HOLMAN, J.A. 1967. A Pleistocene herpetofauna from Ladds, Georgia. Bull. Georgia Acad. Sci. 25:154-166.
- HOLMAN, J.A. 1977. The Pleistocene (Kansan) herpetofauna of Cumberland Cave, Maryland. Ann. Carnegie Mus. Nat. Hist. 46:157-172.
- JANZEN, F.J., HOOVER, S.L., AND SHAFFER, H.B. 1997. Molecular phylogeography of the western pond turtle (*Clemmysmarmorata*): preliminary results. Chelonian Conservation and Biology 2:623-626.
- LEVELL, J. P. 2000. Commercial exploitation of Blanding's turtle, *Emydoidea blandingii*, and the wood turtle, *Clemmys insculpta*, for the live animal trade. Chelonian Conservation and Biology 3:665-674.
- LEWIS, T.L. AND FAULHABER, C.A. 1999. Home ranges of spotted turtles (*Clemmys guttata*) in southwestern Ohio. Chelonian Conservation and Biology 3:430-434.
- Lewis, T.L. AND RITZENTHALER, J. 1997. Characteristics of hibernacula use by spotted turtles, *Clemmys guttata*, in Ohio. Chelonian Conservation and Biology 2:611-615.
- LITZGUS, J.D. AND BROOKS, R.J. 1998. Reproduction in a northern population of *Clemmys guttata*. J. Herpetol. 32:252-259.

- LOVICH, J.E. AND HERMAN, D.W. 1992. Seasonal activity and movements of bog turtles (*Clemmys muhlenbergii*) in North Carolina. Copeia 1992:1107-1111.
- LOVICH, J.E., LAEMMERZAHL, A.F., ERNST, C.H., AND MCBREEN, J.F. 1991. Relationships among turtles of the genus *Clemmys* (Reptilia: Testudines: Emydidae) as suggested by plastron scute morphology. Zoologica Scripta 20:425-429.
- McDowell, S.B. 1964. Partition of the genus *Clemmys* and related problems in the taxonomy of the aquatic Testudinidae. Proc. Zool. Soc. London 143:239-279.
- MERKLE, D.A. 1975. A taxonomic analysis of the *Clemmys* complex (Reptilia: Testudines) utilizing starch gel electrophoresis. Herpetologica 31:162-166.
- MILLER, W.E. 1971. Pleistocene vertebrates of the Los Angeles Basin and vicinity (exclusive of Rancho La Brea). Bull. Los Angeles Co. Mus. Nat. Hist. 10:1-24.
- MILSTEAD, W.S. 1969. Studies on the evolution of box turtles (genus *Terrapene*). Bull. Florida State Mus. Biol. Sci. 14:1-113.
- NIEDERBERGER, A.J. AND SEIDEL, M.E. 1999. Ecology and status of a wood turtle (*Clemmys insculpta*) population in West Virginia. Chelonian Conservation and Biology 3:414-418.
- PARMALEE, P.W. AND KLIPPEL, W.E. 1981. Remains of the wood turtle *Clemmys insculpta* (LeConte) from a Late Pleistocene deposit in middle Tennessee. Amer. Midl. Nat. 105:413-416.
- PERILLO, K.M. 1997. Seasonal movements and habitat preferences of spotted turtles (*Clemmys guttata*) in northcentral Connecticut. Chelonian Conservation and Biology 2:445-447.
- QUAMMEN, R. 1992. A Late Cretaceous (Maestrictian) lower vertebrate faunule from the Hell Creek Formation of North Dakota. North Dakota Acad. Sci. Proc. 46:41.
- RATHBUN, G.B., SIEPEL, N., AND HOLLAND, D.C. 1992. Nesting behavior and movements of western pond turtles, *Clemmys* marmorata. Southwest. Nat. 37:319-324.
- RICHMOND, N.D. 1964. Fossil amphibians and reptiles of Frankstown Cave, Pennsylvania, Ann. Carnegie Mus. Nat. Hist. 36:225-228.
- RITGEN, F.A. 1828. Versuch einer natürlichen Eintheilung der Amphibien. Nova Acta Physico-Medica Acad. Caes. Leopold.-Carol. Natur. Curio. 14:246-284.
- RUSSELL, L.S. 1934. Fossil turtles from Saskatchewan and Alberta. Trans. Royal Soc. Canada Ser. (3)28:101-111.
- SAUMURE, R.A. AND BIDER, J.R. 1998. Impact of agricultural development on a population of wood turtles (*Clemmys insculpta*) in southern Québec, Canada. Chelonian Conservation and Biology 3:37-45.
- SEELIGER, L.M. 1945. Variation in the Pacific pond turtle. Copeia 1945:150-159.
- SEIDEL, M.E. AND ADKINS, M.D. 1989. Variation in turtle myoglobins (subfamily Emydinae: Testudines) examined by isoelectric focusing. Comp. Biochem. Physiol. 94B:569-573.
- TUTTLE, S.E. 1996. Ecology and natural history of the wood turtle (*Clemmys insculpta*) in southern New Hampshire. Master's Thesis, Antioch College New England Graduate School.
- TUTTLE, S.E. AND CARROLL, D.M. 1997. Ecology and natural history of the wood turtle (*Clemmys insculpta*) in southern New Hampshire. Chelonian Conservation and Biology 2:447-449.
- WILSON, P.R. 1989. Clemmys guttata (spotted turtle). Reproduction. Herpetol. Review 20:69-70.
- Zug, G.R. 1969. Fossil chelonians, *Chrysemys* and *Clemmys*, from the Upper Pliocene of Idaho. Great Basin Nat. 29:82-87.

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