Catalogue of American Amphibians and Reptiles.

Seidel, M.E. and C.H. Ernst. 1996. *Pseudemys*.

Pseudemys Gray
Cooters and Red-bellied Turtles

Pseudemys Gray, 1855 (1856a):197. Type-species, *Pseudemys concinna* (= *Testudo concinna* Le Conte, 1830), designated by Baur, 1893:221.

Ptychemys Agassiz, 1857a:431. Type-species, *Pseudemys concinna* (= *Testudo concinna* Le Conte, 1830), designated by Baur, 1893:221.

Ptychemys Pomel, *in* Agassiz, 1857b:642. *Nomen nudum*.

Nectemys: Agassiz, 1857b:642. Substitute name for *Ptychemys* Pomel.

Clemmys: Strauch, 1862:28 (part).

Emys: Wied-Neuwied, 1865:23 (part).

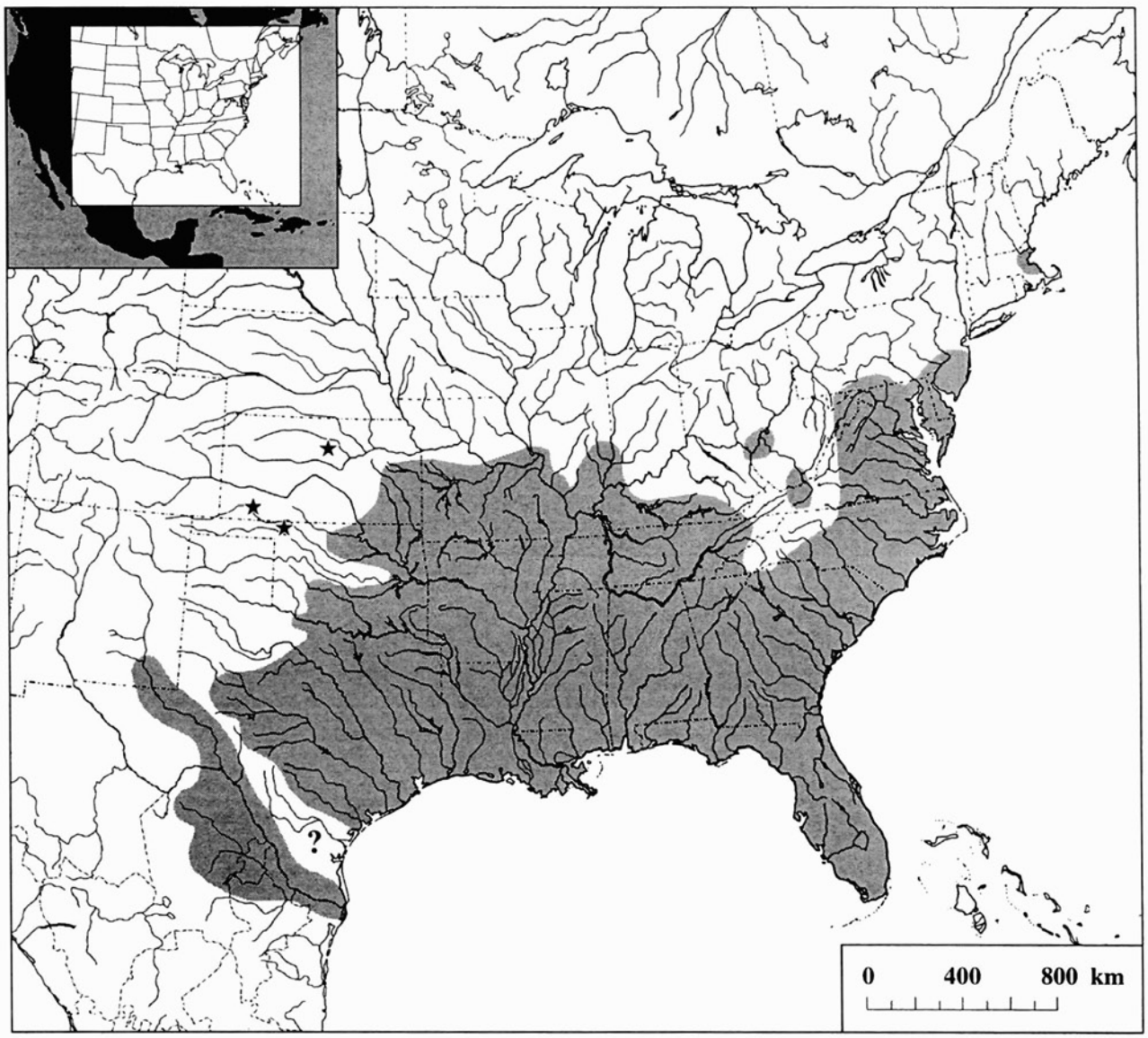
Chrysemys: Boulenger, 1889:69 (part).

Chrysemys (*Pseudemys*): Lindholm, 1929:279.

Pseudomys: Brown, Giuliano, and Hough, 1974:205. *Ex error*.

• **Content.** Seven species are recognized in two species groups: *Pseudemys alabamensis*, *P. nelsoni*, *P. rubriventris* (red-bellied turtles) and *P. concinna*, *P. gorzugi*, *P. peninsularis*, and *P. texana* (cooters). Alternative interpretations of species taxonomy exist for *Pseudemys*. See Remarks.

• **Definition.** Turtles in the genus *Pseudemys* are moderate to large aquatic emydine turtles. Sexually dimorphic size is evident, maximum adult carapace length for males is 33 cm and that of females is 43 cm. The carapace of young individuals is serrated posteriorly and bears a medial keel, whereas older adults are often flat or concave along the midline of the vertebral scutes. The ground color of the carapace is olive, brown, or black, and has a pattern of yellow to orange or red bars, wavy lines, or



Map. Present range of the genus *Pseudemys*. The stars mark extralimital fossil localities; see species accounts for other fossil records. The question mark indicates a region in southern Texas (Nueces River System) which has not been thoroughly surveyed for *Pseudemys*.

concentric circles which may be obscured in older individuals. In hatchlings, the ground color is green. The plastron is relatively large and hingeless with a posterior medial notch. It is pale yellow to orange or coral-colored, and some populations have a dark, dendritic, symmetrical pattern that generally follows the seams. The skin may be brown, olive, green, or black. Yellow stripes are usually present on the head, neck, and limbs, except in some old individuals.

The ventral surface of the lower jaw is relatively flat, and tuberculate denticles are prominent on the median ridge of the alveolar surface of the upper jaw. The cranium has a relatively wide narial opening and large orbits. It is deep anterior to the basisphenoid (36-40% of the condylobasal length) and the zygomatic arch is broad. The tomium of the upper jaw is either rounded or cusped medially.

Adult males have elongated foreclaws and thicker tails with the cloacal vent situated posterior to the carapacial rim. Females have a more vaulted carapace, and their vent is positioned beneath the posterior marginals. Old males in some populations develop a form of melanism or pigment change that is characterized by loss of yellow lines on the soft parts and carapace, accompanied by development of a vermiculated (worm-like) pattern of dark speckled markings on the head, carapace, and plastron.

• **Descriptions and Illustrations.** The genus *Pseudemys* has been described in Ward (1984), Seidel and Smith (1986), Ernst and Barbour (1989), and Ernst et al. (1994). Other descriptions or illustrations pertaining to the genus are: bone (Enlow, 1969), skull (Romer, 1956; McDowell, 1964; Gaffney, 1979), shell (Zangerl, 1969), cervical vertebrae (Williams, 1950), muscles (Guthe, 1981), blood (Dessauer, 1970), pacemaker system of heart (Berger and Burnstock, 1979), brain (Starck, 1979), stereotypic behavior (Carpenter and Ferguson, 1977), and retina (Detwiler et al., 1978).

• **Distribution.** The genus *Pseudemys* is found in the United States from central New Jersey and southern Pennsylvania throughout the Southeast (including peninsular Florida), north to Indiana and Illinois, and west through central Missouri, southeastern Kansas, central Oklahoma, and Texas. Isolated populations occur in eastern Massachusetts and West Virginia. *Pseudemys* is also found in the Rio Grande River system of southeastern New Mexico, southwestern Texas, and northeastern México. Single records for the upper Rio Grande system, Socorro County, New Mexico (Stuart, 1995) and the Monongahela River, Marion County, northern West Virginia (Seidel, 1994) are probable introductions.

• **Fossil Record.** Pleistocene records of *Pseudemys* (referred to *P. nelsoni*) are known from peninsular Florida (Jackson, 1964, 1978; Holman and Clausen, 1984; Holman, 1996), Bartow County, Georgia (Holman, 1985), northwestern Mississippi (Holman, 1995), and Colleton County, South Carolina (Dobie and Jackson, 1979). Pliocene fossils (Early Hemphilian) of an extinct species, *P. caelata*, have been recovered from Levy (Hay, 1908) and Alachua counties, Florida. The latter was originally described as *P. carri* by Rose and Weaver (1966). According to Jackson (1976), *P. caelata* is ancestral to *P. nelsoni*.

Pleistocene fossils of *Pseudemys concinna* have been recovered from Bartow County, Georgia (Holman, 1967), Columbia-Gilchrist County, Florida (Jackson, 1975), Colleton County, South Carolina (Roth and Laerm, 1980), Colbert County, Alabama (Holman et al., 1990), Daviess County, Indiana (Holman, 1995), and Ellsworth, Meade, and Seward counties, Kansas (Holman, 1995). According to Holman (1995), the Pleistocene species, *P. hibbardi*, described by Preston (1979) from Harper County, Oklahoma probably is *P. concinna*. The extinct species, *P. williamsi*, which Rose and Weaver (1966) described from Pliocene remains (Alachua County, Florida), presumably is ancestral to *P. concinna* (Jackson, 1976).

Pleistocene remains of *Pseudemys peninsularis* (*P. floridana*) were reported from Levy, Indian River, and Sarasota counties, Florida (Holman, 1959, 1995, 1996; Holman and Clausen, 1984).

A Pleistocene fossil *Pseudemys* from Bee County, Texas (presumably *P. texana*) was reported by Preston (1979).

Shell fragments from the Lower Miocene, Gilchrist County, Florida may represent a turtle that is ancestral to *Pseudemys* and/or *Trachemys* (Jackson, 1988a).

• **Pertinent Literature.** Species accounts published in the Catalogue of American Amphibians and Reptiles include: *Pseudemys alabamensis* (McCoy and Vogt, 1985), *P. concinna* (Seidel and Dreslik, 1996), *P. gorzugi* (Ernst, 1990a), *P. nelsoni* (Jackson, 1978), *P. rubriventris* (Graham, 1991), and *P. texana* (Etchberger and Iverson, 1990). General accounts relating to both the genus and species are in Smith and Smith (1980), Obst (1985), Ernst and Barbour (1989), Conant and Collins (1991), and Ernst et al. (1994). Other papers are listed by topic as follows: systematics (Carr, 1952; McDowell, 1964; Weaver and Rose, 1967; Holman, 1977; Ernst and Ernst, 1980; Vogt and McCoy, 1980; Dobie, 1981; Seidel, 1981, 1994, 1995; Ward, 1984; Seidel and Smith, 1986; Gaffney and Meylan, 1988; King and Burke, 1989; Ernst, 1990b; Seidel and Jackson, 1990; Fritz, 1991; McCoy and Jacobs, 1991; Seidel and Palmer, 1991; David, 1994; Jackson, 1995; Bickham et al., 1996), common names (Iverson, 1985, 1992; Collins, 1990; Liner, 1994; Frank and Ramus, 1995), karyotype (Stock, 1972; Gorman, 1973; Killebrew, 1977; Bickham and Carr, 1983), hybridization (Mertens, 1968), distribution (Iverson, 1992), phalangeal formulae (McCoy and Jacobs, 1991), neurology (Cosans and Ulinski, 1990), retinal function (Detwiler et al., 1978; Neyton et al., 1981; Piccolino et al., 1981), iodine metabolism (Shellabarger et al., 1956), blood clotting (Brambel, 1941; Dessauer, 1974), immunology (Dahl et al., 1985), protein polymorphism (Seidel, 1994), and nucleotide sequencing (Bickham et al., 1996).

The following additional pertinent literature regarding *Pseudemys alabamensis*, *P. gorzugi*, *P. nelsoni*, *P. rubriventris*, and *P. texana* either was not included or has appeared since those accounts were published: *P. alabamensis* — general accounts (Dobie, 1986) and federal protection (Langton, 1987); *P. gorzugi* — taxonomy (Seidel, 1994) and distribution (Stuart, 1995); *P. nelsoni* — distribution (Powers, 1977; Vitt and Dunham, 1980; Meshaka, 1988; Iverson and Etchberger, 1989; Stevenson and Crowe, 1992), development (Kam, 1993a, 1993b, 1994; Kam and Lillywhite, 1994), behavior (Kramer, 1984, 1989), movements (Kramer, 1995), ecology (Meylan et al., 1992), reproduction (Goodwin and Marion, 1977; Iverson, 1977; Deitz and Jackson, 1979; Kushlan and Kushlan, 1980; Jackson, 1988b, 1989; Kramer and Fritz, 1989; Hunt and Ogden, 1991; Forsman and Shine, 1995), osmoregulation (Dunson and Seidel, 1986), digestion (Bjorndal and Bolten, 1990, 1992, 1993), feeding (Hunt, 1989), predation (Beissinger, 1990), and parasites (Boyce, 1985; Nickol and Ernst, 1987; Boyce and Kazacos, 1991); *P. rubriventris* — geographic variation (Iverson and Graham, 1990), paleoecology (Parris, 1987), predation (Schwab, 1989), oxygen consumption (Graham and Guimond, 1995), thermal relationships (Nutting and Graham, 1993), blood collection methods (Haskell and Pokras, 1994), and headstarting (Stevens, 1988); *P. texana* — distribution (Bridegam et al., 1991), size (Killebrew and Porter, 1989), parasites (McAllister and Upton, 1989, 1992), egg morphology (Rose et al., 1996), nesting (Whiting, 1994), and captive care (Peters, 1989).

Figure. Currently recognized extant species in the genus *Pseudemys*. Cooters (left column, top to bottom): *P. concinna* from Meriwether County, Georgia; *P. gorzugi* from the Rio Grande at Del Rio, Del Rio County, Texas; *P. peninsularis* from Florida; and *P. texana* from central Texas. Red-bellied Turtles (right column, top to bottom): *P. alabamensis* from Baldwin County, Alabama; *P. nelsoni* from the Corkscrew Swamp Sanctuary, Collier County, Florida, and *P. rubriventris* from Baltimore County, Maryland. Photographs of *P. concinna*, *P. gorzugi*, *P. peninsularis*, *P. alabamensis*, and *P. rubriventris* by Suzanne L. Collins and Joseph T. Collins (courtesy of The Center for North American Amphibians and Reptiles); photograph of *P. texana* by Carl H. Ernst; photograph of *P. nelsoni* by Roger W. Barbour (courtesy of Carl H. Ernst).

• **Key to Species.** The catalogue account numbers (when available) are given in parentheses after the species name.

1. a. Tooth-like cusps on upper jaw tomium prominent, length 3-7% of head width 2
   b. Cusps on upper jaw tomium absent or short, less than 2% of head width 6

2. a. Ventral side of cervical scute (underlap) long, usually >50% of dorsal length; distance between inguinal scute and pectoral abdominal sulcus (seam) >8% of carapace length; supratemporal stripes narrow, 5-9% of head width; plastral ground color in living specimens pink, coral, or yellow with an orange tint. Carapace of adults often very dark with orange or red bars, and distinctly rugulose 3
   b. Ventral underlap of cervical scute not long, <50% of dorsal scute length; inguinal scute long, distance from pectoral abdominal sulcus <8% of carapace length; supratemporal stripe width greater than 9% of head width; plastral ground color pale yellow with some orange near edges. Carapace of adults olive with light yellow irregular or concentric lines, and not often rugulose 5

3. a. Gular stripes broad, post-symphyseal stripes >9% of head width; paramedial stripes end in back of eyes; carapace of adults vaulted posteriorly, 55-65° slope in males, 65-75° slope in females .... *P. nelsoni* (210)
   b. Gular stripes not broad, post-symphyseal stripes <9% of head width; paramedial stripes extend forward between the eyes and onto the snout; posterior carapace of adults gradually sloped, less than 50° in males and 58° in females 4

4. a. Carapace of adults flattened medially, vertebral scutes flat to concave; gular stripes narrow, post-symphyseal stripes <7% of head width . *P. rubriventris* (510)
   b. Carapace of adults elevated medially; gular stripes not narrow, post-symphyseal stripes >7% of head width ..... *P. alabamensis* (371)

5. a. Supratemporal stripe broad, >13% of head width; interfemoral sulcus short, <10% of plastron length ... . *P. gorzugi* (461)
   b. Supratemporal stripe not broad, <13% of head width; interfemoral sulcus >10% of plastron length .... *P. texana* (485)

6. a. Anterior margin of carapace retuse, indented toward midline with nuchal bone recessed; dorsal surface of cervical scute narrow posteriorly, <4.5% of carapace length; supratemporal and paramedian head stripes not joined behind eye ..... *P. concinna* (626)
   b. Anterior margin of carapace not indented toward midline (nuchal bone projected forward); dorsal surface of cervical scute wide posteriorly, >4.5% of carapace length; supratemporal and paramedian head stripes confluent behind eye ..... *P. peninsularis*

• **Remarks.** Although the first published reference to *Pseudemys* has often been attributed to Gray's (1855 [1856b]) "Catalogue of Shield Reptiles ...," Webb (1995) stated that the name was first used in Gray (1855 [1856a]).

Gray (1855 [1856a, b]) included *Pseudemys concinna*, *P. hieroglyphica* (= *concinna*), and *P. serrata* (= *rubriventris*) in the genus *Pseudemys* (*sensu stricto*). Prior to that, various species of *Pseudemys* (cooter and red-bellied turtles) were assigned to other composite groups of emydines under *Emys*, *Clemmys*, *Chrysemys*, *Terrapene*, or *Testudo*. Agassiz (1857a) recognized *Ptychemys* (= *Pseudemys*) and assigned slider turtles (*scripta* series) to the genus *Trachemys*. However, Cope (1875) placed the sliders (*Trachemys*) into *Pseudemys* (*sensu lato*), and later Boulenger (1889) lumped both *Trachemys* and *Pseudemys* with painted turtles, under a composite genus *Chrysemys* (*sensu lato*). Boulenger's designation was not readily accepted, but Cope's designation of *Pseudemys*, which included *Trachemys*, prevailed until 1964.

Using skeletal characters, McDowell (1964) resurrected Boulenger's arrangement, *Chrysemys* (*sensu lato*). However, application of *Pseudemys* and *Chrysemys* remained very inconsistent. In 1984, Ward concluded from skeletal analysis that three genera be recognized: *Pseudemys*, *Trachemys*, and *Chrysemys*. Based on a broad survey of characters, Seidel and Smith (1986) determined that slider turtles (*Trachemys*) share as many derived character states with map turtles (*Graptemys*) as they do with cooter and red-bellied turtles (*Pseudemys*). They proposed returning to Agassiz's (1857a) concept (followed by Ward, 1984) of *Pseudemys* (*sensu stricto*), separate from *Trachemys* and painted turtles, *Chrysemys*. This arrangement of three genera has received general acceptance and is now further supported by studies of courtship behavior (Kramer and Fritz, 1989; Seidel and Fritz, in press) and nucleotide sequence data (Bickham et al., 1996).

Ward (1984) partitioned *Pseudemys* into two subgenera: cooters were placed in *Pseudemys*, which included *P. concinna* and *P. floridana*; red-bellied turtles were placed in *Ptychemys*, which included *P. alabamensis*, *P. nelsoni*, *P. rubriventris*, and *P. texana*. Iverson (1992) questioned the placement of *P. texana* in *Ptychemys*, and Seidel (1994) transferred it to the subgenus *Pseudemys*. Nevertheless, Ward's use of the name *Ptychemys* for red-bellied turtles posed a problem. Because Agassiz was first to use *Ptychemys* (= *Pseudemys*) and *P.* (*Testudo*) *concinna* is the type-species (designated by Baur, 1893), *Ptychemys* is not an available name for a subgenus of *P. alabamensis*, *P. nelsoni*, and *P. rubriventris*. Therefore, although red-bellied turtles and cooters appear to represent separate lineages (McDowell, 1964; Seidel, 1994), nomenclatural designation of subgenera in *Pseudemys* should be avoided at present.

Species taxonomy in *Pseudemys* has also had a tumultuous history (see Smith and Smith, 1980; and Seidel, 1981, for reviews). Levels of reproductive isolation and gene flow appear to be variable and difficult to characterize by traditional taxonomic paradigms. Currently other interpretations are available regarding species composition in *Pseudemys*. These include relegation of *P. alabamensis* and *P. nelsoni* to subspecies of *P. rubriventris* (Obst, 1985), recognition of *P. floridana* with *P. peninsularis* as a subspecies (Jackson, 1995), and elevation of *P. c. suwanniensis* to species (Seidel, 1994, 1995).

• **Etymology.** *Pseudemys* derives from the Greek *pseudes*, false or deceptive, and *emys* or *emydos*, a freshwater turtle, hence false turtle, meaning not a member of the genus "*Emys*."

Literature Cited

Agassiz, L. 1857a. The natural history of the United States of America. First monograph. In three parts. Vol. 1, part 2. North American Testudinata. Little, Brown and Co., Boston, Massachusetts.

—. 1857b. The natural history of the United States of America. First monograph. In three parts. Vol. 2, part 3. Embryology of the turtle. Little, Brown and Co., Boston, Massachusetts.

Baur, G. 1893. Notes on the classification and taxonomy of the Testudinata. Proc. Amer. Phil. Soc. 31:210-225.

Beissinger, S.R. 1990. Alternative foods of a diet specialist, the snail kite. Auk 107:327-333.

Berger, P.J. and G. Burnstock. 1979. Autonomic nervous system, p. 1-57. *In* C. Gans, R.G. Northcutt, and P. Ulinski (eds.), Biology of the Reptilia, neurology B, Vol. 10. Academic Press, New York.

Bickham, J.W. and J.L. Carr. 1983. Taxonomy and phylogeny of the higher categories of cryptodiran turtles based on a cladistic analysis of chromosomal data. Copeia 1983:918-932.

—, T. Lamb, P. Minx, and J.C. Patton. 1996. Molecular systematics of the genus *Clemmys* and the intergeneric relationships of emydid turtles. Herpetologica 52:89-97.

Bjorndal, K.A. and A.B. Bolten. 1990. Digestive processing in a herbivorous freshwater turtle: consequences of small-intestine fermentation. Physiol. Zool. 63:1232-1247.

— and —. 1992. Body size and digestive efficiency in a herbivorous freshwater turtle: advantages of small bite size. Physiol. Zool. 65:1028-1039.

— and —. 1993. Digestive efficiencies in herbivorous and omnivorous freshwater turtles on plant diets: do herbivores have a nutritional advantage? Physiol. Zool. 66:384-395.

Boulenger, G.A. 1889. Catalogue of the chelonians, rhynchocephalians, and crocodiles in the British Museum (Natural History). The Trustees (Brit. Mus. Nat. Hist.), London.

Boyce, W.M. 1985. The prevalence of *Sebekia mississippiensis* (Pentastomida) in American alligators (*Alligator mississippiensis*) in north Florida and experimental infection of paratenic hosts. Proc. Helminthol. Soc. Washington 52:278-282.

— and E.A. Kazacos. 1991. Histopathology of nymphal pentastomid infections (*Sebekia mississippiensis*) in paratenic hosts. J. Parasitol. 77:104-110.

Brambel, C.E. 1941. Prothrombin activity of turtle blood and the effect of a synthetic vitamin K derivative. J. Cell Comp. Physiol. 18:221-232.

Bridegam, A.S., A..T. Patterson, B.E. Smith, C.M. Garrett, and M.R. Mateja. 1991. Geographic distribution. *Pseudemys texana*. Herpetol. Rev. 22:25.

Brown, P.S., R. Giuliano, and G. Hough. 1974. Pituitary regulation of appetite and growth in the turtles *Pseudomys* (*sic*) *scripta elegans* and *Chelydra serpentina*. J. Exp. Zool. 187: 205-215.

Carpenter, C.C. and G.W. Ferguson. 1977. Variation and evolution of stereotyped behavior in reptiles, p. 335-554. *In* C. Gans and D.W. Tinkle (eds.), Biology of the Reptilia, ecology and behaviour A, Vol. 7. Academic Press, London.

Carr, A.F. 1952. Handbook of turtles: the turtles of the United States, Canada, and Baja California. Comstock Publ. Assoc. (Cornell Univ. Press), Ithaca, New York.

Collins, J.T. 1990. Standard common and current scientific names for North American amphibians and reptiles. 3rd ed. SSAR Herpetol. Circ. (19):iv + 1-41.

Conant, R. and J.T. Collins. 1991. A field guide to reptiles and amphibians of eastern and central North America. 3rd ed. Houghton Mifflin Co., Boston.

Cope, E.D. 1875. Check-list of North American Batrachia and Reptilia; with a systematic list of the higher groups, and an essay on geographical distribution. Bull. U.S. Natl. Mus. (1):1-104.

Cosans, C.E. and P.S. Ulinski. 1990. Spatial organization of axons in turtle visual cortex: intralamellar and interlamellar projections. J. Comp. Neurol. 296:548-558.

Dahl, D., C.J. Crosby, J.S. Sethi, and A. Bignami. 1985. Glial fibrillary acidic (GFA) protein in vertebrates: immunofluorescence and immunoblotting study with monoclonal and polyclonal antibodies. J. Comp. Neurol. 239:75-88.

David, P. 1994. Liste der reptiles actuels du monde I. Chelonii. Dumerilia 1:7-127.

Deitz, D.C. and D.R. Jackson. 1979. Use of American Alligator nests by nesting turtles. J. Herpetol. 13:510-512.

Dessauer, H.C. 1970. Blood chemistry of reptiles: physiological and evolutionary aspects, p. 1-72. *In* C. Gans and T.S. Parsons (eds.), Biology of the Reptilia, morphology C, Vol. 3. Academic Press, London.

—. 1974. Plasma proteins of Reptilia, p. 187-216. *In* M. Florkin and B.T. Scheer (eds.), Chemical ecology, Vol. 9, Amphibia and Reptilia. Academic Press, New York.

Detwiler, P.B., A.L. Hodgkin, and P.A. McNaughton. 1978. A surprising property of electrical spread in the network of rods in the turtle's retina. Nature (London) 274:562-565.

Dobie, J.L. 1981. The taxonomic relationship between *Malaclemmys* Gray, 1844 and *Graptemys* Agassiz, 1857 (Testudines: Emydidae). Tulane Stud. Zool. Bot. 23:85-102.

—. 1986. Alabama Red-bellied Turtle, p. 38-39. *In* R.H. Mount (ed.), Vertebrate animals of Alabama in need of special attention. Alabama Agric. Exp. Stat., Auburn, Alabama.

— and D.R. Jackson. 1979. First fossil record for the diamondback terrapin, *Malaclemys terrapin* (Emydidae), and comments on the fossil record of *Chrysemys nelsoni* (Emydidae). Herpetologica 35:139-145.

Dunson, W.A. and M.E. Seidel. 1986. Salinity tolerance of estuarine and insular emydid turtles (*Pseudemys nelsoni* and *Trachemys decussata*). J. Herpetol. 20:237-245.

Enlow, D.H. 1969. The bone of reptiles, p. 45-80. *In* C. Gans, A. d'A. Bellairs, and T.S. Parsons (eds.), Biology of the Reptilia, morphology A, Vol. 1. Academic Press, London.

Ernst, C.H. 1990a. *Pseudemys gorzugi*. Cat. Amer. Amphib. Rept.:461:1-461:2.

—. 1990b. Systematics, taxonomy, variation, and geographic distribution of the slider turtle, p. 57-67. *In* J.W. Gibbons (ed.), Life history and ecology of the slider turtle. Smithson. Inst. Press, Washington, D.C.

— and R.W. Barbour. 1989. Turtles of the world. Smithson. Inst. Press, Washington, D.C. and London.

— and E.M. Ernst. 1980. Relationships between North American turtles of the *Chrysemys* complex as indicated by their endoparasitic helminths. Proc. Biol. Soc. Washington 93: 339-345.

—, J.E. Lovich, and R.W. Barbour. 1994. Turtles of the United States and Canada. Smithson. Inst. Press, Washington, D.C. and London.

Etchberger, C.R. and J.B. Iverson. 1990. *Pseudemys texana*. Cat. Amer. Amph. Rept.:485:1-485:2.

Forsman, A. and R. Shine. 1995. Sexual size dimorphism in relation to frequency of reproduction in turtles (Testudines: Emydidae). Copeia 1995:727-729.

Frank, N. and E. Ramus. 1995. A complete guide to scientific and common names of reptiles and amphibians of the world. NG Publ., Inc., Pottsville, Pennsylvania.

Fritz, U. 1991. Balzverhalten und Systematik in der Subtribus Nectemydina 2. Vergleich Oberhalb des Artniveaus und Anmerkungen zur Evolution. Salamandra 27:129-142.

Gaffney, E.S. 1979. Comparative cranial morphology of Recent and fossil turtles. Bull. Amer. Mus. Nat. Hist. 164:65-376.

— and P.A. Meylan. 1988. A phylogeny of turtles, p. 157-219. *In* M.J. Benton (ed.), The phylogeny and classification of the tetrapods, Vol. 1, amphibians, reptiles, birds. Syst. Assoc. Spec. Vol. 35A, Clarendon Press, Oxford, England.

Goodwin, T.M. and W.R. Marion. 1977. Occurrence of Florida Red-bellied Turtle eggs in north-central Florida alligator nests. Florida Sci. 40:237-238.

Gorman, G.C. 1973. The chromosomes of the Reptilia, a cyto-

taxonomic interpretation, p. 349-424. *In* A. B. Chiarelli and E. Capanna (eds.), Cytotaxonomy and vertebrate evolution. Academic Press, London and New York.
Graham, T.E. 1991. *Pseudemys rubriventris*. Cat. Amer. Amph. Rept.:510:1-510:4.
— and R.W. Guimond. 1995. Aquatic oxygen consumption by wintering red-bellied turtles. J. Herpetol. 29:471-474.
Gray, J.E. 1855 (1856a). On some new species of freshwater tortoises from North America, Ceylon and Australia in the British Museum. Proc. Zool. Soc. London 1855:197-202.
—. 1855 (1856b). Catalogue of shield reptiles in the collection of the British Museum. Part I. Testudinata (tortoises). The Trustees (Brit. Mus. Nat. Hist.), London.
Guthe, K.F. 1981. Reptilian muscle: fine structure and physiological parameters, p. 265-354. *In* C. Gans and T.S. Parsons (eds.), Biology of the Reptilia, morphology F, Vol. 11. Academic Press, New York.
Haskell, A. and M.A. Pokras. 1994. Nonlethal blood and muscle tissue collection from redbelly turtles for genetic studies. Herpetol. Rev. 25:11-12.
Hay, O.P. 1908. The fossil turtles of North America. Carnegie Inst. Washington Publ. (75):1-568.
Holman, J.A. 1959. Amphibians and reptiles from the Pleistocene (Illinoian) of Williston, Florida. Copeia 1959:96-102.
—. 1967. A Pleistocene herpetofauna from Ladds, Georgia. Bull. Georgia Acad. Sci. 25:154-166.
—. 1977. Comments on turtles of the genus *Chrysemys* Gray. Herpetologica 33:274-276.
—. 1985. Herpetofauna of Ladds Quarry. Natl. Geog. Res. 1:423-436.
—. 1995. Pleistocene amphibians and reptiles in North America. Oxford Univ. Press, New York.
—. 1996. The large Pleistocene (Sangamonian) herpetofauna of the Williston IIIA site, north-central Florida. Herpetol. Nat. Hist. 4:35-47.
—, G. Bell, and J. Lamb. 1990. A late Pleistocene herpetofauna from Bell Cave, Alabama. Herpetol. J. 1:521-529.
— and C.J. Clausen. 1984. Fossil vertebrates associated with Paleo-Indian artifacts at Little Salt Spring, Florida. J. Vert. Paleontol. 4:146-154.
Hunt, R.H. 1989. Predators of alligator eggs in Okefenokee Swamp National Wildlife Refuge, Georgia. AAZPA Reg. Conf. Proc. 1989:594-596.
— and J.J. Ogden. 1991. Selected aspects of the nesting ecology of American Alligators in the Okefenokee Swamp. J. Herpetol. 25:448-453.
Iverson, J.B. 1977. Reproduction in freshwater and terrestrial turtles of north Florida. Herpetologica 33:205-212.
—. 1985. Checklist of the turtles of the world with English common names. SSAR Herpetol. Circ. (14):1-14.
—. 1992. A revised checklist with distribution maps of the turtles of the world. Priv. printed, Richmond, Indiana.
— and C.R. Etchberger. 1989. The distributions of the turtles of Florida. Florida Sci. 52:119-144.
— and T.E. Graham. 1990. Geographical variation in the redbelly turtle, *Pseudemys rubriventris* (Reptilia: Testudines). Ann. Carnegie Mus. 59:1-13.
Jackson, C.G., Jr. 1964. The status of *Deirochelys floridana* Hay with comments on the fossil history of the genus. Tulane Stud. Geol. 2:103-106.
Jackson, D.R. 1975. A Pleistocene *Graptemys* (Reptilia: Testudines) from the Santa Fe River of Florida. Herpetologica 31:213-219.
—. 1976. The status of the Pliocene turtles *Pseudemys caelata* Hay and *Chrysemys carri* Rose and Weaver. Copeia 1976: 655-659.
—. 1978. *Chrysemys nelsoni*. Cat. Amer. Amph. Rept.:210:1-210:2.
—. 1988a. A re-examination of fossil turtles of the genus *Trachemys* (Testudines: Emydidae). Herpetologica 44:317-325.
—. 1988b. Reproductive strategies of sympatric freshwater emydid turtles in northern peninsular Florida. Bull. Florida St. Mus., Biol. Sci. 33:113-158.
—. 1989. Turtles' use of alligator nests, p. 145. *In* C.A. Ross (ed.), Crocodiles and alligators. Facts on File, New York.
—. 1995. Systematics of the *Pseudemys concinna–floridana* complex (Testudines: Emydidae): an alternative interpretation. Chel. Conserv. Biol. 1:329-333.
Kam, Y.-C. 1993a. Physiological effects of hypoxia on metabolism and growth of turtle embryos. Resp. Physiol. 92:127-138.
—. 1993b. Critical oxygen tension of reptilian embryos. Comp. Biochem. Physiol. 105A:777-783.
—. 1994. Effects of simulated flooding on metabolism and water balance of turtle eggs and embryos. J. Herpetol. 28:173-178.
— and H.B. Lillywhite. 1994. Effects of temperature and water on critical oxygen tension of turtle embryos. J. Exp. Zool. 268:1-8.
Killebrew, F.C. 1977. Mitotic chromosomes of turtles. IV. The Emydidae. Texas J. Sci. 29:245-253.
— and D. Porter. 1989. Size maximum. *Pseudemys texana*. Herpetol. Rev. 20:70.
King, F.W. and R.L. Burke. 1989. Crocodilian, tuatara, and turtle species of the world. A taxonomic and geographic reference. Assoc. Syst. Coll., Washington, D.C.
Kramer, M. 1984. Behavior. *Pseudemys nelsoni*. Herpetol. Rev. 15:113-114.
—. 1989. Individual discrimination in juveniles of two turtles, *Pseudemys nelsoni* and *Pseudemys floridana* (Chelonia, Emydidae). Biol. Behav. 14:148-156.
—. 1995. Home range of the Florida Red-bellied Turtle (*Pseudemys nelsoni*) in a Florida spring run. Copeia 1995:883-890.
— and U. Fritz. 1989. Courtship of the turtle *Pseudemys nelsoni*. J. Herpetol. 23:84-86.
Kushlan, J.A. and M.S. Kushlan. 1980. Everglades alligator nests: nesting sites for marsh reptiles. Copeia 1980:930-932.
Langton, T. (ed.). 1987. Federal protection for two U.S. turtles (terrapins). Herpetofauna News (10):2.
Le Conte, J. 1830. Description of the species of North American tortoises. Ann. Lyceum Nat. Hist. New York 3:91-131.
Lindholm, W.A. 1929. Revidiertes Verzeichnis der Gattungen der rezenten Schildkröten nebst Notizen zur Nomenklatur einiger Arten. Zool. Anz. 81:275-295.
Liner, E.A. 1994. Scientific and common names for the amphibians and reptiles of Mexico in English and Spanish. SSAR Herpetol. Circ. (23):1-113.
McAllister, C.T. and S.J. Upton. 1989. The Coccidia (Apicomplexa: Eimeriidae) of Testudines, with descriptions of three new species. Can. J. Zool. 67:2459-2467.
—. 1992. A new species of *Eimeria* (Apicomplexa: Eimeriidae) from *Pseudemys texana* (Testudines: Emydidae) from north-central Texas. Texas J. Sci. 44:37-41.
McCoy, C.J. and J.F. Jacobs. 1991. Phalangeal formulae in the turtle genera *Chrysemys*, *Pseudemys*, and *Trachemys* (Testudines: Emydidae). J. Herpetol. 25:211-212.
— and R.C. Vogt. 1985. *Pseudemys alabamensis*. Cat. Amer. Amph. Rept.:371:1-371:2.
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.

Mertens, R. 1968. Über Reptilienbastarde, IV. Senckenb. Biol. 49:1-12.

Meshaka, W.E., Jr. 1988. Life history notes. *Pseudemys nelsoni* (mutualism). Herpetol. Rev. 19:88.

Meylan, P.A., C.A. Stevens, M.E. Barnwell, and E.D. Dohm. 1992. Observations on the turtle community of Rainbow Run, Marion County, Florida. Florida Sci.55:219-228.

Neyton, J., M. Piccolino, and H.M. Gerschenfeld. 1981. Involvement of small field horizontal cells in the feedback effects on green cones. Vision Res. 21:1599.

Nickol, B.B. and C.H. Ernst. 1987. *Neoechinorhynchus lingulatus* sp. n. (Acanthocephala: Neoechinorhynchidae) from *Pseudemys nelsoni* (Reptilia: Emydidae) of Florida. Proc. Helminthol. Soc. Washington 54:146-149.

Nutting, W.L. and T.E. Graham. 1993. Preferred body temperatures in five Nearctic freshwater turtles: a preliminary study. Comp. Biochem. Physiol. 104A:243-246.

Obst, F.J. 1985. Schmuckschildkröten. Die Gattung *Chrysemys*. Rev. ed. A. Ziemsen, Wittenberg Lutherstadt.

Parris, D.-C. 1987. Paleosalinity of the lower Hudson River: evidence from zooarchaeology. Dakoterra 3:105-107.

Peters, U.W. 1989. Zwei amerikanische Schildkröten *Pseudemys concinna texana* and *Rhinoclemys pulcherrima incisa*. Aquarium (235):45-56.

Piccolino, M., J. Neyton, and H.M. Gerschenfeld. 1981. Peripheral antagonism in the small field L-horizontal cells (L2-HC) of turtle retina. Vision Res. 21:1579-1580.

Powers, A. 1977. Geographic distribution. *Chrysemys nelsoni*. Herpetol. Rev. 8:84.

Preston, R.E. 1979. Late Pleistocene cold-blooded vertebrate faunas from the mid-continental United States. I. Reptilia; Testudines, Crocodilia. Univ. Michigan Mus. Paleontol. Pap. Paleontol. (19):1-53.

Romer, A.S. 1956. Osteology of the reptiles. Univ. Chicago Press, Chicago, Illinois.

Rose, F.L., T.R. Simpson, and R.W. Manning. 1996. Measured and predicted egg volume of *Pseudemys texana* with comments on turtle egg shape. J. Herpetol. 30:433-435.

— and W.G. Weaver. 1966. Two new species of *Chrysemys* (= *Pseudemys*) from the Florida Pliocene. Tulane Stud. Geol. 5:41-48.

Roth, J.A. and J. Laerm. 1980. A late Pleistocene vertebrate assemblage from Edisto Island, South Carolina. Brimleyana (3):1-29.

Schwab, D. 1989. *Pseudemys rubriventris rubriventris* (Red Bellied Turtle). Catesbeiana 9:33.

Seidel, M.E. 1981. A taxonomic analysis of pseudemyd turtles (Testudines: Emydidae) from the New River, and phenetic relationships in the subgenus *Pseudemys*. Brimleyana (6): 25-44.

—. 1994. Morphometric analysis and taxonomy of cooter and red-bellied turtles in the North American genus *Pseudemys* (Emydidae). Chel. Conserv. Biol. 1:117-130.

—. 1995. How many species of cooter turtles and where is the scientific evidence? — A reply to Jackson. Chel. Conserv. Biol. 1:333-336.

— and M.J. Dreslik. 1996. *Pseudemys concinna*. Cat. Amer. Amph. Rept.:626.1-626.11.

— and U. Fritz. In press. Courtship behavior provides additional evidence for a monophyletic *Pseudemys*, and comments on Mesoamerican *Trachemys* (Testudines: Emydidae). Herpetol. Rev.

— and D.R. Jackson. 1990. Evolution and fossil relationships of slider turtles, p. 68-73. *In* J.W. Gibbons (ed.), Life history and ecology of the slider turtle. Smithson. Inst. Press, Washington, D.C.

— and W.M. Palmer. 1991. Morphological variation in turtles of the genus *Pseudemys* (Testudines: Emydidae) from central Atlantic drainages. Brimleyana (17):105-135.

— and H.M. Smith. 1986. *Chrysemys*, *Pseudemys*, *Trachemys* (Testudines: Emydidae): did Agassiz have it right? Herpetologica 42:242-248.

Shellabarger, C.J., A. Gorbman, F.C. Schatzlein, and D. McGill. 1956. Some quantitative and qualitative aspects of metabolism in turtles. Endocrinology 59:331-339.

Smith, H.M. and R.B. Smith. 1979 (1980). Synopsis of the herpetofauna of Mexico. Vol. 6. Guide to Mexican turtles. Bibliographic addendum III. John Johnson, North Bennington, Vermont.

Starck, D. 1979. Cranio-cerebral relations in Recent reptiles, p. 1-38. *In* C. Gans, R.G. Northcutt, and P. Ulinski (eds.), Biology of the Reptilia, neurology A, Vol. 9. Academic Press, New York.

Stevens, L. 1988. Headstarting the Plymouth Red-bellied Turtle. AAZPA Reg. Conf. Proc. 1988:643-646.

Stevenson, D. and D. Crowe. 1992. Geographic distribution. *Pseudemys nelsoni*. Herpetol. Rev. 23:88.

Stock, A.D. 1972. Karyological relationships in turtles (Reptilia: Chelonia). Can. J. Genet. Cytol. 14:859-868.

Strauch, A. 1862. Chelonologische Studien, mit besonderer Beziehung auf die Schildkrötensammlung der kaiserlichen Akademie der Wissenschaften zu St. Petersburg. Mém. Acad. Imper. Sci. St. Pétersbourg (7th ser.) 5(7):1-196.

Stuart, J.N. 1995. Notes on aquatic turtles of the Rio Grande drainage, New Mexico. Bull. Maryland Herpetol. Soc. 31: 147-157.

Vitt, L.J. and A.E. Dunham. 1980. Geographic distribution. *Chrysemys nelsoni*. Herpetol. Rev. 11:80.

Vogt, R.C. and C.J. McCoy. 1980. Status of the emydine turtle genera *Chrysemys* and *Pseudemys*. Ann. Carnegie Mus. 49:93-102.

Ward, J.P. 1984. Relationships of chrysemyd turtles of North America (Testudines: Emydidae). Spec. Publ. Mus. Texas Tech. Univ. (21):1-50.

Weaver, W.G., Jr. and F.L. Rose. 1967. Systematics, fossil history, and evolution of the genus *Chrysemys*. Tulane Stud. Zool. 14:63-73.

Webb, R.G. 1995. The date of publication of Gray's *Catalogue of Shield Reptiles*. Chel. Conser. Biol. 1:322-323.

Wied-Neuwied, M.A.P. 1865. Verzeichniss der Reptilien, welche auf einer Reise im nördlichen America beobachtet wurden. Nova Acta Acad. Caeser Leopold Verz.-Carol. 32(1):viii + 146 p. + 7 pl.

Whiting, M.J. 1994. Natural history notes. *Pseudemys texana* (nesting interference). Herpetol. Rev. 25:25.

Williams, E.E. 1950. Variation and selection in the cervical central articulations of living turtles. Bull. Amer. Mus. Nat. Hist. 94:505-562.

Zangerl, R. 1969. The turtle shell, p. 311-339. *In* C. Gans, A. d'A. Bellairs, and T.S. Parsons (eds.), Biology of the Reptilia, morphology A, Vol. 1. Academic Press, London.

Michael E. Seidel, Department of Biological Sciences, Marshall University, Huntington, WV 25755, and **Carl H. Ernst**, Department of Biology, George Mason University, Fairfax, VA 22030-4444, USA.

Primary editor for this account, George R. Zug.

Published 20 December 1996 and Copyright © 1996 by the Society for the Study of Amphibians and Reptiles.