Catalogue of American Amphibians and Reptiles.

Zug, G.R. and C.H. Ernst. 1994. *Lepidochelys*.

Lepidochelys Fitzinger
Ridley Sea Turtles

Lepidochelys Fitzinger, 1843:30. Type-species, *"Thalass. olivacea* Fitz.", by monotypy.

Cephalochelys: Gray, 1873a:408. Type-species, *Cephalochelys oceanica* Gray, 1873a (= *Chelonia olivacea* Eschscholtz, 1829), by monotypy.

Colpochelys: Garman, 1880:124. Type-species, *Thalassochelys Kempii* Garman, 1880, by monotypy. Proposed as subgenus for *kempii*, specifically excluded *caouana* and *olivacea*.

Lepidochelis: Tamayo, 1962:373. *Ex error.*

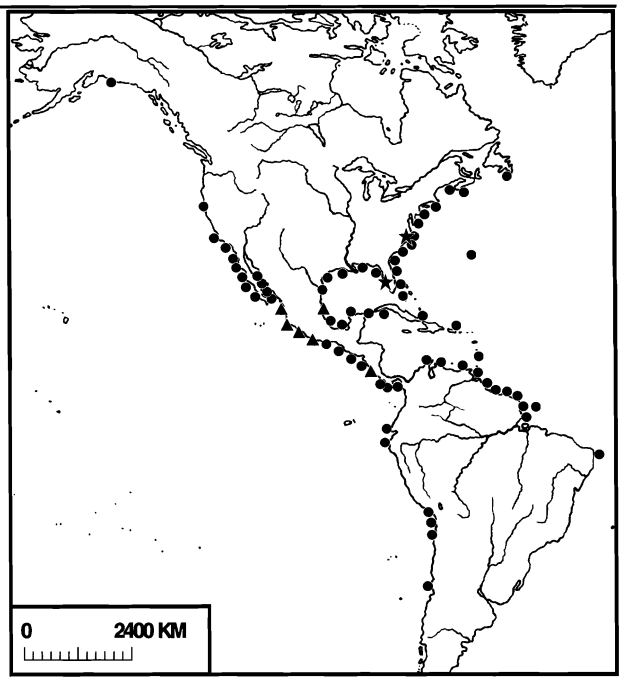
• **Content.** Two species, *Lepidochelys kempii* and *Lepidochelys olivacea*, are recognized.

• **Definition.** Adults range from 595-749 mm in straight carapace length with no apparent sexual dimorphism in body size. These turtles are streamlined for an aquatic existence. The carapace is dorsoventrally depressed, circular to obovate in horizontal outline, and fusiform in vertical outline, thickest anteriorly. The head is moderately enlarged and not retractable into the shell. The neck is thick, broadly and smoothly joining the shell to create a smooth, streamlined surface from head to shell. Forelimbs are modified into flippers for aquatic-flight locomotion. Antibrachium, carpus, and manus are dorsoventrally flattened and fused into a rigid aerofoil shape; no digits are free and 1-2, sometimes 3, claws are present. The hindlimb retains the typical testudine morphology, although the pes is somewhat enlarged and fully webbed with only the claws and proximal-most part of penultimate phalanges projecting from the web. Only the two outermost hindtoes bear claws. The tail is relatively short; its posterior tip just extending beyond the posterior carapace rim in females, and, in males, the tip extends about 50% the length of the last vertebral scute beyond the carapace rim.

The carapace bears a moderately-sized cervical scute that touches the first vertebral and first pleural scutes posteriorly and the first marginal scutes laterally. The five vertebral scutes are large and bordered laterally by 5-7 pairs of pleurals (occasionally to nine in *L. olivacea*). In juveniles, each vertebral bears a narrow, medial projection or partial keel; these projections gradually disappear in older (larger) individuals, and typically only the projection on the fifth vertebral is evident in adults. Eleven to 14 pairs of marginals form the outer edge of the carapace, and usually 3-4 inframarginal scutes occur ventrally on the bridge. Five or six pores (musk or Rathke glands) occur within the inframarginal series of the bridge, typically at the posterior medial edge of each inframarginal scute. The posterior rim of the carapace is slightly serrate in hatchlings and juveniles, but is nearly a smooth curve in adults. The anterior rim of the carapace is slightly indented over the neck. The large nuchal bone lacks a costiform process, but has a ventral area for attachment to the neural arch of cervical vertebra VIII. The carapace is comprised of 12-13 pairs of peripheral bones, eight pairs of costal bones, and 9-15 neurals formed by secondary fragmentation; lateral fontanelles are absent (Zangerl, 1958). The neurals are shortest anteriorly, and either tetragonal or hexagonal in shape.

The rigid plastron usually bears only nine scutes, with a single, triangular gular followed posteriorly by four scute pairs, but occasionally two gulars or an interanal scute may be present. Plastral bones include an entoplastron and two pairs each of epiplastra, hypoplastra, hyoplastra, and xiphiplastra. All plastral elements are reduced, and the hyo- and hypoplastral elements are separated by a large fontanelle.

The medium-sized, triangular-shaped head is covered by a variable number of scales. Major scales include dorsally a pair of nasals, two (sometimes three) pairs of prefrontals, a single frontal, a pair of parietals, and laterally several supraoculars and postoculars bordering the orbit on each side. In the palate, the vomer separates the maxillae and abuts the premaxillae anteriorly. A ridge occurs on the triturating surface of each maxilla, but not on the premaxillae. Both vomers and palatines are smooth and slightly concave. The tomen is unserrated. Both upper and lower jaws are medially hooked. The descending processes of the prefrontals touch only the vomers ventrally. The frontal bone forms the posterodorsal portion of the orbit. Epipterygoidal processes are expanded, and the supraoccipital process is long and lacks a shelf.



Map 1. Distribution of *Lepidochelys* in the Atlantic and eastern Pacific oceans. Triangles represent major nesting beaches; dots mark records of occurrence; stars denote fossil localities.

Cervical vertebrae are as follows: II, anteriorly convex; III, anteriorly convex, posteriorly concave; IV, both anteriorly and posteriorly convex; V-VIII, anteriorly concave, posteriorly convex, occasionally VII is posteriorly doubly convex (Williams, 1950).

Coloration varies between the two species. *Lepidochelys kempii* has a grey, yellowish-grey, or greenish-grey carapace; that of *L. olivacea* is olive to olive-brown or brown. The skin of *L. kempii* is greyish, that of *L. olivacea* olive to brownish. Flipper margins are darker in both species. Hatchlings are dark grey and not countershaded as in other genera.

Adult males have concave plastra, long tails extending well beyond the posterior carapacial rim, and a recurved claw on each foreflipper.

• **Descriptions.** The genus *Lepidochelys* is described in Ernst and Barbour (1989), Ernst et al. (1994), and Pritchard and Trebbau (1984); and both *L. kempii* and *L. olivacea* are described in these same publications. Additional references to the descriptive literature of *L. kempii* are summarized in Wilson and Zug (1991). Descriptions pertaining to the genus are: developmental stages (Crastz, 1982), skull (Bellairs and Kamal, 1981), choanal structure (Parsons, 1968), buccopharyngeal mucosa (Winokur, 1988), limb muscles and movements (Walker, 1971, 1973), kidney tubules (Fraser, 1950), esophageal spines (Yoshie and Honma, 1976), and histology of Rathke's glands (Weldon and Cannon, 1992). The karyotype (of *L. olivacea*) is described by Bhunya and Mohanty-Hejmadi (1986) and Nakamura (1937).

• **Illustrations.** Both *Lepidochelys kempii* and *L. olivacea* are illustrated in Ernst and Barbour (1989) and Ernst et al. (1994), and several life history stages of *L. olivacea* appear in Pritchard and Trebbau (1984). Additional references to the illustrative literature of *L. kempii* are included in Wilson and Zug (1991). The following illustrations pertain to the genus: developmental stages (Crastz, 1982), shell (Deraniyagala, 1939; Obst, 1986), skull (Bellairs and Kamal, 1981; Carr, 1952; Deraniyagala, 1939; Gaffney, 1979), vertebrae, humerus, and femur (Romer, 1956), pelves (Deraniyagala, 1939), pectoral muscles (Walker, 1973), esophageal spines (Yoshie and Honma, 1976); Rathke's gland (Weldon and Cannon, 1992), submarginal pores (Deraniyagala, 1939), head scales (Obst, 1986),

egg shell (Packard and Packard, 1988), hatchlings, juveniles and subadults (Deraniyagala, 1939), and karyotype of *L. olivacea* (Bhunya and Mohanty-Hejmadi, 1986).

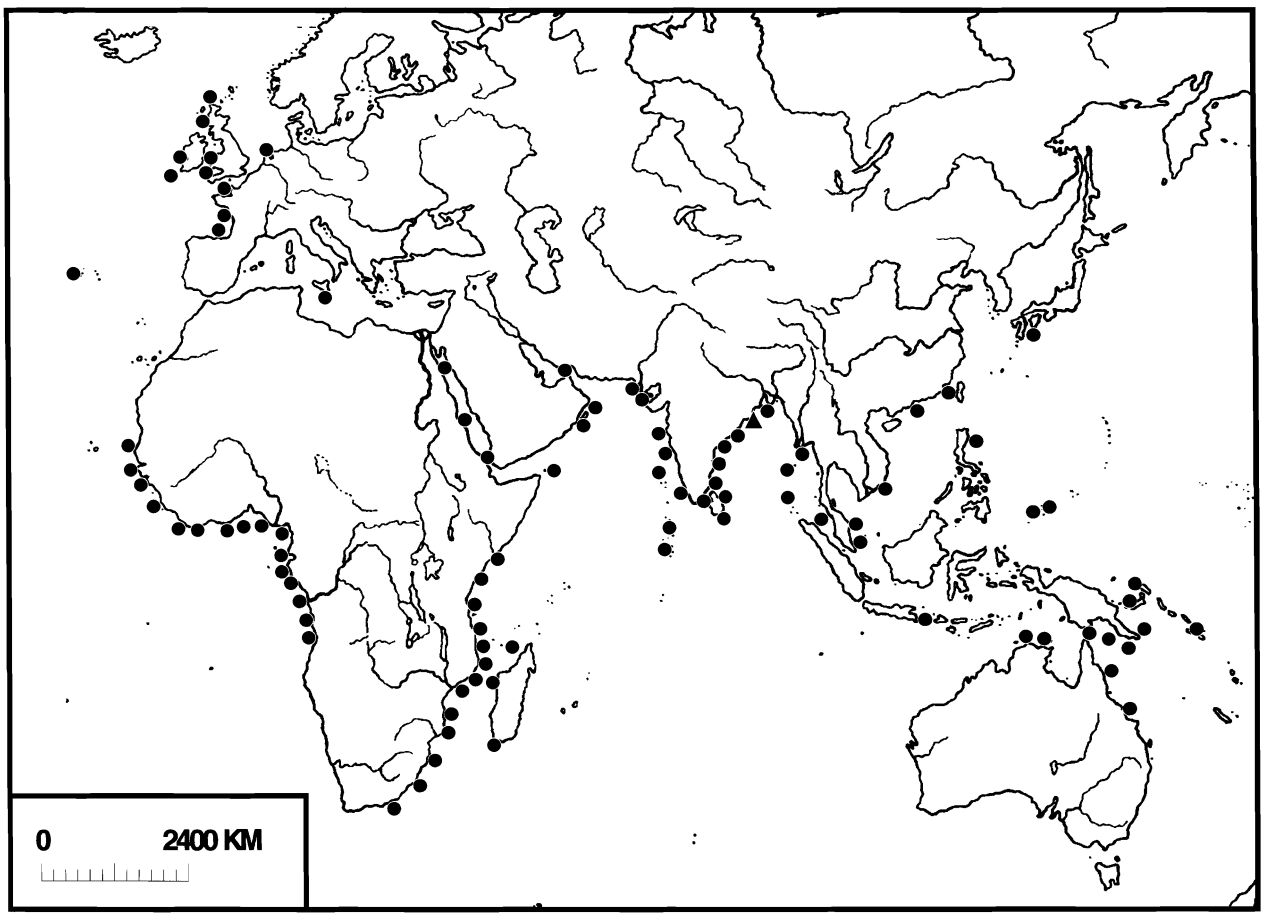
• **Distribution.** Geographic ranges of the two species are largely complementary and non-overlapping (see Wilson and Zug, 1991, and Iverson, 1992). The distribution of *L. kempii* is centered on the Gulf of Mexico and eastern coast of North America south of Cape Cod; also the Gulf Stream likely plays a prominent role in the movements of juveniles. Their occurrence in the east Atlantic and Mediterranean Sea (Brongersma and Carr, 1983) likely represents juveniles that have moved there naturally and not lost individuals that have strayed from the normal range. In contrast, *L. olivacea* populations occur pantropically in all oceans, and have their greatest abundance in the eastern Pacific off Central America, in the Bay of Bengal adjacent to eastern India, in the southwestern Indian Ocean near Mozambique, and the Gulf of Guinea adjacent to West Africa.

• **Fossil Record.** *Lepidochelys* fossils are known from two marine formations in eastern North America: the Pliocene York Creek Formation of North Carolina (Zug, in press), and the Pleistocene Bone Valley Formation of Florida (Dodd and Morgan, 1992). In both sets of fossils, the fossil elements appear to derive from *L. kempii*. *Lepidochelys kempii* has also been reported from an American Indian burial mound in southeastern Florida (Johnson, 1952).

• **Pertinent Literature.** Literature pertaining to the genus is as follows: systematics and evolution (Avise et al., 1992; Bowen et al., 1991), origin of common name (Carr, 1942; Dundee, 1992), karyotype (Bhunya and Mohanty-Hejmadi, 1986; Nakamura, 1937), development (Crastz, 1982; Deraniyagala, 1939; Ewert, 1985; Fraser, 1950; Miller, 1985), shell (Deraniyagala, 1939; Mlynarski, 1961; Zangerl, 1969), cervical vertebrae (Williams, 1950), histology (Gabe, 1970; Yamamoto, 1960; Yoshie and Honma, 1976), endocrinology (Chester Jones et al., 1959; Follett, 1967), blood components and physiology (Bartlett, 1978; Dessauer, 1970), osmoregulation (Dunson, 1969; Thorson, 1968), reproductive physiology (Licht et al., 1982; Owens, 1980), and temperature dependent sex determination (Raynaud and Pieau, 1985; Standora and Spotila, 1985).

Selected additional references for this genus (a more extensive list of references pertaining to *L. kempii* may be found in Wilson and Zug, 1991) include: general accounts (Caldwell, 1966; Carr, 1942, 1952; Carr and Caldwell, 1958; Chavez et al., 1968a; Hildebrand, 1963, 1982; Meylan, 1986; Pope, 1939; Pritchard, 1976; Pritchard and Márquez, 1973), systematics and taxonomy (Carr, 1942; Deraniyagala, 1943, 1961; Dozy et al., 1964; Frair, 1969, 1979; Mertens and Wermuth, 1961; Smith, 1954), conservation (Klima and McVey, 1982), ecology (Burchfield, 1981; Burchfield and Foley, 1983; Burchfield and Mongrell, 1986; Carr and Caldwell, 1956; Chavez, 1969; Chavez et al., 1968b; Dobie et al., 1961; Márquez et al., 1982), embryology, growth, and age (Caldwell, 1962; McVey and Wibbels, 1984), movement and activity patterns (Burchfield, 1981; Burchfield and Foley, 1983; Burchfield and Mongrell, 1986; Carr, 1963; Carr and Caldwell, 1956; Chavez, 1969; Chavez et al., 1968a, 1968b; Henwood and Ogren, 1987; Hildebrand, 1963; McVey and Wibbels, 1984; Mendonça and Pritchard, 1986; Shoop, 1980; Walker, 1971), physiology and endocrinology (Dozy et al., 1964; Frair, 1969; Grassman et al., 1984; Lenhardt et al., 1983, 1986; Rostal et al., 1990; Schwartz, 1978), reproduction (Chavez et al., 1968b; Chavez, 1969; Hirth, 1980; Werler, 1951).

The following additional pertinent literature regarding *Lepidochelys kempii* was either not included in or was published since Wilson and Zug (1991): general accounts (Carr, 1980; Ernst et al., 1994; National Research Council Committee on Sea Turtle Conservation, 1990; Ogren, 1992; USFWS & NMFS, 1992); distribution (Brongersma and Carr, 1983; Duguy, 1990; Duron-Dufrenne, 1989; Gramentz, 1989; Iverson, 1992; Manzella, 1991; Manzella and Williams, 1991, 1992; Morreale et al., 1992; Penhallurick, 1990; Schmidt, 1945); circulatory physiology (Davis, 1991; Stanbenau et al., 1990, 1991); blood cell morphology (Cannon, 1992); gland structure and secretions (Rostal et al., 1991; Weldon and Cannon, 1992); thermal ecology (Burke et al., 1991; Morreale et al., 1992); reproductive biology (Márquez et al., 1992; Rostal et al., 1990); sex determination



Map 2. Distribution of *Lepidochelys* in the Indian and western Pacific oceans. Symbols are as in Map 1. Locality records for this and Map 1 rely on data in Frazier (1990), Iverson (1992), Márquez et al. (1992), and Wilson and Zug (1991).

(Paukstis and Janzen, 1990); growth and aging (Zug, 1991); survivorship and longevity (Iverson, 1991; Snider and Bowler, 1992); pathology (Fontaine et al., 1990); status (Fretey, 1987; Fretey and Lescure, 1992; Márquez et al., 1992; National Research Council Committee on Sea Turtle Conservation, 1990); conservation (Allen, 1990, 1992; Amos, 1989; Eckert, 1991; National Research Council Committee on Sea Turtle Conservation, 1990; Shaver and Fletcher, 1992; Taubes, 1992a, 1992b; Whitaker, 1977; Wibbels, 1992; Woody, 1990, 1991); management and care in captivity (Fontaine et al., 1988; Koi, 1989; Malone et al., 1990; Schroeder, 1989).

• **Key to the Species.** The pertinent catalogue account number is given in parentheses after the species name.

1. a. Color gray; usually only five pairs of pleurals; longitudinal maxillary ridge prominent ..... *Lepidochelys kempii* (509)
   b. Color olive or brown; usually more than five pairs of pleurals; longitudinal maxillary ridge weakly developed or absent ..... *Lepidochelys olivacea*

• **Etymology.** *Lepidochelys* derives from the Greek *lepis* (combining form *lepid-*) for scale and *chelus* for turtle, hence scaled-turtle.

• **Comments, Taxonomic History.** The name *Lepidochelys* has had a chequered history of use and disuse. Fitzinger (1843) divided his earlier *Thalassochelys* into *Halichelys* for his *T. atra* (= *Testudo caretta* Linnaeus) and *Lepidochelys* for his *Thalassochelys olivacea*; he also restricted *Thalassochelys* for his *Thalassochelys Caouana* (= *T. caretta*). The epithets *atra*, *olivacea*, and *caouana* derive from earlier workers, yet Fitzinger appended his name to these species names in the type-species designations.

Shortly thereafter, Gray (1844), with his seeming reluctance to use any nomenclature but his own, proposed *Caouana* for the species *caretta*, *elongata*, and *olivacea*, respectively. He did not specify a type species and definitely considered *Caouana* as having priority over *Thalassochelys*, which is listed in small type beside *Caouana*. The name "*Caouana*" or its derivations had a variety of earlier usages in the systemic literature. The earliest use is likely *Testudo cauanna* Edwards (1771, *in* Catesby, Vol. 2), although *Testudo caouana* Daudin (1802) is more commonly cited. Others used this epithet, including Agassiz (1857) and Günther (1864), who seems to have been one of the last. The usage of these latter authors largely encompassed the sea turtles of the current taxon *Caretta caretta*. If Smith and Smith (1980) are correct that Cocteau (in Cocteau and Bibron, 1843; erroneously listed by Smith and Smith as 1838) proposed *Caouana* for *Testudo caouana* Lacepède, *Caouana* is unquestionably a junior synonym of *Caretta*.

In his monumental study of North American turtles, Agassiz (1857) carefully reviewed the content and characterization of all North American families, genera, and species. He noted his uncertainty about the placement of *Chelonia olivacea* Eschscholtz in either *Thalassochelys* or *Lepidochelys*. Because this "Pacific" sea turtle was outside his geographic area, he made no attempt to resolve its generic placement.

Girard (1858) offered a more definite statement on *Lepidochelys*. He provided an insightful review of cheloniid classification and chose *Lepidochelys* for *olivacea* and *dussumieri* (= *olivacea*). Girard's comments on the historical usage of the generic and specific names remain valuable for anyone tracing the tortuous use-pattern of sea turtle names.

Strauch (1862) thought Girard's choice of generic characters too variable to recognize *Lepidochelys* as a genus and placed *olivacea* in *Thalassochelys*. Günther (1864) offered no explanation for his return to or retention of *Caouana* for Indian Ocean *olivacea*.

Gray (1855, 1870) continued to follow his own 1844 classification. Soon thereafter, he re-examined the relationships of sea turtles, and perhaps with more specimens now available to him, then altered his classification and recognized Fitzinger's *Lepidochelys* and used the combination *Lepidochelys olivacea* (Gray, 1873a, 1873b). He also proposed a new genus *Cephalochelys* for a new species *Cephalochelys oceanica* (= *Chelonia olivacea* Eschscholtz, *fide* Brongersma, 1961). Smith and Smith (1980) cited *C. oceanica* as a *nomen nudum*, assuming Gray's Hand-List... (1873b) preceded his article in the Proceedings... (1873a). The dates in the two publications available to us indicate that this assumption is incorrect.

Garman (1880) recognized the distinctiveness of the "bastard" sea turtle of the Gulf of Mexico and named it *Thalassochelys Kempii*. He noted at the end of his species description that the differences between *kempii* and *olivacea* are "more than specific importance" and proposed the subgeneric name *Colpochelys*.

In 1889, Boulenger took a conservative position in his Catalogue of Chelonians... and recognized four species and two genera (*Chelone*, *Thalassochelys*) of hard-shelled sea turtles. He recognized *kempii* as a distinct species but considered *olivacea* a synonym of *caretta*. Baur (1890) noted in a brief, data-packed article that skeletal morphology suggested a greater sea turtle diversity than that recognized by Boulenger. He specifically recommended the use of *Lepidochelys* for *kempii* and *olivacea*. Boulenger (1890) responded by observing that one of Baur's key characters was variable, thus confirming his use of *Thalassochelys*. Nonetheless, Boulenger's usage was not universally adopted. Van Denburgh (1896) used *Lepidochelys olivacea* in his survey of the Lower Californian herpetofauna.

Stejneger (1907) reassigned *olivacea* to *Caretta*, citing the nomenclatural discussion in his 1902 Herpetology of Porto Rico. The latter discussion, however, addresses only the seniority of *Caretta* as the generic name for *caretta* and its synonyms. Subsequently, *Caretta* was used regularly for the two ridley species (e.g., Siebenrock, 1909). As exceptions, Wieland (1902) adopted *Colpochelys* and was followed by Hay (1908). *Caretta* became firmly embedded in the literature when it appeared in the first edition of the Check List of North American Amphibians and Reptiles (Stejneger and Barbour, 1917).

Deraniyagala (1934) examined the relationships of loggerhead turtles and recognized three genera, *Caretta*, *Colpochelys*, and *Lepidochelys*. He reconfirmed this usage in his exhaustive work on Sri Lankan turtles (1939), and his generic designation was adopted by Pope (1939) in his popular book on North American turtles. Carr (1942) re-examined Deraniyagala's analysis, and though agreeing with the distinctiveness of the three "loggerheads," also recognized the close similarities of *kempii* and *olivacea* and recommended their congeneric status as *Lepidochelys*. Meanwhile Deraniyagala (1943) also reviewed the nomenclature of species assigned to *Caretta* and recognized *Lepidochelys olivacea* with two subspecies. Stejneger and Barbour (1943) adopted Carr's (1942) recommendation and used *Caretta* exclusively for *caretta* and *Lepidochelys* for the two ridley species in the fifth edition of their Checklist. This listing established modern usage, and *Lepidochelys* certainly became firmly fixed with Carr's 1952 Handbook... and his subsequent research articles.

Brongersma (1961) provided an in depth review of the synonyms for the species of *Caretta* and *Lepidochelys*. This publication is an important source for the nomenclature of all cheloniid species.

Literature Cited

Agassiz, L. 1857. Contributions to the natural history of the United States of America, Vol. 1, part 2. North American Testudinata. Little, Brown and Co., Boston. p. 233-452d.

Allen, C.H. 1990. Give 'headstarting' a chance. Marine Turtle Newsl. (51):12-16.

——. 1992. It's time to give Kemp's Ridley head-starting a fair and scientific evaluation! Marine Turtle Newsl. (56):21-24.

Amos, A.F. 1989. Trash, debris and human activities: potential hazards at sea and obstacles to Kemp's Ridley Sea Turtle nesting, p. 42. *In* C.N. Caillouet, Jr. and A.M. Landry, Jr. (eds.), Proceedings of the First International Symposium on Kemp's Ridley Sea Turtle Biology, Conservation and Management. Texas A & M Univ., Sea Grant College Prog. Spec. Publ.

Avise, J.C., B.W. Bowen, T. Lamb, A.B. Meylan, and E. Bermingham. 1992. Mitochondrial DNA evolution at a turtle's pace: evidence for low genetic variability and reduced microevolutionary rate in the Testudines. Mol. Biol. Evol. 9:457-473.

Bartlett, G.R. 1978. Phosphate compounds in reptilian and avian blood cells: developmental changes. Comp. Biochem. Physiol. 61A:191-202.

Baur, G. 1890. The genera of the Cheloniidae. Amer. Nat. 24:486-487.

Bellairs, A. d'A. and A.M. Kamal. 1981. The chondocranium and the development of the skull, p. 1-263. *In* C. Gans and T.S. Parsons (eds.), Biology of the Reptilia, morphology F, Vol. 11. Academic Press, New York.

Bhunya, S.P. and P. Mohanty-Hejmadi. 1986. Somatic chromosome study of a sea turtle, *Lepidochelys olivacea* (Chelonia, Reptilia). Chromosome Info. Serv. (40):12-14.

Boulenger, G.A. 1889. Catalogue of the chelonians, rhynchocephalians, and crocodiles in the British Museum (Natural History). The

Trustees (Brit. Mus., Nat. Hist.), London.
——. 1890. Exhibition of, and remarks upon, the skull of a large sea-snake (*Distira cyanocincta*) and three skulls of the Green Turtle. Proc. Zool. Soc. London 1890:617-618.
Bowen, B.W., A.B. Meylan, and J.C. Avise. 1991. Evolutionary distinctiveness of the endangered Kemp's Ridley Sea Turtle. Nature (London) 352:709-711.
Brongersma, L.D. 1961. Notes upon some sea turtles. Zool. Verh., Leiden (51):1-46.
—— and A.F. Carr. 1983. *Lepidochelys kempi* (Garman) from Malta. Proc. Koninkl. Nederl. Akad. Wetensch. - Amsterdam 86:445-454.
Burchfield, P.M. 1981. Report on United States/Mexico conservation of Kemp's ridley sea turtle at Rancho Nuevo, Tamaulipas, Mexico. 1981. Preliminary report USFWS contract #14-16-0002-81-913.
—— and F.J. Foley. 1983. Report on United States/Mexico conservation of Kemp's ridley sea turtle at Rancho Nuevo, Barra Coma, Tamaulipas, Mexico, 1982. Preliminary Report to Inst. Nac. de la Pesca, México.
—— and J.V. Mongrell. 1986. Report on Republic of Mexico/United States of America conservation effort on behalf of Kemp's ridley sea turtle at Playa de Rancho Nuevo, Tamaulipas, México, 1986.
Burke, V.J., E.A. Standora, and S.J. Morreale. 1991. Factors affecting strandings of cold-stunned juvenile Kemp's ridley and loggerhead sea turtles in Long Island, New York. Copeia 1991:1136-1138.
Caldwell, D.K. 1962. Growth measurements of young captive Atlantic sea turtles in temperate waters. Contr. Sci. Los Angeles Co. Mus. (50):1-8.
——. 1966. A nesting report on the American ridley. Int. Turtle Tortoise Soc. J. 1(1):10-13, 30.
Cannon, M.S. 1992. The morphology and cytochemistry of the blood leukocytes of Kemp's ridley sea turtle (*Lepidochelys kempi*). Can. J. Zool. 70:1336-1340.
Carr, A.F. 1942. Notes on sea turtles. Proc. New England Zoöl. Club 21:1-16.
——. 1952. Handbook of turtles: the turtles of the United States, Canada, Baja California. Comstock Publ. Assoc., Cornell Univ. Press, Ithaca, New York.
——. 1963. Panspecific reproductive convergence in *Lepidochelys kempi*. Ergebn. Biol. 26:298-303.
——. 1980. Some problems of sea turtle ecology. Amer. Zool. 20:489-498.
—— and D.K. Caldwell. 1956. The ecology and migrations of sea turtles, 1. Results of field work in Florida, 1955. Amer. Mus. Novit. (1793):1-23.
—— and ——. 1958. The problem of the Atlantic Ridley turtle (*Lepidochelys kempi*) in 1958. Rev. Biol. Trop., Costa Rica 6:245-262.
Catesby, M. 1771. The Natural History of Carolina, Florida and the Bahama Islands; containing the figures of birds, beasts, fishes, serpents..., with their description in English and French, etc. 2 Vols. 3rd ed. London.
Chavez, H. 1969. Tagging and recapture of the Lora turtle (*Lepidochelys kempi*). Int. Turtle Tortoise Soc. J. 3(4):14-19, 32-36.
——, M. Contreras, and E. Hernandez. 1968a. On the coast of Tamaulipas. Part 1. Int. Turtle Tortoise Soc. J. 2(4):20-29.
——, ——, and ——. 1968b. On the coast of Tamaulipas. Part 2. Int. Turtle Tortoise Soc. J. 2(5):16-19.
Chester Jones, I., J.G. Phillips, and W.N. Holmes. 1959. Comparative physiology of the adrenal cortex, p. 582-612. *In* A. Grobman (ed.), Comparative endocrinology. John Wiley & Sons, New York.
Cocteau, J.T. and G. Bibron. 1843. Reptiles, pp. 1-242 + 30 la. [pl.]. *In* Ramon de La Sagra, fisica, politica y natural de la isla de Cuba. Segunda parte, Historia natural. Tomo IV, Reptiles y peces. Arthus Bertrand, Paris.
Crastz, F. 1982. Embryological stages of the marine turtle *Lepidochelys olivacea* (Eschscholtz). Rev. Biol. Trop. 30:113-120.
Daudin, F.M. 1802. Histoire naturelle, générale et particulière des reptiles. 2. F. Dufart, Paris.
Davis, B.J. 1991. Developmental changes in the blood oxygen transport system of Kemp's ridley sea turtle, *Lepidochelys kempi*. Can. J. Zool. 69:2660-2666.
Deraniyagala, P.E.P. 1934. Relationships among loggerhead turtles (Carettidae). Ceylon J. Sci., sect. B Zool. Geol. 18:207-209.
——. 1939. The tetrapod reptiles of Ceylon. Vol. 1. Testudinates and crocodilians. Dulau and Co., Ltd., London.
——. 1943. Subspecies formation in loggerhead turtles (Carettidae). Spolia Zeylan. 23:79-92.
——. 1961. Some little known characters of the two subspecies of *Lepidochelys olivacea*. Spolia Zeylan. 29:196-201.
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.
Dobie, J.L., L.H. Ogren, and J.F. Fitzpatrick. 1961. Food notes and records of the Atlantic ridley turtle (*Lepidochelys kempi*) from Louisiana. Copeia 1961:109-110.
Dodd, C.K., Jr. and G.S. Morgan. 1992. Fossil sea turtles from Early Pliocene Bone Valley Formation, Central Florida. J. Herpetol. 26:1-8.
Dozy, A.M., C.A. Reynolds, J.M. Still and T.H.J. Huisman. 1964. Studies on animal hemoglobins. I. Hemoglobins in turtles. J. Exp. Zool. 155:343-348.
Duguy, R. 1990. Observations de tortues marines en 1990 (Manche et Atlantique). Ann. Soc. Sci. Nat. Charente-Marit. 7:1053-1057.
Dundee, H.A. 1992. The etymological riddle of the ridley sea turtle. Marine Turtle Newsl. (58):10-12.
Dunson, W.A. 1969. Electrolyte excretion by the salt gland of the Galapagos marine iguana. Amer. J. Physiol. 216:995-1002.
Duron-Dufrenne, M. 1989. *Lepidochelys kempii*, p. 104-105. *In* J. Castanet and R. Guyetant (eds.), Atlas Repartition des Amphibiens et Reptiles de France. Soc. Herpetol. France, Paris.
Eckert, K.L. 1991. Sea turtles recommended for protection in the Caribbean. Marine Turtle Newsl. (52):30.
Ernst, C.H. and R.W. Barbour. 1989. Turtles of the world. Smithsonian Inst. Press, Washington, D.C.
——, J.E. Lovich, and R.W. Barbour. 1994. Turtles of the United States and Canada. Smithsonian Inst. Press, Washington, D.C.
Eschscholtz, J.F. 1829. Zoologischer Atlas, enthaltened Abbildungen und Beschreibungen neuer Thierarten, während des Flottcapitains von Kotzebue zweiter Reise um die Welt, auf der Russisich-Kaiserlichen Kreigsschlupp Predpriaetie in den Jahren 1823-1826, part 1, iv + 17 + 15. G. Reimer, Berlin.
Ewert, M.A. 1985. Embryology of turtles, p. 75-267. *In* C. Gans, F. Billett, and P.F.A. Maderson (eds.), Biology of the Reptilia, development A, Vol. 14. John Wiley & Sons, New York.
Fitzinger, L. 1843. Systema Reptilium. Fasciculus Primus. Amblyglossae. Braumüller et Seidel Bibliopolas, Vindobonae.
Follett, B.K. 1967. Neurohypophysial hormones of marine turtles and of the grass snake. J. Endocrinol. 39:293-294.
Fontaine, C.T., K.W. Indelicato, and J.P. Flanagan. 1990. A congenital lung disorder in a juvenile head-started Kemp's ridley sea turtle, *Lepidochelys kempi*. Herpetol. Rev. 21:80-81.
——, T.D. Williams, and D.B. Revera. 1988. Care and maintenance standards for Kemp's ridley sea turtles (*Lepidochelys kempi*) held in captivity. NOAA Tech. Mem. NMFS-SEFC (202):1-9.
Frair, W. 1969. Aging of serum proteins and serology of marine turtles. Bull. Serol. Mus., New Brunswick, New Jersey (42):1-3.
——. 1979. Taxonomic relations among sea turtles elucidated by serological tests. Herpetologica 35:239-244.
Fraser, E.A. 1950. The development of the vertebrate excretory system. Biol. Rev. 25:150-187.
Frazier, J. 1990. Biology and conservation of sea turtles in the Indian Ocean, p. 364-386. *In* J.C. Daniel and J.S. Serro (eds.), Conservation in developing countries: problems and prospects. Oxford Univ. Press, Bombay, India.
Fretey, J. 1987. Les tortues. Inv. Faune Flore (France) 44:57-106.
—— and J. Lescure. 1992. New protection for sea turtles in France. Marine Turtle Newsl. (57):11-12.
Gabe, M. 1970. The adrenal, p. 263-318. *In* C. Gans and T.S. Parsons (eds.), Biology of the Reptilia, morphology C, Vol. 3. Academic Press, New York.
Gaffney, E.S. 1979. Comparative cranial morphology of Recent and fossil turtles. Bull. Amer. Mus. Nat. Hist. 164:65-376.
Garman, S. 1880. On certain species of Chelonioidae. Bull. Mus. Comp. Zoöl. 6:123-126.
Girard, C. 1858. United States Exploring Expedition, during the years 1838, 1839, 1840, 1841, 1842, under the command of Charles Wilkes, U.S.N. Vol. 20. Herpetology. J. B. Lippincott & Co., Philadelphia.
Gramentz, D. 1989. Marine turtles in the central Mediterranean Sea. Centro (Msida) 1:41-56.
Gray, J.E. 1844. Catalogue of the tortoises, crocodiles, and amphisbaenians in the collection of the British Museum. The Trustees

(Brit. Mus., Nat. Hist.), London.
——. 1855 (1856). Catalogue of the shield reptiles in the collection of the British Museum. Part 1. Testudinata (tortoises). The Trustees (Brit. Mus., Nat. Hist.), London.
——. 1870. Supplement to the catalogue of shield reptiles in the collection of the British Museum. Part 1. Testudinata (tortoises). The Trustees (Brit. Mus., Nat. Hist.), London.
——. 1873a. Notes on the genera of turtles (Oiacopodes) and especially on their skeletons and skulls. Proc. Zool. Soc. London 1873: 395-411.
——. 1873b. Hand-list of the specimens of shield reptiles in the British Museum. The Trustees (Brit. Mus., Nat. Hist.), London.
Grassman, M.A., J.P. McVey, and R. Márquez M. 1984. Olfactory based orientation in artificially imprinted sea turtles. Science 224:83-84.
Günther, A.C.L.G. 1864. The reptiles of British India. The Ray Society, London.
Hay, O.P. 1908. On the existing species of sea turtles, one of them (*Caretta remivaga*) new. Proc. U.S. Natl. Mus. 34:183-198.
Henwood, T.A., and L.H. Ogren. 1987. Distribution and migrations of immature Kemp's ridley turtles (*Lepidochelys kempi*) and green turtles (*Chelonia mydas*) off Florida, Georgia, and South Carolina. Northeast Gulf Sci. 9:153-159.
Hildebrand, H.H. 1963. Hallazgo del área de anidación de la tortuga marina "lora", *Lepidochelys kempi* (Garman), en la costa occidental del Golfo de México (Rept., Chel.). Ciencia (México) 22:105-112.
——. 1982. A historical review of the status of sea turtle populations in the western Gulf of Mexico, p. 447-453. *In* K.A. Bjorndal (ed.), Biology and conservation of sea turtles. Smithsonian Inst. Press, Washington, D.C.
Hirth, H.F. 1980. Some aspects of the nesting behavior and reproductive biology of sea turtles. Amer. Zool. 20:507-523.
Iverson, J.B. 1991. Patterns of survivorship in turtles (Order Testudines). Can. J. Zool. 69:385-391.
——. 1992. A revised checklist with distribution maps of the turtles of the world. Privately printed, Richmond, Indiana.
Johnson, W.R. 1952. *Lepidochelys kempii* and *Caretta caretta caretta* from a south Florida Indian mound. Herpetologica 8:36.
Klima, E.F. and J.P. McVey. 1982. Headstarting the Kemp's ridley turtle, *Lepidochelys kempi*, p. 481-487. *In* K.A. Bjorndal (ed.), Biology and conservation of sea turtles. Smithsonian Inst. Press, Washington, D. C.
Koi, D.B. 1989. Captive-reared Kemp's ridley sea turtle data base management, p. 152. *In* C.W. Caillouet, Jr. and A.M. Landry, Jr. (eds.), Proceedings of the First International Symposium on Kemp's Ridley Sea Turtle Biology, Conservation and Management. Texas A. & M Univ., Sea Grant College Prog. Spec. Publ.
Lenhardt, M.L., S. Bellmund, R.A. Byles, S.W. Harkins, and J.A. Musick. 1983. Marine turtle reception of bone-conducted sound. J. Aud. Res. 23:119-125.
——, R.C. Klinger, and J.A. Musick. 1986. Marine turtle middle-ear anatomy. J. Aud. Res. 25:66-72.
Licht, P., D.W. Owens, K. Cliffton, and C. Penaflores. 1982. Changes in LH and progesterone associated with the nesting cycle and ovulation in the olive ridley sea turtle, *Lepidochelys olivacea*. Gen. Comp. Endocrinol. 48:247-253.
Malone, R.F., K.A. Rusch, and G. Burden. 1990. Kemp's ridley sea turtle waste characterization study: precursor to a recirculating holding system design. J. World Aquacult. Soc. 21:137-144.
Manzella, S. 1991. Head-started Kemp's ridley recaptured in Caribbean. Marine Turtle Newsl. (54):13-14.
—— and J. Williams. 1991. Juvenile head-started Kemp's ridleys found in floating grass mats. Marine Turtle Newsl. (52):5-6.
—— and ——. 1992. The distribution of Kemp's ridley sea turtles (*Lepidochelys kempi*) along the Texas coast: an atlas. NOAA Tech. Rept. NMFS (110).
Márquez M., R., A.P. Sepesca, M. Sánchez P., J. Diaz F., J. Vasconcelos, I. Flores, D.G. Pesca, I. Arquello, M.A. Carrasco, and A. Villanueva. 1992. Research at Ranch Nuevo, Tamaulipas, Mexico in 1990. Marine Turtle Newsl. (58):15.
——, A. Villanueva O., and M. Sánchez Perez. 1982. The population of the Kemp's ridley sea turtle in the Gulf of Mexico - *Lepidochelys kempii*, p. 159-164. *In* K.A. Bjorndal (ed.), Biology and conservation of sea turtles. Smithsonian Inst. Press, Washington, D.C.
McVey, J.P. and T. Wibbels. 1984. The growth and movements of captive-reared Kemp's ridley sea turtles, *Lepidochelys kempi*, following their release in the Gulf of Mexico. NOAA Tech. Memo. NMFS-SEFC-145.
Mendonça, M.T. and P.C.H. Pritchard. 1986. Offshore movements of post-nesting Kemp's ridley sea turtles (*Lepidochelys kempi*). Herpetologica 42:373-381.
Mertens, R. and H. Wermuth. 1961. Proposed use of the Plenary Powers to suppress eight specific names of turtles (Reptilia, Testudines). Bull. Zool. Nomencl. 18:211-213.
Meylan, A.B. 1986. Riddle of the ridleys. Nat. Hist. 95(11):90-96.
Miller, J.D. 1985. Embryology of marine turtles, p. 269-328. *In* C. Gans, F. Billett, and P.F.A. Maderson (eds.), Biology of the Reptilia, development A, Vol. 14. John Wiley & Sons, New York.
Mlynarski, M. 1961. Bemerkungen zur Morphologie des Panzers der Seeschildkröten (Cheloniidae). Zool. Jb. Syst. 88:551-562.
Morreale, S.J., A.B. Meylan, S.S. Sadove, and E.A. Standora. 1992. Annual occurrence and winter mortality of marine turtles in New York waters. J. Herpetol. 26:301-308.
Nakamura, K. 1937. On the chromosomes of some chelonians. (A preliminary note). Japanese J. Genetics 13:240.
National Research Council Committee on Sea Turtle Conservation. 1990. Decline of the sea turtle; causes and prevention. Natl. Acad. Press, Washington, D.C.
Obst, F.J. 1986. Turtles, tortoises and terrapins. St. Martin's Press, New York.
Ogren, L.H. 1992. Atlantic ridley turtle *Lepidochelys kempii* (Garman) family Cheloniidae order Testudines, p. 100-104. *In* P.E. Moler (ed.), Rare and endangered biota of Florida. Vol. III. Amphibians and reptiles. Univ. Press of Florida, Gainesville.
Owens, D.W. 1980. The comparative reproductive physiology of sea turtles. Amer. Zool. 20:549-563.
Packard, G.C. and M.J. Packard. 1988. The physiological ecology of reptilian eggs, p. 523-605. *In* C. Gans and R.B. Huey (eds.), Biology of the Reptilia, ecology B, defense and life history, Vol. 16. Alan R. Liss, Inc., New York.
Parsons, T.S. 1968. Variation in the choanal structure of Recent turtles. Can. J. Zool. 46:1235-1263.
Paukstis, G.L. and F.J. Janzen. 1990. Sex determination in reptiles: summary of effects of constant temperatures of incubation on sex ratios of offspring. Smithson. Herpetol. Inform. Serv. (83):1-28.
Penhallurick, R.D. 1990. Turtles off Cornwall, the Isles of Scilly and Devonshire. Dyllansow Pengwella, Trispen Truro.
Pope, C.H. 1939. Turtles of the United States & Canada. Alfred A. Knopf, New York.
Pritchard, P.C.H. 1976. Endangered species: Kemp's Ridley turtle. Florida Nat. 49(3):15-19.
—— and R. Márquez M. 1973. Kemp's ridley turtle or Atlantic ridley, *Lepidochelys kempi*. IUCN Monogr. (2):1-30.
—— and P. Trebbau. 1984. Turtles of Venezuela. Soc. Stud. Amphib. Rept. Contrib. Herpetol. 2:1-414.
Raynaud, A. and C. Pieau. 1985. Embryonic development of the genital system. p. 149-300. *In* C. Gans and F.B. Billett (eds.), Biology of the Reptilia, development B, Vol. 15. John Wiley & Sons, New York.
Romer, A.S. 1956. Osteology of the reptiles. Univ. Chicago Press, Chicago, Illinois.
Rostal D.C., J.S. Grumbles, and D.W. Owens. 1990. Nesting physiology of wild Kemp's ridley sea turtles, *Lepidochelys kempi*. Amer. Zool. 30:123A.
——, J.A. Williams, and P.J. Weldon. 1991. Rathke's gland secretion by loggerhead (*Caretta caretta*) and Kemp's ridley (*Lepidochelys kempi*) sea turtles. Copeia 1991:1129-1132.
Schmidt, K.P. 1945. Problems in the distribution of the marine turtles. Marine Life 1(3):7-10.
Schroeder, B.A. 1989. Marine turtle data base management: National Marine Fisheries Service — Miami Laboratory, p. 153-156. *In* C.W. Caillouet, Jr. and A.M. Landry, Jr. (eds.), Proceedings of the First International Symposium on Kemp's Ridley Sea Turtle Biology, Conservation and Management. Texas A & M Univ., Sea Grant College Prog. Spec. Publ.
Schwartz, F.J. 1978. Behavioral and tolerance responses to cold water temperatures by three species of sea turtles (Reptilia, Cheloniidae) in North Carolina. Florida Mar. Res. Publs. (33):16-18.
Shaver, D.J. and M.R. Fletcher. 1992. Response to Taubes (1992a). Science 257:465-466.
Shoop, C.R. 1980. Sea turtles in the northeast. Maritimes (Univ. of Rhode Island), November 1980:9-11.
Siebenrock, F. 1909. Synopsis der rezenten Schildkröten mit Berücksichtigung der in historischer Zeit ausgestorbenen Arten. Zool.

Jahrb., suppl. 10:427-618.
Smith, F.G.W. 1954. Taxonomy and distribution of sea turtles. Fishery Bull. Fish Wildl. Serv. 55:513-515.
Smith, H.M. and R.B. Smith. 1980. Synopsis of the herpetofauna of Mexico. Vol. 6. Guide to Mexican turtles. Bibliographic addendum III. (1979) John Johnson, North Bennington, Vermont.
Snider, A.T. and J.K. Bowler. 1992. Longevity of reptiles and amphibians in North American collections. 2nd ed. Soc. Stud. Amphib. Rept. Herpetol. Circ. (21):1-40.
Stabenau, E.K., T.A. Heming, and J.F. Mitchell. 1991. Respiratory, acid-base and ionic status of Kemp's ridley sea turtles (*Lepidochelys kempi*) subjected to trawling. Comp. Biochem. Physiol. 99A:107-111.
——, C.G. Vanoye, and T.A. Heming. 1990. HCO3-/Cl-exchange in Kemp's ridley sea turtle erythrocytes. The Physiologist 33(4):A-63.
Standora, E.A. and J.R. Spotila. 1985. Temperature dependent sex determination in sea turtles. Copeia 1985:711-722.
Stejneger, L. 1904. The herpetology of Porto Rico. Rep. U.S. Natl. Mus. for 1902:551-724.
——. 1907. Herpetology of Japan and adjacent territory. U.S. Natl. Mus. Bull. (58):xx +577 p.
—— and T. Barbour. 1917. A check list of North American amphibians and reptiles. Harvard Univ. Press, Cambridge, Massachusetts.
—— and T. Barbour. 1943. A check list of North American amphibians and reptiles. 5th ed. Bull. Mus. Comp. Zoöl. 93:xix + 260 p.
Strauch, A. 1862. Chelonologische Studien, mit besonderer Beziehung auf die Schildkrötensammlung der kaiserlichen Akademie der Wissenschaften zu St.-Petersburg. Mem. Acad. Imp. Sci. St.-Petersbourgh, Series 7, 5(7):1-196.
Tamayo, J. 1962. Geografía general de México. 2nd ed. Tomo III. Geografía, biológica y humana. Inst. Méx. Inv. Económicas, México, D.F.
Taubes, G. 1992a. A dubious battle to save Kemp's ridley sea turtle. Science 256:614-616.
——. 1992b. Response to Shaver and Fletcher (1992) and Wibbels (1992). Science 257:466-467.
Thorson, T.B. 1968. Body fluid partitioning in Reptilia. Copeia 1968: 592-601.
U.S. Fish & Wildlife Service and National Marine Fisheries Service. 1992. Recovery plan for the Kemp's ridley sea turtle (*Lepidochelys kempii*). Natl. Mar. Fish. Serv., St. Petersburg, Florida.
Van Denburgh, J. 1896. Additional notes on the herpetofauna of Lower California. Proc. California Acad. Sci., Second Series, 5:1004-1008.
Walker, W.F., Jr. 1971. Swimming in sea turtles of the family Cheloniidae. Copeia 1971:229-233.
——. 1973. The locomotor apparatus of Testudines, p. 1-100. *In* C. Gans and T.S. Parsons (eds.), Biology of the Reptilia, morphology D, Vol. 4. Academic Press, London.
Weldon, P.J. and M.S. Cannon. 1992. Histology and histochemistry of Rathke's glands of juvenile Kemp's ridley sea turtle (*Lepidochelys kempi*). Zool. Jb. Anat. 122:in press.
Werler, J.E. 1951. Miscellaneous notes on the eggs and young of Texas and Mexican reptiles. Zoologica (New York) 36:37-48.
Whitaker, R. 1977. Notes on turtle conservation in India. Marine Turtle Newsl. (3):3.
Wibbels, T. 1992. Response to Taubes [1992a]. Science 257:465.
Wieland, G.R. 1902. Notes on the Cretaceous turtles, *Toxochelys* and *Archelon*, with a classification of the marine Testudinata. Amer. J. Sci. 14:95-108.
Williams, E.E. 1950. Variation and selection in the cervical central articulations of living turtles. Bull. Amer. Mus. Nat. Hist. 94:505-562.
Wilson, R.V. and G.R. Zug. 1991. *Lepidochelys kempii* (Garman). Cat. Amer. Amphib. Rept.:509.1-509.8.
Winokur, R.M. 1988. The buccopharyngeal mucosa of the turtles (Testudines). J. Morphol. 196:33-52.
Woody, J.B. 1990. Is 'headstarting' a reasonable conservation measure? 'On the surface, yes; in reality, no.' Marine Turtle Newsl. (50):8-11.
——. 1991. Guest editorial: it's time to stop headstarting Kemp's ridley. Marine Turtle Newsl. (55):7-8.
Yamamoto, Y. 1960. Comparative histological studies of the thyroid gland of lower vertebrates. Folia Anat. Japon. 34:353-387.
Yoshie, S. and Y. Honma. 1976. Light and scanning electron microscopic studies on the esophageal spines in the Pacific ridley turtle, *Lepidochelys olivacea*. Arch. Histol. Japon 38:339-346.
Zangerl, R. 1958. Die oligocanen Meerschildkröten von Glarus. Schweiz. Päleontol. Abh. 73:1-56.
——. 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.
Zug, G.R. 1991. Estimates of age and growth in *Lepidochelys kempii* from skeletochronological data. Proceedings of the Tenth Annual Workshop on Sea Turtle Biology and Conservation. NOAA Tech. Mem. NMFS-SEFC (278):285-286.
——. In press. Turtles of the Lee Creek Mine (Pliocene: North Carolina). Smithsonian Contrib. Paleobiol.

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