



**FLORIDA
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BULLETIN

**A NEW FOSSIL LAND TORTOISE IN THE
GENUS *CHELONOIDIS* (TESTUDINES: TESTUDINIDAE)
FROM THE NORTHERN BAHAMAS, WITH AN OSTEOLOGICAL
ASSESSMENT OF OTHER NEOTROPICAL TORTOISES**

Richard Franz and Shelley E. Franz

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**Send communications concerning purchase or exchange
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Managing Editor of the BULLETIN
Florida Museum of Natural History
University of Florida
PO Box 117800
Gainesville, FL 32611-7800 U.S.A.
Phone: 352-392-1721
Fax: 352-846-0287
e-mail: lrfranz08@gmail.com

IN MEMORIUM
SHELLEY ETHERIDGE FRANZ
1952-2008



We dedicate this issue of the Bulletin of the Florida Museum of Natural History on Bahamian fossil tortoises to Shelley E. Franz, who passed away on 1 July 2008, following a prolonged illness. Shelley worked as a volunteer researcher since 1984 in the fields of herpetology and vertebrate paleontology at the Florida Museum of Natural History. She participated in museum-sponsored research in Haiti, Cayman Islands, The Bahamas, Florida, Nebraska, New Mexico, and Wyoming. Shelley was most recently engaged with her husband Dick in the descriptions of fossil tortoise faunas from The Bahamas, Turks and Caicos Islands, and the White River Badlands of northwestern Nebraska.

Shelley Franz was first and foremost an educator. She had taught in public schools in Florida, North Carolina, and Virginia for more than 15 years. Shelley received her BS in geology and teaching from East Carolina State University in 1979 and her MA in museum education from the College of William and Mary in 2004. Prior to her illness, Shelley was enrolled in a PhD program in the College of Education at the University of Florida.

During her career, Shelley worked for Florida Sea Grant and Florida Environmental Education Service Project (both at the University of Florida), U.S. Geological Survey (Water Resources, Tampa), Morningside Nature Center, Samuel Harn Art Museum, Watermen's Museum (in Yorktown, Virginia), and Synergy Design Group (a Tallahassee design firm developing museum exhibits). She was a volunteer researcher at the Ordway-Swisher Biological Station, conducting botanical surveys, sampling amphibians and reptiles, and participating in interviews with local families and in searches of historic documents for a study on the environmental and cultural history of the station. Shelley was also a co-author on several scientific papers and abstracts on Florida crayfishes, tortoises, and most recently fossil vertebrates associated with Bahamian blue holes, the latter appearing in the Proceedings of the National Academy of Sciences (PNAS) and the Bulletin of the Florida Museum of Natural History.

Shelley was a member of the writing team with ecologists Peter Feinsinger and Maria Minno, who produced the *Handbook to Schoolyard Plants and Animals of North Central Florida*, sponsored by the Bingham Environmental Education Foundation and the Nongame Wildlife Program of the Florida Game and Fresh Water Fish Commission. Upon her death, Pete Feinsinger wrote, "It was a pleasure and honor to work with Shelley so long ago, when we, a ragtag bunch of rebels with a cause, started the local natural history movement, which has since grown into a many pronged, pedagogically complete initiative in 14 countries, all in Latin America. Without Shelley's enthusiasm and drive that might never have happened. I will always remember her."

Shelley Franz is survived by her husband Richard (Dick) Franz, three adult children (Jeffrey Franz, Lara Hollberg, and Cooper Partin), and six grandchildren. She is missed.

R. Franz

A NEW FOSSIL LAND TORTOISE IN THE GENUS *CHELONOIDIS* (TESTUDINES: TESTUDINIDAE) FROM THE NORTHERN BAHAMAS, WITH AN OSTEOLOGICAL ASSESSMENT OF OTHER NEOTROPICAL TORTOISES

Richard Franz and Shelley E. Franz¹

ABSTRACT

An extinct tortoise, *Chelonoidis alburyorum* n. sp., is described from nearly complete, beautifully preserved fossils from Sawmill Sink, a deep inland blue hole and cave system, on Great Abaco Island, Little Bahama Bank, in the northern Bahamas. This tortoise is part of an extensive fossil fauna in peat deposits associated with an immense debris cone in the entry shaft of this water-filled cave. The peat fauna also includes intact skeletons, skulls, and isolated bones of Cuban crocodiles (*Crocodylus rhombifer*), large birds, native rodents (*Geocapromys ingrahami*), and bats. The turtle remains include the first complete skull, first intact shells, and first associated vertebrae and appendicular skeletons of a tortoise from The Bahamas and/or West Indies. A morphological assessment of this tortoise and other Neotropical tortoises shows greater similarity of this new species with modern *Chelonoidis nigra* from the Galápagos Islands and fossils from the greater Caribbean area, than with the Cuban *Chelonoidis cubensis* or living and fossil continental *Chelonoidis*.

AMS radiocarbon dates obtained from bones from the holotype and female paratype of the new tortoise, and from three Cuban crocodiles from Sawmill Sink, indicate a late Holocene age (2,580-3,820 yrs BP) for the peat deposits that produced the fossils of *Chelonoidis alburyorum*. Two other fossil faunas from this sink are thought to be older, possibly Pleistocene in age. These older fossils lack sufficient carbon to permit reliable radiometric dating. *Chelonoidis alburyorum* is one of a series of tortoise fossils recently found in blue holes, caves, and archaeological sites in the Bahamian archipelago, including the Turks and Caicos Islands, BWI. Two other fossil species from Abaco and the Turks and Caicos Islands, both in the genus *Chelonoidis*, are also new to science and will be described elsewhere. Affinities of the fossils from other Bahamian banks remain unstudied. A morphological assessment of Neotropical tortoises shows greater similarities between the new species, modern *Chelonoidis nigra*, and to a lesser degree fossils from the greater Caribbean than with the Cuban *Chelonoidis cubensis* and continental *Chelonoidis*.

Key Words: new fossil tortoise, Testudinidae, *Chelonoidis*, inland blue holes, Abaco, The Bahamas, late Holocene.

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¹ Florida Museum of Natural History, University of Florida, P.O. Box 117800, Gainesville, FL 32611-7800

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INTRODUCTION

Fossil reptiles from the Bahamian archipelago have been reported from Banana Hole sinkhole on New Providence Island, caves on north Andros, both on the Great Bahama Bank (Auffenberg 1967, Pregill 1982), a cave on San Salvador (Olson, Pregill, & Hilgartner 1990), and an archeological site and a cave from the Turks and Caicos Islands (Carlson 1999, Franz, et al. 2001). The first reports of vertebrate fossils from Bahamian inland blue holes were two specimens of Cuban crocodiles (*Crocodylus rhombifer*) from Dan's Cave, near Sawmill Sink, on Abaco, collected by divers in 1994 (Franz, et al. 1995). This was the first report of *C. rhombifer* from the Bahamian archipelago. Fossil Cuban crocodiles were previously known from Cuba (Leidy 1868, Varona 1966, 1984) and Grand Cayman (Morgan & Patton 1979, Morgan, et al. 1993, Morgan 1994). Natural populations still exist in southwestern Cuba (Varona 1966, Morgan, et al. 1993).

Cave diver Brian Kakuk made the initial discoveries of vertebrate fossils at Sawmill Sink on Great Abaco Island, Little Bahama Bank, The Bahamas, in December 2004 (Fig.1). The first tortoise fossils were recov-

ered in the sink by Kakuk in February 2005. Physical descriptions of Dan's Cave and Sawmill Sink have been published elsewhere (Franz, et al. 1995, Steadman, et al. 2007).

Extensive bone accumulations, partially exposed in plant-rich peat deposits, were revealed by intense diving efforts in Sawmill Sink between 2005 and 2008. The peat fauna consists of tortoises, Cuban crocodiles, native rodents (*Geocapromys ingrahami abaconis*), and birds (Steadman, et al. 2007). Radiocarbon dates reveal a late Holocene age (2,580-3,820 yrs BP) for two tortoises and three crocodiles (Steadman, et al. 2007).

Peat forms a thick mantle over a massive debris cone that nearly fills the flooded entrance shaft of Sawmill Sink. The peat consists of well-preserved wood, leaves, flowers, fruits, seeds, pollen, and insects. Florida Museum paleobotanists have identified 40 taxa of fungi, spike mosses, ferns, gymnosperms, monocots, and dicots from three cores and several grab samples collected at three different water depths in Sawmill Sink (Steadman, et al. 2007). Pine fossils dominated the upper core, but were absent from the two deeper cores. Plant species of the coppice (tropical dry forest) were

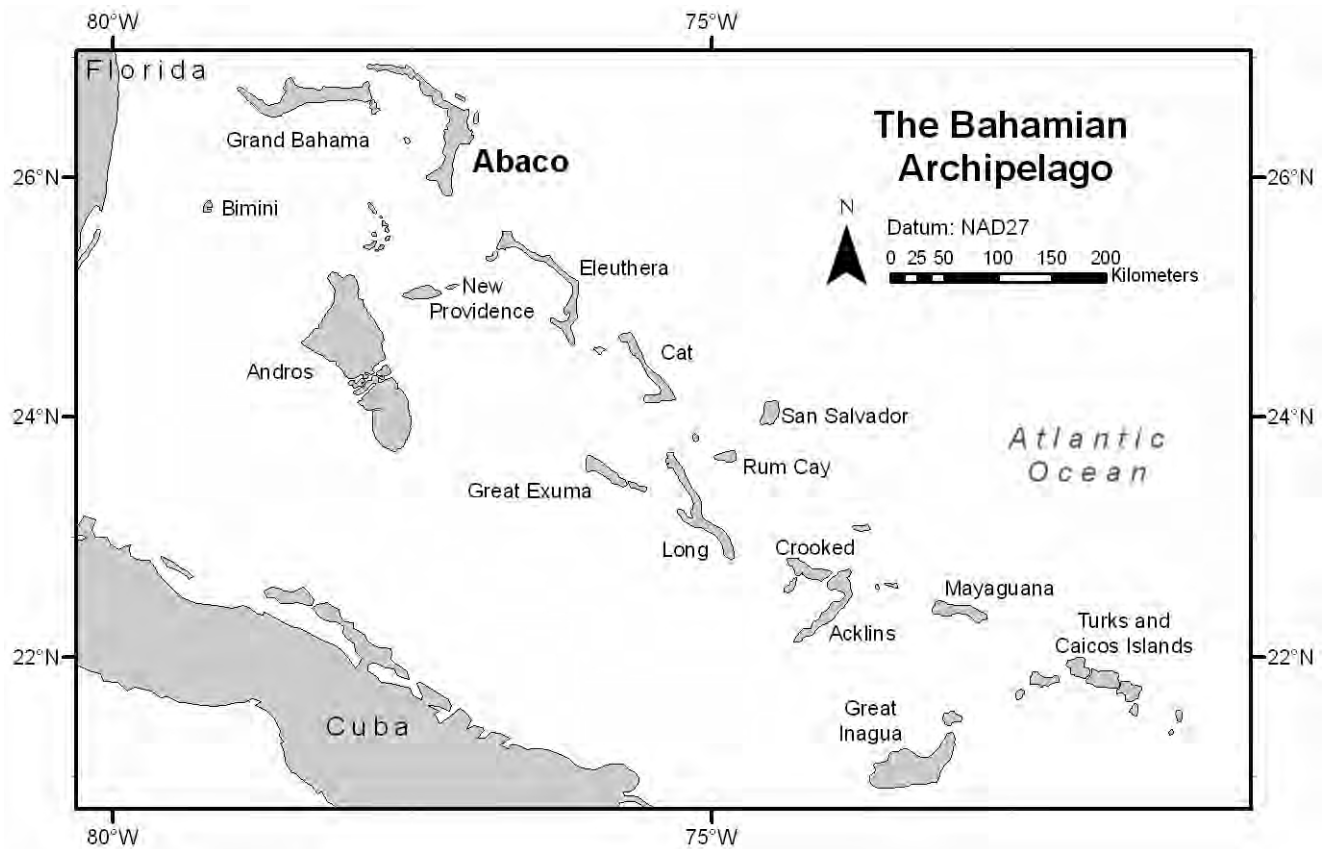


Figure 1. Map of the Bahamas, showing the location of Abaco Island.

abundant in all samples. This suggests an abrupt change in plant communities from hardwoods to more open pine-dominated forests in the vicinity of Sawmill Sink during the late Holocene. No radiocarbon dates are available for the plant macrofossils in the peat at this time.

A second, presumably older fauna, rich in microfossils, occurs as yellow-colored bone layers on rock ledges at the bottom of the sink at water depths between 27-29 m. This fauna consists of individual bones from birds, native rodents, bats, lizards, snakes, and small fishes (Steadman, et al. 2007). Tortoises, crocodiles, large birds, or plant material are not associated with this deposit. We believe this fauna was deposited by roosting predatory birds, probably barn owls (*Tyto* sp.). The unidentified fish component may have been added by Audubon shearwaters (*Puffinus lherminieri*) or other piscivorous birds. Both owls and shearwaters are known to roost and nest in caves of The Bahamas. We suspect that the bones of the yellow layer accumulated when sea levels stood at least 29 m lower than present-day levels, based on the location and structural nature of the deposit. Samples of bones from this layer lack sufficient carbon for radiocarbon analysis to substantiate this proposed late Pleistocene time interval (Steadman, et al. 2007).

A third fauna also exists at Sawmill Sink. This fauna consists of a series of isolated, highly mineralized bones that represent very large individuals of a sea turtle (*Chelonia mydas*), tortoise (*Chelonoidis* n. sp.), and crocodile (*Crocodylus* sp.). A tortoise humerus has an accumulation of what appears to be limestone attached to its distal end. The provenance of this group of fossils is unclear at this time.

Recent collections at Nancy's Cave near Sawmill Sink have revealed the first sample of fossil rock iguanas (*Cyclura* sp.) (ID by D.W. Steadman) to a growing list of vertebrates found in inland blue holes on the Little Bahama Bank. *Cyclura* fossils are also known from a dry cave at Hole-in-the-Wall on the south end of Abaco (Franz, et al. 1996, G.S. Morgan, pers. comm.). Their ages are unknown. *Cyclura* no longer occurs on islands of the Little Bahama Bank and probably disappeared prior to human occupation. We suspect that the list of fossil species will continue to grow as more blue holes are explored.

The Sawmill Sink study is designated as an official project of the Bahamian government under the direction of The Antiquities, Monuments, and Museums Corporation and the National Museum of The Bahamas. The sink has been declared an important archaeological/paleontological site by the Bahamian government because of the site's well-preserved fossils, and visitation is re-

stricted. The exceptional fossils are currently under study by a team of researchers from the University of Florida and other institutions. The ultimate goals of the project are to describe the Sawmill fossil biotas and reconstruct the environmental history of the northern Bahamas as recorded by these specimens and fossil materials from other blue holes on the Little Bahama Bank.

BAHAMIAN AND WEST INDIAN TORTOISE FOSSILS

Fossil tortoises are reported from springs, inland blue holes, caves, cow wells, fissures, and archaeological sites in the Bahama Islands, the Greater Antilles, and the Lesser Antilles. Specific Records: THE BAHAMAS: (Great Bahama Bank) Andros, New Providence (Auffenberg 1967), Eleuthera (unpublished records); (Little Bahama Bank) Abaco (this paper), Moore's Island (formerly known as Mores Island) (unpublished records); (Crooked-Acklins Bank) Acklins (unpublished records); (Mayaguana Bank) Mayaguana (unpublished records); and (San Salvador Bank) San Salvador (Olson, et al. 1982). TURKS AND CAICOS ISLANDS, BWI: (Caicos Bank) Middle Caicos (Franz, et al. 2001); (Turks Bank) Grand Turk (Carlson 1999). GREATER ANTILLES: Cuba (Leidy 1868, Williams 1950a, Auffenberg 1967), Mona Island between Puerto Rico and Hispaniola (Williams 1952), Navassa Island off the west coast of Haiti (Auffenberg 1967), and eastern Dominican Republic (Franz & Woods 1982). LESSER ANTILLES: Sombrero Island in the Anegada Passage between the Leeward and Virgin islands (Leidy 1868, Williams 1950a, Auffenberg 1967), Barbados (Ray 1964), and Anguilla (Lazell 1993). COASTAL VENEZUELA: Curacao (Hooijer 1963). EXTRALIMITAL RECORD: Bermuda (Meylan & Sterrer 2000).

Three names are available in the literature for tortoise fossils from the Bahamas and the West Indies: *Testudo cubensis* Leidy (1868) for the Cuban species, *Emys sombrenensis* Leidy (1868) for the Sombrero Island species, and *Testudo monensis* Williams (1952) for the Mona Island species. The Anguilla fossils were reported as the living species *Geochelone carbonaria* by Lazell (1993).

Most fossil tortoise specimens from the Bahama Islands and the Antilles are fragmentary and difficult to diagnosis. Conversely, the Sawmill Sink fossils are well preserved and essentially complete. They provide the first opportunity in more than 140 years of paleontological exploration and research in the West Indian region to study complete skeletons of extinct tortoises.

The Pleistocene land tortoise (*Hesperotestudo bermudae*) from Bermuda is considered to have originated in North America (Meylan and Sterrer 2000).

Bermuda is an oceanic island in the Atlantic Ocean that lies approximately 1,500 km northeast of Abaco. Abaco is considered the most northern point in the West Indian region of the Neotropics.

Recent fossil discoveries in inland blue holes on the Bahamian archipelago include undescribed tortoise populations from Abaco, Moore's Island, Eleuthera, Mayaguana, Middle Caicos, and Grand Turk. One of them, from Sawmill Sink, Lost Reel Cave, and other caves on Abaco, attained a much larger size than the late Holocene species from Sawmill Sink described here. We believe that this larger species may be geologically older, although we have been unable to verify its age with radiocarbon dates because of insufficient bone collagen. Until these new discoveries are studied, we feel that a general review of the region's fossil tortoises would be premature; therefore, we limit the current discussion to the similarities among the late Holocene Sawmill Sink population, its living and fossil South American relatives, and the Cuban, Hispaniola, and Mona fossils, and refrain from conducting a phylogenetic analysis. In any case, because of their completeness and superb preservation, the Sawmill Sink specimens provide a morphological data set against which all other Bahamian and West Indian tortoise fossils will be compared.

HISTORY OF NEW WORLD GENERA

Loveridge & Williams (1957) placed many of the world's fossil and living land tortoises in the genus *Geochelone* and divided this genus into subgenera. Auffenberg (1974) embraced their concept, but modified their subgeneric arrangement. Bramble (1971) suggested that *Geochelone*, as conceived by Loveridge & Williams (1957) and by inference Auffenberg (1974), did not represent "a natural, phyletic unit."

Loveridge & Williams (1957) and Auffenberg (1974) included all fossil and living West Indian and South American tortoises in the subgenera *Chelonoidis* and *Monachelys* in the genus *Geochelone*. Bramble (1971) regrouped them in the genus *Chelonoidis*. He further asserted that Nearctic and Neotropical tortoises were monophyletic with origins in nuclear Central America. Meylan & Sterrer (2000) kept the generic concept of *Chelonoidis* for all South American tortoises. They considered *Chelonoidis* to be the sister group to certain Old World tortoises and did not find evidence for monophyly of living and extinct North and South American land tortoises.

A recent molecular assessment of the phylogeny of living tortoises includes a basal lineage with the Asian *Manouria* and North American *Gopherus*, a second

clade with *Indotestudo* + *Malacochersus* + *Testudo*, and a diverse third clade with *Pyxis*, *Aldabrachelys*, *Homopus*, *Chersina*, *Psammobates*, *Kinixys*, and *Geochelone* (including *Chelonoidis*) (Le, et al. 2006). Further, *Geochelone* was found to be polyphyletic with four independent clades, and the hypothesis of South American tortoises originating in North America was rejected (Le, et al. 2006). Thus, we follow recent publications and consider *Chelonoidis* as the preferred generic name for Neotropical tortoises. We also apply this name to the Abaco fossils and by implication to all Bahamian and West Indian tortoises.

Williams (1952) erected the subgenus *Monachelys* to accommodate his Mona Island fossil, *Testudo monensis*. Auffenberg (1974) considered *Monachelys* to be an endemic West Indian subgenus within the genus *Geochelone*. The Abaco and Mona specimens share some shell features, but differ in aspects of the skull and the configuration of the first dorsal vertebra. We consider the subgenus *Monachelys* to be part of the genus *Chelonoidis*, although its phylogenetic position within this group needs further clarification.

METHODS AND MATERIALS

The tortoise fossils described below were recovered by professional divers from the salt water zone below a hydrogen sulfide layer and halocline in the entrance shaft of Sawmill Sink (Steadman, et al. 2007). The bones were lifted by divers to the surface in plastic recovery boxes that were filled with water and sediment from the site of collection. Lids were sealed on the recovery boxes immediately following the collection to prevent contamination of the bones as they were brought to the surface through layers of water with different water qualities. At the surface, the water in the boxes was removed and stored in plastic bags. The shells and bones were wrapped in wet cloth towels to immobilize them during transport. Towels were removed at the preparation facility and the original water was reintroduced to the containers following cleansing of loose sediment. Care was taken to insure the shells and bones were fully immersed.

The original salt water was gradually replaced with freshwater over the course of the next 11 days. The freshwater bath was then changed daily for an additional 14 days to insure that shells and bones were completely leached of their remaining salt content. Following this process, water was drained from the specimens, and the bones were allowed to air dry slowly for the next 28 days to prevent cracking. Shells and bones were turned twice each day to insure uniform drying. Bones were inspected daily for mold growth and

signs of degradation. Shells, skull, and most appendicular bones were then immersed in a thin solution of Butvar B-76 and dried. The first treatment was followed by a second application several days later, and thoroughly dried again. Certain bones were air-dried, but not immersed in Butvar for dating and DNA recovery. The bones are maintained in plastic boxes at the preparation facility. The fossils were assigned individual field numbers, based on the collection site and order of their collection. Selected specimens were imported to the United States with appropriate permits from The Antiquities, Museums, and Monuments Corporation, The Bahamas Department of Agriculture, and the United States Fish and Wildlife Service, and are curated in the Vertebrate Paleontology Collection of the Florida Museum of Natural History. The majority of specimens are retained in Marsh Harbour, Abaco, where they are the property of the AMMC.

Abbreviations and Terminology: **UF**, Florida Museum of Natural History (formerly Florida State Museum), University of Florida, Gainesville; **USNM**, United States National Museum (Smithsonian Institution); **AMMC**, The Antiquities, Monuments, and Museums Corporation; **NMB**, The National Museum of The Bahamas (under **AMMC**) (The Bahamas is the official name of the country), Nassau. **ABACO**, AMMC preparation center at Marsh Harbour, Abaco; **BNM.AB50.T**, The National Museum of The Bahamas field numbers for tortoise fossils (ex. AB50.T2=code for Abaco, Sawmill Sink [50], specific tortoise ID [T2]). The Florida and Bahamian museum numbers are shortened to Ts in the body of the text. AMS or accelerator mass spectrometry method was used for radiocarbon (¹⁴C) dating.

Terminology for scutes and bones follows Bramble (1971) and Hutchison (1998); for skulls see Bramble (1971) and Gaffney (1979). Shell measurements for the Sawmill Sink fossils and living species are shown in Table 1 and Appendices I-IV. Skull measurements are shown in Table 2. Specialized descriptive terminology has been used for aspects of the shell, which deviates from other proposed terminologies. (1) The gular and anal extensions are termed apices (= projections). (2) The epiplastron consists of two shapes in *Chelonoidis*: a) an epiplastral excavation that forms a prominent shelf on the interior surface of the epiplastron that can be partially or deeply undercut in three of four living *Chelonoidis*; and b) a flattened epiplastral surface without the presence of a shelf in Bahamian fossils and *C. nigra*. (3) We use the name gular branching to describe the treelike branching of gular sulci from the midline sulcus. The tree is positioned on the external surface of the anterior lobe

of the plastron and can occur either on the epiplastron or entoplastron. The location of this feature has been used in species recognition. (4) Interclavicular sculpture includes an anterior elevated mass, a strong interclavicular keel or ridge, a detached blade dorsal to the HYO, and a pair of fossa lateral to the midline ridge. We describe the sculpture in the context of a bird face pattern. This feature is distinctive in *Chelonoidis*. The “bird face” analogy was used by anthropologists and us in discussing the various fossil species (Carlson 1999, W. Keegan and N. Albury pers. comm., and the Bahamian field team). The patterns are consistent among individual specimens within a species, but are distinctive among species.

The following list of abbreviations for scutes and shell bones is repeated in text at their first use. Abbreviations for other features not listed here are identified in the text at their first use. Roman numerals following abbreviations indicate bone order. CARAPACE SCUTES: Cervical = CER, Vertebral = VER, Pleural = PLE, Marginal = MAR. PLASTRON SCUTES: Gular = GUL, Humeral = HUM, Pectoral = PEC, Abdominal = ABD, Femoral = FEM, Anal = ANA, Auxiliary = AXI, Inguinal = ING. CARAPACE SHELL BONES: Nuchal Plate = NUC, Neural = NEU, Suprapygial I = SPY I, Suprapygial II = SPY II, Pygal = PYG, Costal = COS, Periperal = PER. PLASTRON SHELL BONES: Epiplastron = EPI, Entoplastron = ENT, Hyoplastron = HYO, Hypoplastron = HYP, Xiphoplastron = XIP. COMMON MEASUREMENTS: Standard Carapace (midline) Length = CL, Over-shell Carapace Length = OCL, Standard Plastron Midline Length = PL, Greatest Plastron Length (including gular and anal apices) = GPL, Greatest Shell Height = GSH, Greatest Shell Width = GSW.

SYSTEMATIC PALEONTOLOGY

Class REPTILIA Laurenti 1768
Order TESTUDINES Linnaeus 1758
Suborder CRYPTODIRA Cope 1868
Family TESTUDINIDAE Gray 1825
Genus *CHELONOIDIS* Fitzinger 1835

Chelonoidis alburyorum n. sp.

(Figs. 2-15, Tables 1-2)

Holotype.—UF 225400 (NMB.AB50.T1), adult male, includes a complete shell, complete skull (minus the mandible), 4 cervical and 16 caudal vertebrae, complete pectoral and pelvic girdles, front and hind limbs, and 4 terminal phalanges (Figs. 2, 9, 10, 13, 14, 15). The holotype is on permanent loan to the Florida Museum of Natural History from The National Museum of The Bahamas.

Table 1. Shell measurements (in mm) for five *Chelonoidis alburyorum* specimens from Sawmill Sink, Abaco, Bahamas. T1=holotype. T1 and T4 in UF collection, T2, T3, and T7 in The National Museum of the Bahamas collection.

Character	T1	T2	T3	T4	T7
Sex	Male	Male	Female	Subadult	Male
Standard carapace length	453	466	428	Est 345	424
Over-the-shell carapace length	595	610	550	Est	575
Ento- plus hyoplastral length	151.2	157.8	133.1	111.1	143
Width of shell at midsection	273	297	281	245	277
Greatest height of shell	224	229	215	186	218
Minimum bridge length	181	194	180	156	174
Midline length of plastron	345	359	335	275	328
Greatest length of plastron	354	368	347	286	338
Anterior plastral lobe length	88	86	78	59.7	75
Posterior plastral lobe length	85	89	91	75.4	83
Combined lobe lengths	173	175	169	135.1	158
Nuchal plate length at midline	75.2	78.8	79.2	58.6	67.8
Nuchal plate width at shell margin	72.6	77.4	62.6	47.4	61.6
Greatest width of nuchal plate	108.2	100.2	95.4	79.1	91.4
Length of suture between nuchal plate & neural I	39.3	32.0	27.9	25.1	34.8
Midline length of neural I	57.5	60.3	52.2	50.8	57.0
Width of neural I at transverse sulcus	49.1	55.7	50.2	50.8	51.7
Number of sides on neural I	4	4	4	6	4
Midline length of neural II	53.4	60.0	52.0	46.0	58.3
1 st width on neural II	64.7	74.6	64.8	52.4	67.1
2 nd width on neural II	74.7	83.4	75.6	66.4	76.8
Number of sides of neural II	8	8	8	6	8
Midline length of neural III	52.5	55.3	49.8	38.5	53.0
Width on neural III at transverse sulcus	57.9	65.2	60.8	52.0	59.0
Number of sides on neural III	4	4	4	4	4
Midline length of neural IV	53.4	59.9	52.7	45.9	53.3
Greatest width on neural IV	82.2	87.8	82.1	67.9	78.4
Number of sides of neural IV	8	8	8	8	8
Midline length neural V	46.2	49.4	43.6	34.6	44.8
Width of neural V at transverse sulcus	61.7	62.6	61.0	47.1	54.4
Number of sides on neural V	4	4	5	4	4
Midline length of neural VI	37.1	38.5	32.5	30.5	62.1
Greatest width of neural VI	73.4	77.8	63.1	53.0	70.3
Number of sides on neural VI	8	6	5	6	8
Number of sides of neural VII	6	6	6	6	6

Table 1. Continued.

Character	T1	T2	T3	T4	T7
Sex	Male	Male	Female	Subadult	Male
Number of sides on neural VIII	4	6	4	6	4
Length of sulcus between suprapygal II & pygal	79.7	73.3	62.3	46.4	61.7
Width of pygal at shell margin	45.7	48.5	33.3	na	39.5
Epiplastron length at midline	34.6	29.7	37.6	33.2	30.2
Entoplastron length at midline	45.1	45.8	48.7	47.2	45.6
Entoplastron greatest width	70.8	72.3	64.7	48.9	65.3
Hyoplastron length at midline	106.1	112.0	84.4	63.9	97.4
Hypoplastron length at midline	115.0	114.9	103.8	85.0	101.4
Xiphiplastron length at midline	55.3	59.8	60.0	53.5	61.3
Distance between the entoplastron & humeral/pectoral sulcus	27.7	23.5	11.6	6.0	16.8
Length of nuchal midline sulcus	20.1	25.6	24.7	22.4	25.1
Midline length of vertebral scute I	89.7	91.0	87.4	73.6	81.2
Midline length of vertebral scute II	106.0	110.0	100.0	80.0	103.6
Midline length of vertebral scute III	95.3	108.1	99.1	82.5	101.2
Midline length of vertebral scute IV	111.7	111.6	102.1	86.0	100.0
Midline length of vertebral scute V	118.6	112.2	104.9	84.5	103.5
Greatest width of vertebral scute I	112.5	118.9	106.1	90.5	114.8
Greatest width of vertebral scute II	130.3	147.7	124.6	110.0	136.6
Greatest width of vertebral scute III	154.0	166.5	144.2	126.6	148.3
Greatest width of vertebral scute IV	134.4	125.0	114.8	96.2	126.7
Greatest width of vertebral scute V	123.8	113.7	101.3	93.7	115.5
Midline length of gular scute	31.3	24.1	31.2	30.2	29.3
Midline length of humeral scute	72.8	72.8	63.0	53.5	65.0
Midline length of pectoral scute	22.8	23.4	32.9	23.0	21.5
Midline length of abdominal scute	129.0	147.0	117.0	95.9	118.1
Midline length of femoral scute	77.0	68.0	68.0	52.8	75.4
Midline length of anal scute	20	33	22	21.4	21
Depth of anal notch	8	8	8	6	7

Table 2. Skull measurements (in mm) of *Chelonoidis alburyorum* (T1, holotype, CL = 453mm), recent *C. denticulata* (UF 33670, Colombia, Leticia, CL = 366 mm), recent *C. chilensis* (UF 33611, Argentina, North Cordoba, CL = 184 mm), and recent *C. nigra* (captive population).

Measurements	<i>C. alburyorum</i>	<i>C. denticulata</i>	<i>C. chilensis</i>	<i>C. nigra</i>
Skull length from anterior end of premaxilla to occipital condyle	67.4	60.4	38.6	119.7
Greatest skull width (across quadrotajugals)	58.9	42.1	30.2	93.5
Skull width/length ratio	1:1.12	1:1.43	1:1.28	1:1.28
Skull length from anterior margin of prefrontals to terminus of supraoccipital crest	82.2	71.6	40.7	143.0
Skull width between posteroventral projections of maxilla	43.7	36.8	23.4	73.1
Width between the quadrate condyles	37.2	30.1	17.9	54.9
Width between the outside margins of quadrate condyles	55.6	42.2	26.0	91.6
Width between orbits at prefrontal-frontal sutures	23.5	18.2	8.0	37.1
Width of palate between posterior palatine foramen	21.3	17.9	9.2	28.3
Length of maxillary portion of the triturating surface along median ridge	23.6	21.6	9.9	35.7
Length of median ridge	23.6	16.5	9.0	32.3
Length of maxilla along labial ridge	32.2	27.9	17.2	52.2
Orbit greatest diameter (anteroposterior)	21.0	20.3	11.4	33.4
Breadth of occipital condyle	6.8	5.8	3.2	11.2
Height of foramen magnum	11.3	9.5	6.3	16.5
Breadth across external nares	17.1	12.9	9.3	26.7
Height of skull anterior to orbits	25.9	20.4	15.0	42.8
Length of ear opening	14.0	10.5	5.4	21.3
Height of ear opening	14.5	10.5	6.4	21.4

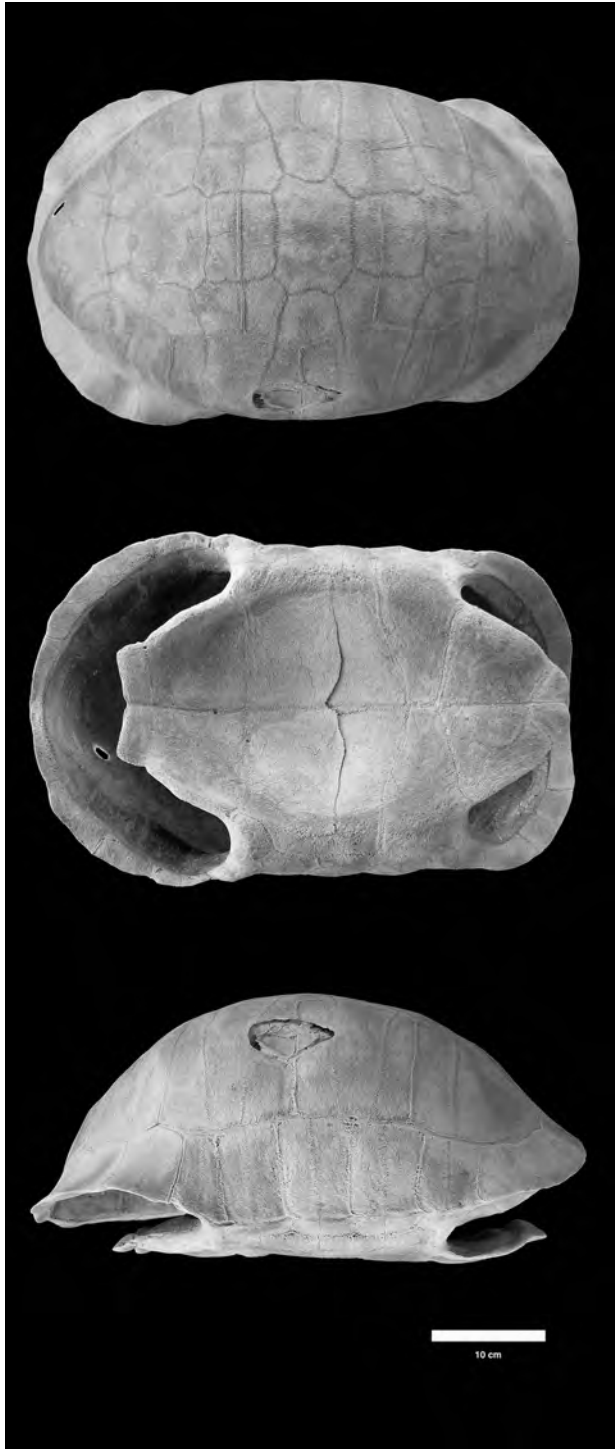


Figure 2. Shell of the fossil tortoise *Chelonoidis alburyorum*, holotype, T1 (UF 225400), from Sawmill Sink, Abaco, The Bahamas. Dorsal, ventral, and lateral views. Scale = 10 cm.

Paratypes.— NMB.AB50.T2, adult male, a complete shell (Figs. 3, 10). NMB.AB50.T3, adult female, complete shell and individual girdle and limb bones (Figs. 4, 10). NMB.AB50.T4, subadult, nearly complete shell (kept as separated carapacial and plastral halves), lacking the pygal and several posterior peripherals (Figs. 5-8, 11, 12). NMB.AB50.T4 is on long-term temporary loan to the Florida Museum of Natural History and as a consequence has not been assigned a UF number. NMB.AB50.T7, adult male, complete shell (with crocodile bite marks), girdle and limb bones, a cervical vertebra, and 14 caudal vertebrae (see photograph of T7 in Steadman, et al. 2007). Paratypes NMB.AB50.T2, T3, and T7 have been retained by The National Museum of the Bahamas and are currently housed at the ABACO facility.

Referred Material.— NMB AB50.T5, adult (sex unknown), partial shell, including a nuchal plate, one partial 8-sided neural, several costals, three peripherals, and the right side of the carapace posterior to the bridge, composed of associated costals, peripherals, pygal and suprapygals. NMB AB50.T6, juvenile, isolated limb and girdle bones (no shell elements) found in the recovery box after flushing organic sediments from the inside of the T1 shell. T5 and T6 have been retained by the NMB.

Generic Allocation.— We consider the new Bahamian tortoise to be a member of the Neotropical genus *Chelonoidis* rather than *Hesperotestudo* or other North American genera for the following reasons. *Chelonoidis* and *C. alburyorum* lack a cervical scute, extensive limb and tail armor, and obvious growth annuli. They have a thin-walled shell, neural formula of 4-8-4-8-6 (but showing considerable variation), enlarged entoplastron, enlarged pectoral scute, and an interior entoplastral sculpture (bird face). Additionally, Bahamian and West Indian land tortoises occur with other fossil vertebrates that have biogeographic affinities with the Neotropics. Previous researchers also have allied these fossil tortoises with Neotropical tortoises (Auffenberg 1974, Williams 1950a).

Diagnosis.— A moderate-sized tortoise (up to 466 mm CL) with an elongate, high-domed, thin-walled shell. Epiplastral shelf absent, gular apices (projections) short and rounded, distinctive entoplastral sculpture, and enlarged pectoral scute. Skull brachycephalic with a strap-like vomer, vaulted palate, undeveloped pedestal for origin of septum, and weak septum-like ridge instead of prominent thin-walled septum as in other *Chelonoidis*. The jugals are either fused to the maxilla or absent. Specific comparisons between *C. alburyorum* and other *Chelonoidis* are found in later sections.



Figure 3. Shell of the fossil tortoise *Chelonoidis alburyorum*, paratype, male, T2 (NMB), from Sawmill Sink, Abaco, The Bahamas. Dorsal, ventral, and lateral views. Scale = 10cm.

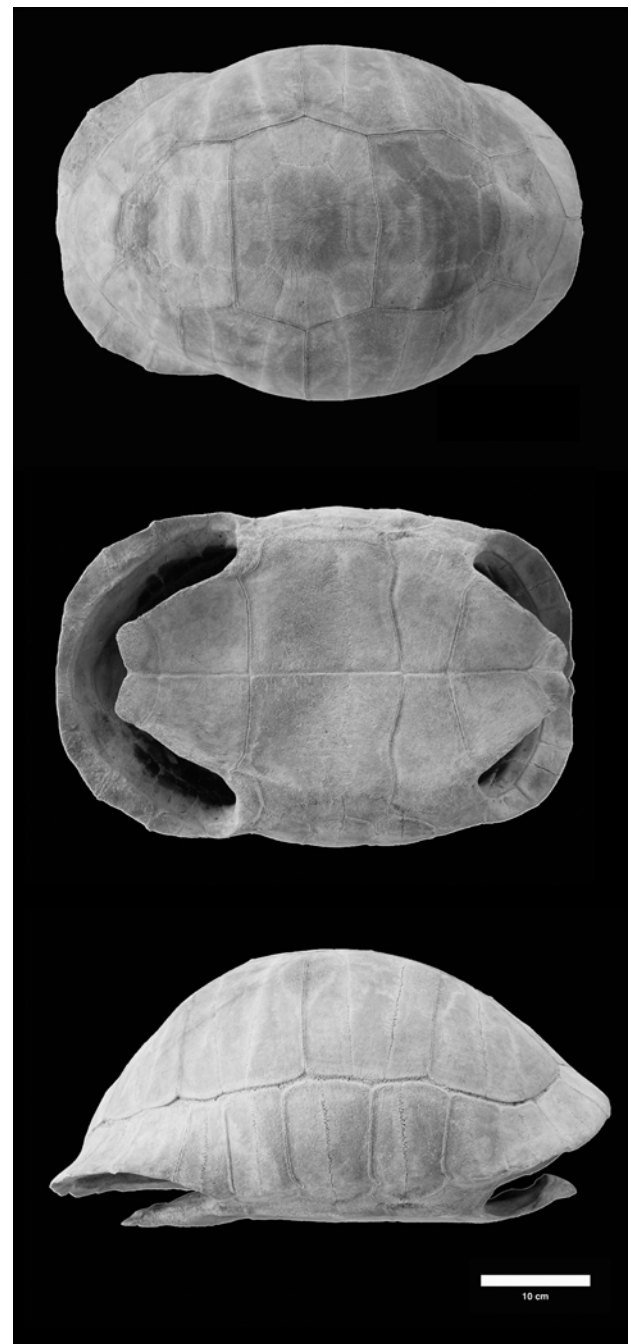


Figure 4. Shell of the fossil tortoise *Chelonoidis alburyorum*, paratype, female, T3 (NMB), from Sawmill Sink, Abaco, The Bahamas. Dorsal, ventral, and lateral views. Scale =10 cm.

Type Locality, Deposition, and Age.— The holotype, four paratypes, and two referred specimens were collected from peat deposits on the debris cone in the water-filled entry shaft of Sawmill Sink (BNM Site Number AB-50), north of Cornwall Point, 37 km (23 mi) S of Marsh Harbour, Great Abaco Island, Little Bahamas Bank, The Bahamas (26°17' N, 77°12' W). The holotype was collected at a water depth of 17 m in Grid A. The skull was found directly beneath the shell, while the postcranial bones were taken from inside the shell. The mandible, remaining cervical vertebrae, and the wrist and ankle bones are missing. No dermal ossicles were found. The paratypes and referred materials were retrieved at water depths between 14-20 m in association with grids A and B. Conventional AMS radiocarbon dates were secured from a scapula and vertebra of two different tortoises by Beta Analytic Radiocarbon Dating Laboratory, Miami, FL: T1 (holotypic male), 2720 ± 40 yr BP (Sawmill -T1, Beta #225508) and T3 (paratypic female), 2580 ± 50 yr BP (Sawmill T3-Beta #225509). Radiocarbon dates were also obtained from a humerus, vertebra, and femur from three individual crocodiles collected in the peat (Steadman, et al., 2007), ranging from 2990 ± 50 to 3820 ± 50 yr BP. A single human bone from the peat was dated at 1040 ± 40 yr BP (Steadman, et al., 2007). A bone sample from T3 was sent to George Amato, Department of Molecular Genetics, American Museum of Natural History, for DNA analysis. The results of the molecular analysis are pending.

Etymology.— We name this new fossil tortoise in honor of Nancy and Michael Albury of Man of War Cay, The Bahamas, in recognition of their efforts to conserve Sawmill Sink and other unique natural features on and near Great Abaco Island. The Alburys are prominent members of the Abaco Friends of the Environment, and Michael Albury serves as President of the Friends group and a council member of the Bahamas National Trust. Nancy Albury was instrumental in bringing international attention to the Sawmill Sink fossils and serves as Coordinator of the Sawmill Sink Project representing the Bahamian government. She also was responsible for cleaning, preserving, curating, and storing the Sawmill Sink fossils and for most of the photographs used in the description.

DESCRIPTION

The following descriptions of the shell, skull, vertebrae, limb bones and girdles of *Chelonoidis alburyorum* are based primarily on the holotype (T1) and one paratype (T4), with supplemental information from the other paratypes (T2, T3 and T7) and two referred specimens (T5 and T6).

GENERAL SHELL FEATURES

The external surfaces of the shell bones are minutely roughened, appearing porous and in some places fibrous. None of the shell bones shows signs of growth annuli or damage from animal gnawings. The edges of the scutes are well delineated by prominent sulcal grooves embedded in the exterior surfaces of the shell bones. Raised edges along the margins of the sulci further accent these channels. The typical tan color of the dried bones of Sawmill Sink tortoises can be seen in the photograph of T7 in Steadman, et al. (2007).

Shell measurements for T1-T4 and T7 are presented in Table 1. The three adult males (T1, T2, and T7) range from 424-466 mm in CL; the only female (T3) measures 428 mm CL; the only subadult (T4) is estimated at 345 mm CL (missing pygal). T5 is represented by a partial shell of an adult (sex unknown), similar in size to T2. T6 is a large juvenile, represented by only limb and girdle bones (shell bones missing). The length of the humerus of T6, missing the head and the ends of the tuberosities, measures 36 mm, and the length of a complete ulna, 25.3 mm. We estimate the CL of T6 to be about 170 mm, when compared to similar limb measurements from small individuals of related living species. Other bones from T6 include a partial femur, tibia, fibula, and parts of the pelvis.

Complete shells are moderately elongate (GSW, 60-66% of CL), bubble-shaped when viewed from above, and domed (GSH, 49-51% of CL) with the GSH measurement taken near at the anterior margin of Neural (NEU) IV (Figs. 2-5). CLs are 74-78 % of OCLs in adults. Most carapacial elongations in shells are products of bone distortions associated with abnormal NEU VI-VIII and a curious “caudal hump” at VER V.

Random measurements of shell thickness in T4 range from 3.6-4.8 mm (carapace) and 8.5-11.5 mm (plastron); some of the thickest measured points on the shell occurred along the skin lines; shell thickness in T5 is 2.3-3.8 mm (carapace). T1-T3 and T7 have similar bone thicknesses, but direct measurements are impossible with articulated shells.

The first dorsal vertebra and the first two costal ribs are exposed in the opened carapace of T4 (Figs. 6, 7). The centrum is robust, rectangular, with a length greater than the greatest width. It has a moderately constricted waist at about mid-point and a strong keel along the midline. First dorsal vertebrae of complete Sawmill Sink specimens are difficult to see, but appear to show similar constructions.

The free portions of the shell ribs are prominent, thin, and flattened laterally (Fig. 6). The ribs originate on the costals, well below the costal-neural sutures. The

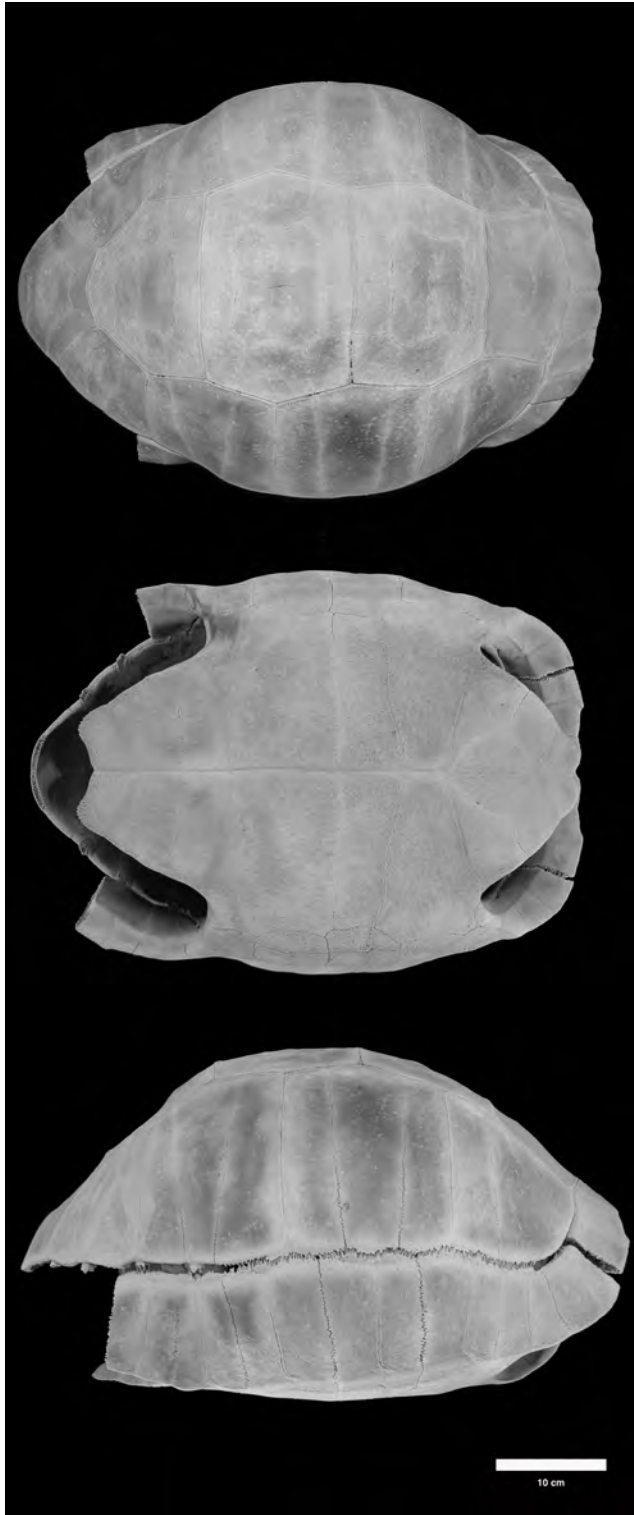


Figure 5. Shell of the fossil tortoise *Chelonoidis alburyorum*, paratype, subadult, T4 (NMB), from Sawmill Sink, Abaco, The Bahamas. Dorsal, ventral, and lateral views. Scale = 10 cm.

shell vertebrae are elevated above the internal surface of the shell on a thin wall of bone (neural spines). The vertebrae and ribs are suspended below the internal surface of the shell, which produces a sizeable space for the passage of large muscles. This elevated configuration exceeds those found in living *Chelonoidis*, except for *C. nigra*.

The presacral vertebral complex consists of the three posterior-most thoracic vertebrae (VIII-X) and the accompanying ribs (Figs. 6, 8). These vertebrae are attached to NEUs VII & VIII. The ribs on vertebra VIII are attached to COSs VII, and vertebrae IX and X, to COSs VIII. These ribs are mounted on thin, elevated wings of bone that arise from these costals (Figs. 6, 8)

Bridge lengths are slightly longer than the combined lengths of the anterior and posterior plastral lobes. The anterior lobe is broadly elongated, tapering from the bridge forward toward the rounded gular apices.

Peripherals (PER) II-III and IX-XI are moderately flared; the NUC, the rest of the peripherals and the pygal (PYG) slope rooflike over their respective plastral lobes and show little or no flaring. Sulcal spurs form as extensions of the sulci along the margins of peripherals in thin-shelled species, presumably to reinforce a protruded scute edge. These spurs are weakly expressed in only the subadult T4 and show no obvious development in adults T1-T3 and T7. The margins of the carapace in *Chelonoidis alburyorum* are entire to wavy or weakly scalloped, but not serrated.

The midline plastron (PL) and the greatest plastron (GPL) lengths are 76-78% and 78-81% of CL, respectively. The differences between GPLs and the PLs are less than 5%, which reflects the limited extent of the gular and anal apices in *C. alburyorum*.

The three males with complete shells (T1, T2, and T7) possess prominent concavities that cover about 65% of the plastron (Figs. 2, 3). T3, the only female, and T4, a subadult, lack this feature (Figs. 4, 5). The concavity of T1 is more evident than that of T2, even though the T2 shell is slightly larger. The bowl-shaped concavity starts at the base of the ENT and extends backward onto the xiphiplastron (XIP). The lateral expansion of the bowl reaches the outer margins of the hyoplastron (HYO) and hypoplastron (HYP) about to the lower bridge suture. Similar bowl-like concavities also occur in *C. nigra*. The shape of this concavity in living *C. denticulata* and *C. carbonaria* are more elongated conforming to their more elongate shells. The plastra of the female (T3) and the subadult (T4) show only slight depressions associated with the anterior part of the xiphiplastron.

SHELL WOUNDS AND PENETRATIONS

T1 and T2 possess single oval holes that penetrate completely the left side of suprapygal I (SPY I) near its suture with costal (COS) VIII. T3, T4, and T7 lack these holes. The holes occur at a point near where the top of the underlying pelvis comes in contact with the carapace. Similar holes are found regularly in other thin-shelled, land-dwelling turtles, such as *Chelonoidis nigra*, *Gopherus polyphemus*, and *Terrapene carolina* (RF pers. obs.). These holes are covered by dermal scutes in living specimens and are not visible in specimens retaining intact scutes. The origins of these holes may lie with wear patterns by the pelvic girdle and hind limbs that form possibly as a consequence of terrestrial locomotion or limb retraction as in the case of box turtles.

T1 also possesses a large, partially healed, oval-shaped bone scar (65 x 45 mm) of unknown origin on COS IV of the right side of the carapace (Fig. 2). The injury must have occurred prior to death, as evidenced by the regrowth of new bone in the former wound.

T7 has a series of shallow dents and scrapes, blind pits, and deep pits with secondary holes completely penetrating the carapace (see photograph in Steadman, et al. 2007). Most of these marks are round in shape, and many line up with respect to one another, suggesting bite wounds inflicted by crocodiles. They are absent on the plastron. All of the wounds show bone regrowth, indicating that the bites were older, and not the immediate cause of death.

SHELL BONES AND SCUTES

Carapace: The NUC of *Chelonoidis alburyorum* lacks a CER scute (Fig. 9). The CER scute is replaced with a midline cervical sulcus that separates the left and right marginals (MAR) I. The length of the midline cervical sulcus is long (20.1-25.6 mm), representing about 27-37 % of the NUC's total midline length. The length of the NUC is shorter (69-83%) than its greatest width. The free margin of the NUC is narrower than its greatest width and its total midline length.

The neural formula for the first five neural bones in T1-T3 and T7 is 4-8-4-8-4 (Fig. 10). NEUs I, III, V, and VIII are each crossed by a transverse vertebral scute sulcus. Significant variation is found in the neural series of the known specimens. The most common variant consists of extra bones embedded in NEUs VI-VIII. Other variants include T1 with a divided SPY I that gives the appearance of an extra neural bone and T3 with a 5-sided NEU VI. T4 shows the greatest variation in the sample: NEU I is split into two bones that, taken together, produce the more typical 4-sided, wedge-shaped combination; NEU II is 6-sided with four of the faces

directed posteriorly; NEUs VI-VIII are broken into four separate bones; and SPY I is also separated into two bones, with the uppermost bone masquerading as an extra neural bone.

The pygal complex typically includes a PYG and a bifurcated SPY I that encloses SPY II. The arms of SPY I come in contact with PERs XI on both side. The suture between PYG and SPY II lies below the sulcus that separates VERT V from the terminal marginal.

Carapacial scute contact patterns among the type series show consistent alignments of COSs I-III, and V with their corresponding neurals and peripherals; however, minor displacements occur between COSs IV, VI-VIII and accompanying NEUs VI-VIII and PERs V-XI. These variants are the results of adjustments in shell architecture to accommodate neural distortions and the caudal hump in the rear of the carapace.

The bridge peripherals are long and form a strong vertical wall that connects the carapace to the plastron. The bridge is neither angular nor keeled as in some other *Chelonoidis*. The auxiliary scute (AXI) is long, narrow, kidney-shaped, and borders PEC and MARs III-IV scutes. The inguinal scute (ING) is weakly 5-sided. It is prominent and broadly borders the abdominal (ABD) scute and MARs VII-VIII scutes and has less contact with the femoral scute (FEM).

Plastron: The ventral (or external) surface of the epiplastron (EPI) is flattened (Fig. 11). The gular apices consist of two weakly rounded lobes with a weak notch between them (Fig. 12). The gular scutes (GUL) are short and lie entirely above the ENT. The interior surfaces of the gular apices are inflated to the skin line. The surface behind the skin line is sloped and lacks the development of an epiplastral shelf. A narrow transverse trough separates the EPI from the brow line of the bird face of the ENT. The lateral margins of the trough rise to meet the marginal skin line where it forms a shallow lip.

The external ENT surface in all four complete specimens is much wider than long, with 1:1.57, 1.58, 1.39 (female), and 1.43 ratios, respectively. The ENTs of T1-T3 are oval; T7, triangular or wedge-shaped. The ENT of T4 is shieldlike, more angular, and about as wide as long. The external ENT surface in all of the shells has a single, unbranched sulcus that passes through the midline axis of this bone. The pectoral-hyoplastral sulcus lies distinctly posterior to the posterior margin of the ENT.

A distinctive interclavicular sculpture is present on the internal surfaces of the ENT of T1-T4, and T7 (see Fig. 11 for best display on the plastron of T4). The



Figure 6. Internal view of carapace of the fossil tortoise *Chelonoidis alburyorum*, T4, from Sawmill Sink, Abaco, The Bahamas, showing the vertebral column. Note the first dorsal vertebra, pelvic vertebrae, and the elevated shell ribs. T4 CL = 345 mm.

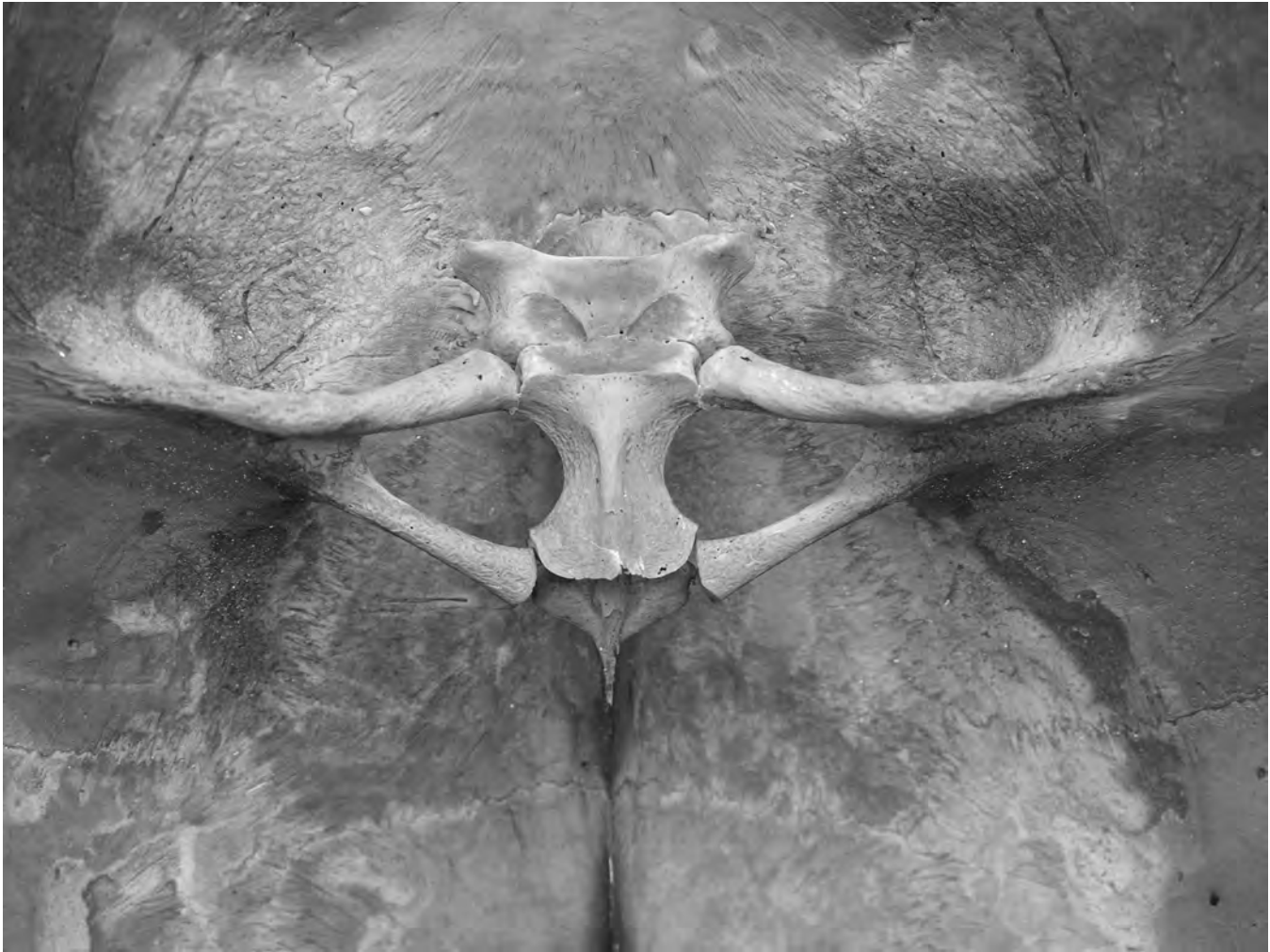


Figure 7. Close up of first dorsal vertebra of *Chelonoidis alburyorum*, T4, from Sawmill Sink, Abaco, The Bahamas, showing the modified centrum and associated first shell ribs. T4 CL = 345mm.

sculpture consists of a compact elevated mass, a strong interclavicular keel that extends posteriorly as a detached blade dorsal to the HYO, and a pair of fossae lateral to the midline ENT keel. Together, this combination produces a strongly elevated structure that is reminiscent of a “bird face.” The components of the face are interpreted as a prominent forehead or brow (mass), an elevated midline ridge with a long flattened beak or bill (keel plus blade), and a pair of shallow eye sockets (fossae) on either side of the midline ridge.

The HUM scute is about as long along the midline suture as the femoral (FEM) scute. A longer HUM scute was used by Williams (1960) to separate *C. denticulata* from *C. carbonaria*. The PEC scutes in *C. alburyorum* are prominent. They represent 6.6% of the midline plastral length. The ABD scutes are 39% longer than the HUM and FEM scutes along the midline suture. The ANA scutes are short and variable in their midline lengths. The anal apices are short, weakly tri-

angular and flattened; the anal notch is weakly wedge-shaped and very shallow.

THE SAWMILL SINK SKULL

The single skull of *Chelonoidis alburyorum* was found in association with the shell of T1 (Fig. 13, 14, Table 2). The skull is strongly brachycephalic, being nearly as wide as long (skull width/length ratios of 1:1.12). The rostrum is essentially square. It is composed of prefrontals and the more posteriorly located frontals. The frontals contribute to the orbit where they form an abrupt orbital angle just anterior to the frontal-postorbital suture. This angular configuration appears to rotate the orbits into a more frontal orientation, a condition that also exists in *C. nigra*, but not in *C. denticulata*, *C. carbonaria*, or *C. chilensis*. An extra bone occurs against the frontal-parietal suture between the two parietals. A prominent trochlear process on the quadrate extends as a ridge onto the prootic terminat-

ing in a smaller secondary process. The trigeminal foramen lies directly under the trochlear ridge. The trigeminal and the more dorsally located anteriomandibular foramen are separated from one another by a prominent, thin-bladed spear of bone that originates high on the internal wall of the orbit.

External narial aperture is moderately large. In a frontal view, several bony structures, visible in the narial aperture, protrude downward from the prefrontal symphysis and upward from the premaxillary symphysis. A pair of very low, crescent-shaped premaxillary ridges extends along the narial floor.

The maxilla ends in a well-developed posterior maxillary process. The suture between the maxilla and the jugal is either missing or obscure on both sides. A missing jugal with the extension of the maxilla to meet the postorbital and the quadratojugal would be very unusual. It is unknown whether this condition is peculiar to this skull or to the species.

The cutting edge of the tomial ridge of the maxilla is weakly serrated. The oral surface of the combined premaxillae forms a deep cup-like fossa at the front of the mouth (Fig. 14). There is no medial transverse ridge at the symphysis of the premaxillae. The triturating ridges do not intrude into the premaxillary cup. A transverse ridge at the suture separates the premaxilla from the maxilla. This ridge is the origin of the medial and lingual triturating ridges, which extend the entire length of the maxilla. The tomial ridge is more than three times as tall as the accompanying triturating ridges. The lateral margin of the lingual surface is straight-edged, not curved or crescent-shaped as in living South American *Chelonoidis*. The triturating surfaces of the maxillae are straight and strongly divergent, exposing an ever-widening palate posteriorly.

A triad of small openings includes two foramen praepalatinum and a nearly closed slit-like vomerine foramen, which terminates posteriorly as a small, rounded



Figure 8. Close up of the pelvic region of *Chelonoidis alburyorum*, T4, from Sawmill Sink, Abaco, The Bahamas, showing the arrangement of the presacral thoracic vertebrae and ribs. T4 CL = 345 mm.

hole along the premaxillary-vomer suture. The vomer ascends steeply into the cranium to form a highly vaulted palate. The anterior part of the vomer is strap-like and flattened. The elevated pedestal found in recent *Chelonoidis* to support the origination of the prominent vomerine septum is absent in *C. alburyorum*. Instead, the septum begins as a low ridge about one-third of the way along the vomer and eventually melds into a slightly more elevated bony ridge about midway and continues onto the anterior edge of the pterygoids. The palatines are positioned laterally with respect to the vomer and are arched to meet the lingual margin of the triturating surfaces. A small posterior palatine foramen occurs near the suture where the palatine intercepts the lateral extensions of the pterygoid. The suture that separates the vomer and palatine bones from the pterygoids is very irregular. The basisphenoid is shield-shaped, about as wide as long, with the obtusely pointed end facing toward the pterygoids.

The sagittal crest begins high on the back of the skull at the base of a slight bony ridge at the merger of the postorbital bar with the parietals (Fig. 13). The crest is slightly lower than the parietal and dips toward the terminal blunted point about 14 mm beyond the end of the occipital condyle.

The opening to the tympanic cavity is large, 14.5 mm in height (longest axis) (Fig. 13). The cavity is divided into a vertically oriented (anterior) precolumellar fossa and a horizontally oriented (posterior) postotic atrium. The division between the tympanic chambers is marked by a low ridge formed by the quadrate. The stapes are fused within the quadrate. Both stapes in the holotype skull are well preserved. They are straight bones with their exposed distal ends white and slightly swollen. The postotic chamber expands posteriorly ending against the thin walls of the quadrate and probably the squamosal bones. A second pair of holes (7.6 x 6.0 mm, right side; 8.3 x 6.1 mm, left side) penetrates into the postotic chambers on both sides of the skull (Fig. 13). These holes would normally be covered by the squamosals. It is unknown whether the squamosals were originally there and fell away with decomposition, or absent to form natural openings. Bony rims around the holes suggest that the squamosals may have been naturally absent and the holes covered with membranous tissue.

VERTEBRAE

Cervical vertebrae: Four cervical vertebrae (atlas, II, VI, and VII) of *Chelonoidis alburyorum* were recovered from inside the shell of T1 (Fig. 9). The atlas is laterally compressed; the centrum length and verte-



Figure 9. Anterior part of carapace of *Chelonoidis alburyorum* showing details of the nuchal plate, holotype, (T1), from Sawmill Sink, Abaco, The Bahamas. T4 CL = 345mm.

bra height are about equal (23 mm). The neural spine is hump-like, which is weakly hooked at the posterior end. The anterior socket of the centrum is small and deeply concave, whereas the posterior end is broadly developed with a slightly raised surface. The haemal keel on the ventral surface of the centrum is also well developed.

The spine on cervical II is absent, although there is a suggestion of strut-like development on the dorsal aspect of the postzygapophysis. Cervicals VI and VII have poorly developed, low, blunted neural spines. These spines have associated rib-like, bifurcated struts that extend posteriorly onto the postzygapophyses. The greatest centrum lengths of cervicals II, VI, and VII measure 33.0, 29.6, and 24.9 mm, respectively; narrowest widths, 15.5, 16.0, and 11.5 mm. The greatest distances between the outer margins of the pre- and postzygapophyses of these cervicals are 31.8, 34.7, and 38.6 mm, respectively. The centrum patterns include II (procoelous, doubled posteriorly), VI (amphicoelous, doubled at both ends), and VII (biconvex, doubled anteriorly) (based on terminology in Williams 1950b, Fig. 1). Short, thickened haemal keels are present on VI and VII; the keel on II is more elongated, thinner, and more bladelike. The keels on VI and VII are strongly bifurcated posteriorly; very strong struts occur along the ventral margins of the centrum in VII without engaging the haemal keel.

First Dorsal Vertebra: The first dorsal vertebra, as viewed inside carapace of T4, has a rectangular centrum with a moderately narrow waist and a strong midline keel. This vertebra is also in place in specimens T1-

T3 and T7. They all appear very similar to the one in T4, but are not as easily observed or measured when they are enclosed inside complete shells.

Caudal Vertebrae: Sixteen procoelous caudal vertebrae were recovered from inside the shell of T1, nine of which have fused transverse processes (Fig. 15). This tail is estimated to be about 18 cm long, based on a reconstruction of the 16 vertebrae. The terminal three caudal vertebrae are the smallest vertebrae and are distinctly flattened dorsoventrally.

LIMBS AND GIRDLES

Front and hind limb bones, scapulae, coracoids, and an articulated pelvic girdle were collected from inside the shell of T1 (Fig. 15).

Anterior Limbs and Pectoral Girdle: The pair of scapulae was separated from the respective coracoids. The straight dorsal blade of the scapula extends dorsally from the glenoid cavity. There is a slight swelling on the lateral surface near the distal end of the blade. The straight acromion process makes a 111° angle to the blade. This angle is greater than the 85° reported by Meylan & Sterrer (2000) for *Chelonoidis*. The short coracoids are prominently fan-shaped with a moderate anterodorsal crest.

The humerus of *C. alburyorum* is strongly recurved in ventral view. The total length of the right humerus is

96.1 mm. The hemispherical head is bent anteriorly at about 90° . The head itself is subspherical, 19.8 x 23.6 mm. The trochanteric tuberosities are moderately divergent and separated by a short, deep intertrochanteric fossa. The lesser trochanter is short, about 24 mm in length, ending at about the level of the base of the head. The greater trochanter extends about 26 mm above the proximal surface of the lesser trochanter and 8 mm above the upper surface of the head. An obvious shallow muscle scar for the attachment of *M. latissimus dorsi*, 8 mm wide x 15 mm long, is located on the outside surface of the greater trochanter in the upper half of the bone. The internal surface of the scar is greatly roughened. The shaft of the humerus at midpoint is nearly rounded with a shaft ratio of 1:1.12. The shaft becomes broader and more flattened distally. Two rib-like reinforcements arise on the posterior surface in the lower quarter of the humerus and diverge toward the distal articulation. The distal articulating surface is continuous, although with a slight suggestion for two facets that correspond to the ulnar and radial articulating surfaces. The greatest width across the distal articulating surface is 37.4 mm, or about 39% of the total length of the humerus.

The ulna is angular and compressed. The greatest length of the right ulna measured 59.7 mm. Its medial surface has a prominently raised bone scar, 8.2 mm long, which serves as the insertion for the biceps. The shaft

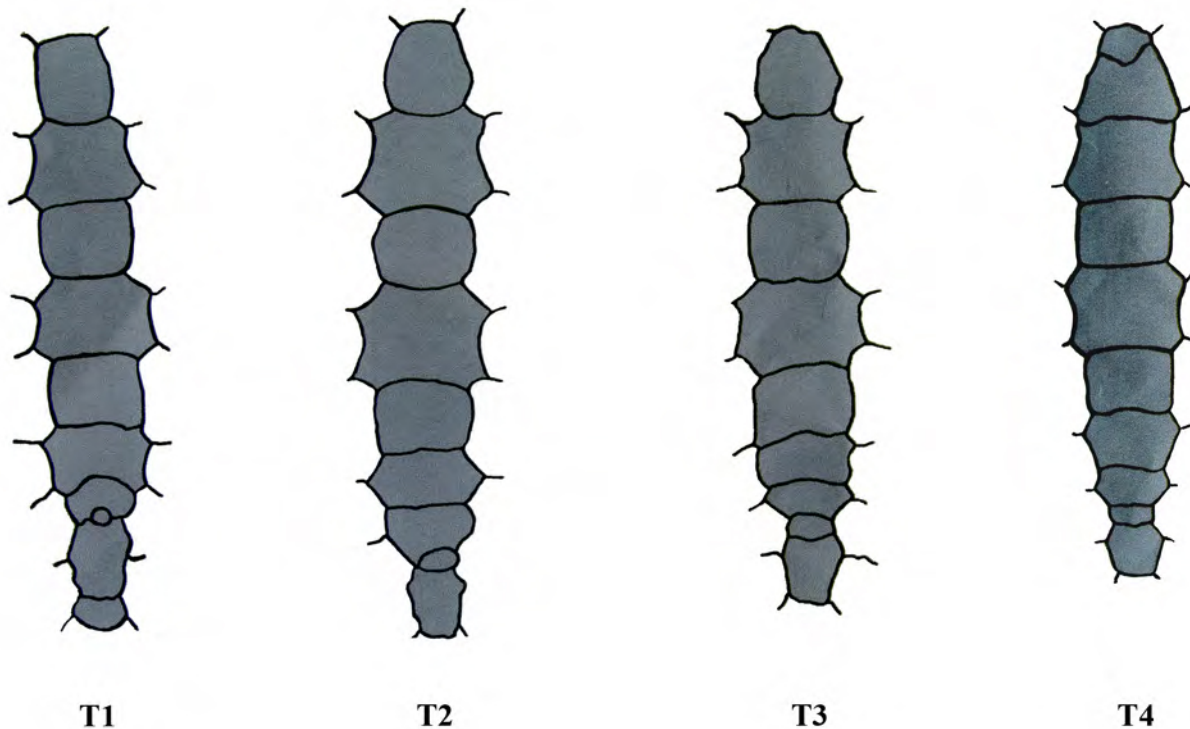


Figure 10. Neural bone aberrations in holotype (T1) and the three paratypes (T2-T4) from Sawmill Sink, Abaco, The Bahamas.

just below the scar is flattened, 5.5 x 10.3, with a shaft ratio of 1:1.87. A second raised scar occurs on the same surface just above the distal articulation. The distal articulating surface is 15.2 x 23.4 mm, the longest dimension including a raised olecranon. The distal articulation is much narrower, 17.5 x 7.3 mm, with two indistinct raised facets and one sunken facet that articulate with the wrist bones.

The radius is moderately slender with an expanded distal end, 18.3 x 23.3 mm. The greatest length of the right radius is 57.5 mm, slightly shorter than the ulna. The shaft is moderately compressed at midpoint, 7.3 x 9.6 mm, with shaft ratio of 1:1.3.

Posterior Limbs and Pelvic Girdle: The pelvic girdle in T1 consists of two articulated halves that fit together to form a complete pelvic architecture (Fig. 15). The bone sutures on both sides of the pelvis are partially ankylosed, probably accounting for their persisting articulations. The ischiopubic fenestrae are wider than long forming oval openings. Viewed from the rear, the ilia flare outward from their contacts with the pubis and ischium and then arc inward again at their distal ends to form a more or less circular interior space between the two pelvic halves. The crest of the ilium is broad, flattened, and flared. The posterior edge of the crest breaks into a broad shoulder that slopes downward to form a prominent elevated nose-like scar. The crest is rotated about 70° laterally bringing it nearly into the orientation plane of the glenoid fossa. The outer edge of the crest is smooth and straight in outline except for a slight hook at the anterior end. The pectineal process on the pubis is long and acute. The posteroventral process on the ischium is broad and slopes gently toward the midline suture. The glenoid fossa is shallow and generally triangular in shape. The ilium provides the greatest contribution to the glenoid cavity.

The greatest length of the femur is 83.7 mm. This represents about 87% of the total length of the humerus. The head of the femur is nearly spherical, measuring 22.1 x 24.8 mm. The trochanters are united behind the head to form a trochanteric crest, which encloses a deep medial trochanteric fossa on the distal surface. The shaft is short, robust, and triangular in cross-section with roughened muscle scars on either side. Shaft width and depth are 10.2 x 10.9 mm at midpoint. The trochanteric crest is about the same width as the distal articular surface. The tibial and fibular condyles are very weakly developed with only a suggestion of a notch between them.

The tibia and fibula measure 57.2 and 55.5 mm, respectively. The proximal and distal articular surfaces of the tibia are rotated about 90° with respect to one

another. The shafts of both the tibia and fibula are robust and angular, measuring 7.1 x 7.2, 5.3 x 6.4 mm, respectively. An enlarged, roughened tuberosity lies at the base of the distal surface of the tibia and extends up the tibial shaft 19.3 mm.

A group of four terminal phalanges, collected with T1, was slightly hooked and measures 11.8-15.7 mm in total lengths.

PRESERVED FOODS

The shells of T1 and T3 contained 146 and 80 fruits with enclosed seeds, respectively, of wild mastic (Sapotaceae, *Mastichodendron foetidissimum*) and satinleaf (or saffron) (Sapotaceae, *Chrysophyllum oliviforme*). We presume that these fruits represented last meals for both tortoises and the food stuffs were released from the gastrointestinal tract upon decay following submergence. The excellent preservation of these fruits indicates that tortoises had a quick death in the sink, possibly from drowning, and rapid burial in deeper, oxygen-depleted, salt water below the hydrogen sulfide layer. The fruits and seeds of both trees were otherwise uncommon in the peat-laden debris cone at Sawmill Sink (Terry Lott, pers. comm.). When fresh, the mastic and satin-leaf fruits are large, plum-like, and sweet (Scurlock 1987, Tomlinson 1986). The fruits ripen on these Bahamian trees from late winter to early summer (Scurlock 1987, D.W. Steadman pers. comm.). Fruits usually drop en masse on the ground under the trees where presumably the tortoises encountered and consumed them. The timing of fruit availability in these tree species suggests spring deaths for T1 and T3.

DESCRIPTIONS OF OTHER SPECIES OF *CHELONOIDIS*

Chelonoidis alburyorum is a member of the modern Neotropical tortoises that currently inhabits South America, Galápagos Islands, and a few scattered islands in the southern Lesser Antilles. Comparisons with fossil and living *Chelonoidis* are essential in determining the position of the Bahamian species within this clade.

FOSSIL TORTOISES

Fragments of fossil tortoises from Cuba, Hispaniola, and Mona Island provide minimal data on the tortoise species that once occurred there (see photographs in Williams 1950a, Franz and Woods 1982, and Williams 1952, respectively). These specimens are only moderately helpful to determine morphological attributes and specific adaptations of these tortoises to island habitats. Better materials are needed before they can be compared meaningfully with the Bahamian specimens.



Figure 11. Internal surface of the plastron of *Chelonoidis alburyorum*, T4, from Sawmill Sink, Abaco, The Bahamas, showing the rounded gulars, entoplastral sculpture, and details of the posterior lobe. T4 CL = 345mm.

The dry cave-derived fossils from Navassa, New Providence, Andros (Auffenberg 1967) and San Salvador (Olson, et al. 1982) also are too fragmentary to provide much more than the knowledge that tortoises occurred there in the past.

Williams (1950a) provided a redescription of the Sombrero species *Testudo sombreroensis*, based on information from Leidy (1868) and Julien (1867, 1878). The following characters for *sombreroensis* were provided in Williams' Table 1 (1950a): large size, xiphialastral notch well marked, and humerus somewhat flattened at middle (ratio of diameter 1.31:1). Auffenberg (1967) reported new material of this species that he and J. C. Dickinson of the Florida State Museum collected in "Pleistocene fissures" on the north end of Sombrero in 1964. Although Auffenberg (1967) provided a sketch of a proposed posterior lobe of this tortoise, little more can be gained from these newer specimens to clarify the relationships of this species.

The Hispanolan fossils include a left humerus (135 mm TL), fragments of carapace, and a single element from the plastron (Franz and Woods 1982). Shell thicknesses range from 2.1-17.9 mm. Nearly rounded in cross section, the humeral shaft has only a very faint scar for the attachment of the *M. latissimus dorsi*. The few peripherals in the series indicate that the margins of the shell were entire, not dentated. The authors estimated that this fossil specimen was about 600 mm CL, based on comparisons with other tortoise species. To our knowledge, these are the only specimens available from Hispaniola, in spite of years of extensive collecting in dry caves by the Florida Museum of Natural History (RF, pers. obs.).

The type material of the Mona Island species, *Testudo* (= *Chelonoidis*) *monensis*, was collected from Lirio Cave and included the remains of at least three individuals (Williams 1952). The holotype is the centrum of a first dorsal vertebra, one of the most distinct bones found in this species. Williams' referred materials included anterior and posterior fragments of a skull, complete and fragmented humeri, glenoid facet fragments, ulna, radius fragments, scapula fragments, broken femur, tibial fragments, pelvic fragments, cervical vertebrae (II-V, and VII), and miscellaneous shell fragments. The distinctive features of the Mona tortoise were listed by the author as follows: centrum of first dorsal vertebra elongate and very narrow; shallow palate with vomer less arched dorsally; margins of carapace not scalloped or dentate; sulci feeble; xiphialastron not notched; and shell thin.

The Cuban fossils are the best preserved tortoises from the Caribbean region, except for the recent mate-

rial from Bahamian blue holes. The type specimen of *Testudo* (= *Chelonoidis*) *cubensis*, was part of a first right costal (listed as pleural) from Chiapepote spring at Baños de Ciego Montero, Santa Clara Province (Leidy 1868). Some of the best materials consist of topotypes from this site in the American Museum of Natural History (Williams 1950a). Other referred materials are from Casimba de Jatibonica, Santa Clara Province and a tar pit near Hato Nuevo, Matanzas Province (Williams 1950a). The most diagnostic pieces are (1) the anterior lobe of the figured plastron (Williams 1950a: Plate 2) showing the well-developed gular apices, a moderately developed EPI shelf and a prominent "bird face" with arching brows on the interior surface of the ENT, external ENT wider than long; (2) left quadrant of the plastron with a thickened anal apices and evidence for a very shallow, wedge-shaped anal notch; (3) NUC without a CER scute; (4) two humeral shafts with large, strongly-developed concavities for the insertion of *M. latissimus dorsi*. Other material includes a complete femur, a series of caudal vertebrae (one of which is similar to the three flattened ones found with the Bahamian holotype), pygal, and other miscellaneous bones and pieces of the shell. This species was of large size, the largest in the sample possibly as much as 900 mm CL (based on the length of the figured anterior lobe, EPI + ENT, at midline in Williams 1950a: Plate 2) and a shell thickness of 8-10 mm (based on Leidy's thickness measurement of 3.5-4.5 lines from his type pleural). Williams (1950a) presented a summary of characters for *cubensis*, which included nuchal scute absent; vertebral and costal sulci on raised ridges; marginal and pleural sulci usually in simple grooves; thinning of shell greatest at neural-pleural junction and in midplastron; areas of thickening under marginal, anal and gular scutes; rib heads strong, arising well within costal bones; shape of carapace markedly elongate; xiphialastral notch minimal or absent; free carapace margins recurved, thin, and dentate; femoral-anal sulcus transverse or posteriorly directed at its middle; anal median line very short; pectoral scutes expanding gradually at axillae; gular scutes never encroaching on entoplastron; humerus short, stout, strongly compressed in plane of head, with large and deep pits for *latissimus dorsi*; femur short, stout, strongly compressed in plane of head; and caudal vertebrae normally testudine except for the extreme dorsoventral thickness of the neural lamina of some anterior caudals, which may exceed dorsoventral thickness of centrum.

The most distinctive differences between *cubensis* and its Bahamian relative include its larger size, epiplastral shelf, and prominent pits on the humerus. The presence

of the epiplastral shelf in *cubensis* suggests an independent invasion of a proto-*cubensis* tortoise from South America, probably via nuclear Central America, into Cuba, and that the Cuban species is not closely related to the rest of the Antillean radiation.

Two continental fossil species are also members of the Neotropical group — *Chelonoidis hesterna* (Auffenberg) (new combination) from Miocene sand and gravels of the Honda group (LaVenta fauna), NE of Villavieja, Huila, Colombia (Auffenberg 1971), and *Chelonoidis gringorum* (Simpson) (new combination) from Miocene site in the Chubut Valley, in central Patagonia, Argentina (Simpson 1943). Auffenberg's species includes a crushed shell, two partial skulls and one mandible, most of the pelvic girdle, and limb bones. He considered *hesterna* to be structurally intermediate between *Chelonoidis denticulata* and *C. carbonaria*. Auffenberg (1971) considered the Simpson shell to be

similar to that of *C. chilensis*. He states that the "type of *T. gringorum* can be separated from *G. chilensis* only on the basis of a proportionately thicker external face of the base of the xiphiplastron when compared to its basal width" (from Table 2 in Auffenberg: Xiphipl W/ Xiphipl H=1.4 versus 3.5-6.7, x 5.1).

The fossil *Testudo costaricensis* Segura from the District Peralto in Costa Rica (Oligocene or Miocene) cannot be placed within the genus *Chelonoidis* since it has a well-defined CER scute, a feature missing in all *Chelonoidis* (Auffenberg 1971). The skull is unknown, and the species is based only on one shell (see fig. 8 for shell diagrams in Auffenberg 1971). Segura (1944) considered this species to be near *Testudo* (= *Stylemys*) *amphithorax*, a late Eocene species from the White River group in the northern Great Plains of the United States. Auffenberg (1971) considered this alignment a possibility, but believed that this species might actually



Figure 12. Close up of the internal surface of the anterior plastral lobe of *Chelonoidis alburyorum*, T4, from Sawmill Sink, Abaco, The Bahamas, showing details of the entoplastral *bird face* sculpture. T4 CL = 345mm.



Figure 13. Skull of *Chelonoidis alburyorum*, holotype, T1 from Sawmill Sink, Abaco, The Bahamas. Dorsal, ventral, and posterior views, note the extra pair of holes that penetrate the postotic cavity in the posterior view. Scale = 1 cm.

be more closely allied to *Indotestudo*, a group of forest tortoises from India and southeast Asia, which in turn he thought may be ancestral to both *costaricensis* and *Chelonoidis*. This hypothesis needs further study, particularly since Auffenberg's diagram of hypothetical relationships shows *Manouria* at the root of this arrangement and not *Indotestudo*. We believe that the *Stylemys* hypothesis has greater credibility, based on shell features and biogeographic grounds.

OSTEOLOGY OF LIVING *CHELONOIDIS*

Osteological descriptions are limited for modern Neotropical tortoises, which makes appropriate comparisons of fossils difficult. Much of the literature dwells on color patterns and/or superficial shell or head morphologies, particularly scute configurations and generalized morphometrics (Auffenberg 1969, Pritchard 1979, Ernst 1998, Fritz & Havas 2006). The best descriptive information is found in Auffenberg (1971), who provides shell descriptions, shell ratios, and skull illustrations for various living South American *Chelonoidis*, his new *Geochelone* (= *Chelonoidis*) *hesterna*, and Segura's *Testudo costaricensis*.

We offer the following descriptions to supplement those of Auffenberg (1971). These characters are based on limited samples from the UF and USNM collections. See lists of skull and shell bone measurements for living *Chelonoidis* in Table 2 and Appendices I-IV.

Red-footed Tortoise, *Chelonoidis carbonaria* (Spix 1824). Modern Range: southeastern Panamá, Colombia, Venezuela, the Guyanas, eastern Brazil, eastern Bolivia, Paraguay, northern Argentina, Trinidad, and some islands in the Lesser Antilles (Fritz & Havas 2006). SHELL FEATURES: shell solid, elongate, and domed; male carapaces often narrow in the midsection producing an hourglass-shape; adult males with a moderately developed plastral concavity; CL rarely exceeding 350 mm (Bonin, et al. 2006); NUC without a CER scute; midline cervical sulcus long; neural series variable; SPY I with long, narrow arms, extending only onto PER XI; SPY II completely enclosed by SPY I and the PYG; bridge angular, but not keeled; ING scute large, 4-sided, rectangular in shape, and bordering both the ABD and FEM scutes; plastron with prominent epiplastral shelf that is undercut; anterior margin of gular apices bifid; dorsal surface of gular apices with one pair of GUL scutes and often with a fluted appearance; gular branching deeply encroaching onto the ENT; external surface of the ENT weakly four-sided and almost rounded; internal entoplastral sculpture weak, having a bird-faced sculpture with horizontal brows, diffused sockets and a weak "bill" that projects as a free slender extension onto

the HYO; PEC scute moderate in size with margins divergent; anal apices triangular and dorsally keeled; anal notch prominently bowed or wedged shaped; HUM scute shorter than FEM scute; growth annuli prominent displayed on the external surfaces of the carapace and plastron. SKULL: dolichocephalic with skull width/length ratio of 1:1.41; rostrum more elongate than in *C. denticulata* and not pinched across orbitals; orbital angle, present in *C. nigra* and *C. alburyorum*, absent in *C. carbonaria* and *C. denticulata*; frontal bone does not reach the orbit; cranial profile, domed with the parietal more elevated than the frontal and prefrontal and the sagittal crest; sagittal crest originates below the crest of the parietal and arches downward toward its terminus; sagittal crest tall and laterally compressed; trigeminal and anteriomandibular foramen widely separated; trochlear process prominent and extending across the quadrate and prootic bones; lateral margin of the lingual surface crescent shaped; foramen praepalatinum small; vomerine foramen closed; vomer ascends into the cranium to form a moderately vaulted palate; the anterior part of the vomer with an elevated pedestal; vomerine septum, prominent and bladefike; basisphenoid, long as wide with an obtuse tip directed towards the pterygoids; stapes slender with a slightly swollen apex; squamosal penetrated by a small irregular hole into the postotic chamber. MISCELLANEOUS FEATURES: First dorsal vertebra: centrum robust and more elongate with a moderately constricted waist; centrum with a weak midline keel. Humerus: strongly recurved; head large, rounded, and joined to the bulbous end of the greater trochanter; greater trochanter extending slightly above head; lesser trochanter long, ending about midway up the head; trochanteric fossa narrow and deep, with slightly diverging trochanters; scar for insertion of the *M. latissimus dorsi* faint; humeral shaft triangular with shaft ratio near 1:1.15. Femur: length 82% of humerus length; shaft ratio 1:1.06. Pectoral girdle: scapular angle 105°; glenoid fossa small and very shallow.

REMARKS: Auffenberg (1971) described *Geochelone hesterna* (= *Chelonoidis hesterna*) from the late middle Miocene LaVenta fauna of Huila, Colombia and considered it related to *C. carbonaria* and *C. denticulata* and possibly ancestral to them.

Yellow-footed Tortoise, *Chelonoidis denticulata* (Linnaeus 1766). Modern range: southern Colombia, Venezuela, the Guyanas, the Amazonian lowlands of Brazil, Trinidad, and some islands in the Lesser Antilles (Bonin, et al. 2006, Fritz & Havas 2006). SHELL FEATURES: shell solid, elongate, and domed; CL may reach 800 mm. (Bonin, et al. 2006); plastron with deep concavity in large males; NUC without CER scute; mid-



Figure 14. Ventral view of the skull of the holotype (T1) from Sawmill Sink, Abaco, The Bahamas, showing the triturating surfaces, arched palate, modified vomer (without pedestal) and the reduced septum.

line cervical sulcus long; neural formula generally 4-8-4-8-4; SPY I with broad arms that contact PERs X-XI, and the PYG; SPY II completely enclosed by SPY I and PYG; plastron with prominent epiplastral shelf that is strongly undercut; bridge angular but not keeled; ING scute large, finger-like with rounded margins, primarily in contact with the ABD scute; anterior margin of gular apices can be bowed inward or outward, straight, or occasionally bifid, but not toothed; dorsal surface of gular often split into four scutes, with two on either side of the midline (not visible on ventral surface), often producing a fluted appearance; gular branching well above the ENT; ENT angular, 5-sided and nearly equal in length and width; internal entoplastral sculpture weakly developed, with the bird face having diverging brows, very shallow sockets, short and embedded bill; internal epiplastral suture meeting the lateral margin of the ENT; PEC scute with nearly parallel margins; anal apices triangular and strongly keeled dorsally; anal notch prominent, either wedged, bowed, or U-shaped; HUM scute longer than FEM scute; growth annuli very weakly defined or absent. SKULLS: dolichocephalic with skull width/length ratio of 1:1.43; rostrum somewhat pinched across orbitals which causes the intra-orbital area to be more narrowed than in *C. nigra* and *C. alburyorum*; dorsal part of orbit crescent-shaped with the orbital angle absent; frontal bone does not reach the orbit; profile of the cranium domed with parietal more elevated than the frontal and prefrontal bones and the sagittal crest; sagittal crest originates below the parietal bone and arches downward toward the terminus of the sagittal crest; trigeminal and anteriomandibular foramen united; trochlear process prominent on the quadrate and prootic bones; lateral margin of the lingual surface crescent shaped; foramina praepalatinum small, and the vomerine foramen absent; vomer ascends into the cranium forming a moderately vaulted palate; the anterior part of the vomer with an elevated pedestal; vomerine septum prominent and blade-like; basiosphenoid lance-shaped, longer than wide; stapes slender with a slightly swollen apex; each postotic chamber penetrated by small, apparently naturally occurring irregular hole through the squamosal. MISCELLANEOUS FEATURES: First dorsal vertebra: centrum roughly square in shape with a narrowly constricted waist; centrum without a prominent keel. Humerus: recurved; head large and rounded; greater trochanter robust extending above head; lesser trochanter short ending at the base of the head; trochanteric fossa wide and diverging; scar for insertion of the *M. latissimus dorsi* prominent, shallow with roughened interior; humeral shaft triangular with shaft ratio near 1:1.05.

Femur: length 90% of humerus length; shaft ratio 1:1.2. Pectoral girdle: scapular angle 113 °; glenoid fossa small and very shallow.

Chaco Tortoise, *Chelonoidis chilensis* (Gray 1870). Modern range: southwestern Bolivia, western Paraguay, and northwestern Argentina southward into northern Patagonia (Fritz & Havas 2006). Auffenberg (1969) provides lists of specific localities for Argentina and Paraguay and includes a brief list of anatomical features including scalation to identify this species. Various names have been applied to the northern and southern populations of *C. chilensis* (*Geochelone donosobarrosi* Freiberg 1973; *Geochelone petersi* Freiberg 1973). Separation of these taxa was based in part on a purported difference in CL length (max CL 450 mm for northern population, CL 250 mm for the southern population), although Buskirk (1993) found no morphometric differences between the two forms. Ernst (1998) listed them as synonyms of *C. chilensis*. In a recent checklist, Fritz & Havas (2006) recommended recognizing “only a monotypic *Ch. chilensis* until a phylogeographic investigation is undertaken to determine geographic variation.” SHELL FEATURES (based on UF specimens from Córdoba, Argentina): Shell very thin with numerous fenestra; shell shape more rounded and not strongly domed; NUC without CER scute; midline cervical sulcus either very short or absent; neural formula extremely variable, although still within the general 4-8-4-8-4 pattern; SPY I rectangular, either with very short arms or arms absent; SPY II much wider than PYG; SPY I may partially enclose SPY II when arms are present; bridge with prominent lateral keel; ING scute triangular, but often not discernible because of shell erosion; plastron with poorly developed concavity in males; epiplastral shelf well excavated; anterior margin of gular apices strongly toothed (often with 4 teeth); dorsal surface of GUL with single pair of scutes; position of gular branching either above or touching the ENT, but never encroaching; ENT often 4-sided, generally rounded, being about as long as wide; entoplastral sculpture weakly developed, with bird face having divergent brows, very shallow sockets, bill either embedded and short or free and more elongate; internal epiplastral suture meeting or slightly encroaching onto the anterior edge of the ENT; PEC scute generally narrow, with margins weakly divergent; anal apices often strongly triangular, flattened and very weakly keeled; anal notch deeply incised and wedge-shaped; HUM scute longer than FEM scute; growth annuli weakly developed on the plastron (absent on carapace). SKULL: moderately brachycephalic with skull width/length ratio of 1:1.28; short; rostrum tends to be pinched



Figure 15. A collage of post-cranial skeletal bones of *Chelonoidis alburyorum*, holotype (T1), from Sawmill Sink, Abaco, The Bahamas. Includes pelvis, caudal vertebrae, cervical vertebrae, scapulae, coracoids, humeri, femora, forelimb bones, toe bones, and terminal phalanges. Scale = 10 cm.

across orbits; suggestion of orbital angle in the orbit; frontal bone does not reach the orbit; profile of the cranium slightly domed and more elevated than the frontal and prefrontal bones and the sagittal crest; sagittal crest short with its origin slightly below the crest of the parietal and arches downward toward the terminus; trigeminal and anteriomandibular foramina widely separated; trochlear process prominent on the quadrate and prootic bones; lateral margin of the lingual surface crescent-shaped; foramen praepalatinum and vomerine foramen very small and open; vomer ascends into the cranium to form a very vaulted palate; anterior part of the vomer with an elevated pedestal; vomerine septum blade-like but not prominent; posterior margin of basiosphenoid, bullet-shaped, with tip rounded, rather than pointed; opening of atrial chamber of the tympanic cavity extends into the postotic chamber; squamosal with several small, apparently naturally occurring, holes that penetrate into the postotic chamber. MISCELLANEOUS FEATURES: First dorsal vertebra: centrum roughly square in shape with a narrowly constricted waist; centrum without a prominent keel. Humerus: recurved; head large and rounded; greater trochanter robust extending above head; lesser trochanter short ending at the base of the head; trochanteric fossa wide and diverging; scar for insertion of the *M. latissimus dorsi* prominent, shallow with roughened interior; humeral shaft triangular with shaft ratio near 1:1. Femur: length 87% of humerus length; shaft ratio 1:1.16. Pectoral girdle: scapular angle 113°; glenoid fossa small and very shallow. Osteoderms: front legs with moderate leg armor made of moderate-sized osteoderms.

REMARKS: Auffenberg (1971) considered *Geochelone gringorum* (Simpson) (= *Chelonoidis gringorum*) of Patagonia close to *Chelonoidis chilensis* and by inference *Chelonoidis nigra*.

Galápagos Tortoise, *Chelonoidis nigra* (Quoy & Gaimard 1824). Modern Range: Restricted to the Galápagos Islands, Ecuador. Nine recognized subspecies (Bonin, et al. 2006). SHELL FEATURES (based on USNM specimens: four saddle-backed *C. n. ephippium* and one domed *C. n. vinca*): shell thin, variable in shape, including domed and saddleback conditions; males larger than females; males with deeply impressed plastral concavities; NUC without CER scute; midline cervical sulcus very short with a notch; free margins of PERs scalloped; SPY I with arms that enclose SPY II; neural formula generally 4-8-4-8 (sometimes 6)-4 (sometimes 6); inguinal scute narrow and obtusely triangular; plastron with flattened EPI without shelf; internal surface of anterior lobe with a prominent

transverse trough just posterior to the gular apices; anterior lobe of plastron long and narrow; bridge not keeled; anterior margin of gular apices poorly developed, blunted, with a weak notch; gular branching encroaching onto the ENT; ENT broadly triangular with 3 or 5 weakly developed sides; internal sculpture of ENT boldly developed, with bird face having divergent brows, prominent sockets (particularly in larger individuals), and a broad, short bill either attached or free, extending slightly onto the HYO; PEC scutes posterior to ENT; PEC scutes narrow with parallel to slightly divergent margins; HUM scutes much longer than FEM scutes; anal apices broadly triangular; anal notch wedge-shaped; growth annuli absent on bones (but prominent on scutes in living specimens). SKULLS (UF19507): moderately brachycephalic with skull width/length ratios of 1:1.28; rostrum square; inner ocular area not pinched; orbital angle strong; frontal bone reaches the orbit at the position of the orbital angle; profile of the cranium flattened across the prefrontal, frontal, parietal bones and sagittal crest; trigeminal and anteriomandibular foramina united; trochlear process slightly elevated across the quadrate and prootic bones; lateral margin of the lingual surface of maxilla straight; foramen praepalatinum small and open; vomerine foramen absent; vomer ascends into the cranium to form a moderately vaulted palate; anterior part of the vomer with an elevated pedestal (Fig. 16); vomerine septum prominent and bladelikey; basiosphenoid lance-shaped, longer than wide; stapes slender and straight without enlargements; squamosal solid without holes penetrating into postotic chamber. MISCELLANEOUS FEATURES: First dorsal vertebra: centrum variable, robust in some specimens, smaller in others, all with a moderately constricted waist; centrum either without midline keel or with a partial weak keel. Humerus: strongly recurved; head large, rounded; greater and lesser trochanters strongly developed and parallel to one another; trochanteric fossa narrow and deep; scar for insertion of the *M. latissimus dorsi* shallow and roughened; humeral shaft angular with shaft ratio 1:1.11. Femur: length 80% of humerus length; shaft ratio 1:1.24. Pectoral girdle: scapular angle 140°; glenoid fossa large and well-developed.

REMARKS: We assume that the flattened epiplastra without a shelf in *C. nigra* and *C. alburyorum* represent pleisomorphic states, although this condition could have arisen independently from an elevated epiplastral shelf species as a response to the thinning of the shell. The presence of an epiplastral shelf in *C. cubensis* suggests a different evolutionary pathway for it and may indicate a stronger and possibly more recent connection to continental *Chelonoidis* species.

A molecular study reports that *C. nigra* is most closely related to *C. chilensis* with a predicted separation time of 6 to 12 mya, which predates the oldest extant islands in the Galápagos (Caccone, et al. 1999).

COMPARISONS WITH *CHELONOIDIS ALBURYORUM*

Shell Dimensions and Sizes. The shell of *Chelonoidis alburyorum* is most similar to that of domed populations of *C. nigra*. It is less elongate than in either *C. carbonaria* or *C. denticulata*, and higher domed than in *C. chilensis*. The bridge peripherals in most *Chelonoidis* form a nearly vertical or slightly angled wall. In *C. chilensis*, the bridge is much less vertical, and the wall is crossed by a strong transverse keel that merges with both the anterior and posterior free peripherals along the shell margin. There is not enough shell material associated with West Indian fossil tortoises to know their shell shapes or their bridge wall features.

The maximum CL of *C. alburyorum* is 466 mm, which is larger than a new *Chelonoidis* from Grand Turk, *C. carbonaria*, and southern populations of *C. chilensis*, about the same size as in most *C. denticulata* populations and northern populations of *C. chilensis*, and smaller than in *C. nigra*, *C. cubensis*, *C. monensis*, *C. sombreroensis*, *Chelonoidis* sp. from the Dominican Republic, and a geologically older undescribed species from Abaco, The Bahamas.

Nuchal Plates. All fossil and living species of *Chelonoidis* lack a CER scute (Fig. 9). The midline cervical sulcus that replaces the CER is long in *C. alburyorum*, *C. denticulata*, and *C. carbonaria*, short in *C. nigra* and *C. cubensis*, and virtually absent in *C. chilensis*. A prominent notch is present at the intersection of the midline cervical sulcus with the anterior margin of the carapace in *C. nigra* and *C. chilensis*; the notch is absent in the other species, including *C. alburyorum* and *C. cubensis*.

Neural Series. The general neural formula for *Chelonoidis* is 4-8-4-8-4, but variation is common, particularly in island populations and in *C. chilensis*. In limited samples of living species, we found some type of neural bone variation in 1 of 7 *C. denticulata*, 3 of 5 *C. carbonaria*, 5 of 5 *C. chilensis*, and 5 of 6 *C. nigra*. Every individual in the type series of *C. alburyorum* showed some type of neural variation, most often affecting NEUs I, VI, VII, VIII, and SPY I (Fig. 10). We suspect that this high rate in *C. alburyorum* is the results of inbreeding within small insular populations. It is uncertain why *C. chilensis* should show such high levels of variation.

Pygal complexes. The pygal complex includes SPY I, SPY II, and the PYG. In most tortoises, SPY I

has a pair of arms that reach the last one or two peripherals. SPY I and PYG usually enclose SPY II. In *C. denticulata*, *C. nigra*, and *C. alburyorum*, the arms are in contact with PER XI and touch the PYG. The more narrow arms of *C. carbonaria* do not touch the PYG. The pygal complex in the sample of *C. chilensis* is unusual; SPY I is box-like without arms, very short with arms, or asymmetric with arms that do not reach the PERs or the PYG.

Peripherals. The peripherals on the anterior and posterior margins of shell in *C. alburyorum* are entire, wavy, or weakly scalloped, not dentate as in some species of *Chelonoidis*. Flaring is minimal in *C. alburyorum*, *C. denticulata*, and *C. carbonaria*, and more pronounced in *C. chilensis* and *C. nigra*.

First Dorsal Vertebrae. The centrum of the first dorsal in *C. alburyorum* is slightly longer than wide and moderately waisted with a strong midline keel (Figs. 6, 7). Most modern species have similar shaped centra, but lack the prominent keel. In *C. nigra*, this feature is variable with some individuals having the centrum more elongated having a waist that is narrow or of moderate width. In *C. nigra* and other living species of *Chelonoidis*, keels may be missing or rarely complete, but if present they are usually weakly developed. The most distinctive first dorsal vertebra occurs in fossil *C. monensis*, where the centrum is exceptionally elongated. These features need further investigation across the genus *Chelonoidis* to determine the range of variability.

Shell Vertebrae and Associated Ribs. The thoracic vertebrae of *C. alburyorum* and *C. nigra* are suspended below the carapacial bones by a tall, thin wall of bone of the neural spine (Fig. 6). The ribs originate on the COSs below the NEU/COS suture. The free rib heads are extremely thin, flattened, and flexed toward the body cavity, which creates a substantial space between them and the internal surface of the shell. This allows for the passage of large longitudinal muscles that probably serve in head and neck extension and retraction.

The thoracic vertebrae of *C. denticulata*, *C. carbonaria*, and *C. chilensis* also are sutured to the carapace via a thin wall of bone, but are shorter; the ribs originate at the margin of the costals and extend onto the neurals. In some individuals, the ribs nearly touch the internal shell surface. In these three species, these configurations of the suspended rib heads allow little space for muscles between the ribs and the shell.

Pelvic Vertebrae and Ribs. The presacral complex consists of Vertebrae VIII, IX, and X and their associated ribs and shell attachments (Fig. 8). In *C.*



Figure 16. Ventral view of the skull of *Chelonoidis nigra* (UF 63414) from the Galápagos Islands, showing typical vomer with the pedestal and well-developed septum. Skull length 119.7 mm.

alburyorum (T4), the presacral ribs are thin and flattened. They emerge from a thin but prominent wing-like wedge of bone that spans the bases of all three ribs. The ribs originate on COS VII and VIII. In *C. denticulata*, *C. carbonaria*, and *C. chilensis*, presacral ribs are also thin and flattened. As in *C. alburyorum*, the ribs in *C. denticulata* and *C. carbonaria* originate from a wing of bone that extends out from the surface of COS VII. The next presacral ribs, however, are attached to a massive foundation of bone on COS VIII. Rib IX attachment is winglike but much thickened; the attachment for the third rib is massive and knoblike. In *C. chilensis*, the 2nd and 3rd presacrals are attached to a single massive knob of bone that is twisted toward the rear. The above descriptions include undescribed characters associated with the pelvic complex that might prove useful in the diagnosis of a wide range of tortoise taxa.

Epiplastron. The EPIs of *C. alburyorum* and *C. nigra* are flattened, not bent dorsally, and do not form an epiplastral shelf as in most living species of *Chelonoidis* (Fig. 12) and the fossil *C. cubensis*. The three living continental species and *C. cubensis* (Williams 1950a: Plate 2) display the more common condition with a well-developed epiplastral shelf that is undercut. Both *C. alburyorum* and *C. nigra* have a shallow transverse trough that crosses the internal surface of the EPI just behind the gular apices. Rounded in *C. alburyorum*, the gular apices are truncated or bifid in other species. The anterior lobe of the plastron in *C. alburyorum* is broadly rounded, not narrowly constructed and protruding as in *C. nigra* and *C. cubensis*.

External Entoplastron Shape. Three adult *C. alburyorum* have strongly oval-shaped ENT, with lengths 63-75% of their widths. T4 and T7 are exceptions; T4 has a more typical shield-like ENT with angular margins, similar to those in *C. denticulata*, whereas the ENT in T7 is wider than long but is more triangular or wedge-shaped, not oval. The midline sulcus on the ENT is unbranched in all *C. alburyorum*, a condition also found in living *C. denticulata*. The gular branching lies well above the ENT, a condition also found in *C. denticulata* but not in *C. chilensis*, *C. carbonaria*, and *C. nigra*, where the gular branching either terminates at the ENT suture or encroaches onto the ENT.

Internal Entoplastral Sculpture. A raised bony sculpture of variable prominence and design occurs on the internal surface of the ENT in Bahamian and other West Indian fossils and in all living species of *Chelonoidis*. All of them bear resemblance to bird faces. The sculptures are faint in living *C. denticulata*, *C. carbonaria*, and *C. chilensis*, consisting of narrowly

developed, divergent brow lines, and shallow fossae. The bills in *C. denticulata* and *C. chilensis* are broad and firmly attached to the HYO. The bill in *C. carbonaria* is free of HYO, narrow, and spine-like.

The sculptures in *C. alburyorum*, *C. nigra*, and *C. cubensis* are boldly raised. The sculpture in *C. alburyorum* consists of a small, compact brow mass, a keel with shallow fossae on each side, and a "bill" that extends as a free spine onto the HYO (Fig. 12). The brow of *C. cubensis* is more massive. In *C. n. ephippium*, it consists of a divergent brow line, deep fossae, and a short, wide bill that extends slightly onto the hyoplastron.

Prominent sculptures also occur in an undescribed fossil tortoise from Grand Turk. This sculpture differs in several aspects from that in *C. alburyorum* and other *Chelonoidis*. The Grand Turk specimens have a sculpture reminiscent of an "owl face." This face includes a pair of broadly arching heavy brows, in contrast to a prominent brow mass as in *C. alburyorum*, an arching brow mass in *C. cubensis* and *C. nigra*, or weakly developed, divergent brow lines in other *Chelonoidis*. There is also a strong midline keel that separates the pair of fossae (Fig. 14). The bill extensions in the Grand Turk specimens are unfortunately missing, but, based on the conditions of HYO and remnant keels, the spines were most likely free of the underlying HYO and thicker and more narrowly constructed than those in *C. alburyorum*.

Xiphiplastron. The anal apices of the XIP in *C. alburyorum* are triangular, short, and very thin; the anal notch between the apices is very shallow and wedge-shaped. The interior surfaces of anal apices are flattened and lack a raised midline keel. Similar shaped apices occur in living species of *Chelonoidis*, but they tend to be thicker and possess a prominent internal keel. The anal notch in the living species is usually much more pronounced than in the Bahamian fossils and can be prominently wedge-, bowed-, or U-shaped. The apices in *C. cubensis* are blocky and laterally protruding; this fossil species also lacks a significant anal notch.

Plastral Scutes. The GULs in *C. alburyorum* lie far forward of the ENT. The GULs can approach the ENT suture as a general condition in most species of *Chelonoidis*, except in *C. carbonaria* where the GULs extend well onto the ENT. This condition is typical in fossil and living North American *Gopherus* and *Hesperotestudo*, but uncommon in *Chelonoidis*. Williams (1960) used a longer HUM scute when compared to the FEM scute to separate *C. denticulata* from *C. carbonaria*. In *C. alburyorum*, the lengths of the HUM and FEM scute are nearly equal. PEC scutes in most

Chelonoidis tend to be narrow with the margins straight or slightly divergent, but the PECs in the Bahamian fossils are robust and greatly inflated, with the scute margins strongly divergent.

Skull Shapes and Palate. The shape of the skull ranges from strongly brachycephalic in *Chelonoidis alburyorum* to moderately brachycephalic in *C. nigra* (Figs. 13,16) to moderately dolicocephalic in *C. denticulata*; *C. carbonaria* and *C. chilensis* show a condition intermediate between those in *C. nigra* and *C. denticulata*. There are no data for other fossil forms.

A pair of natural-appearing holes posterior to the normal ear openings in *C. alburyorum* penetrates into the postotic chambers. One reviewer considered those openings resulting with the loss of the squamosals during the decay process. Whether natural or not, these openings also occur occasionally in *C. nigra*, but have not been observed in our sample of skulls from other *Chelonoidis* species. The extra openings in the *C. alburyorum* skull are similar in shape and size, with both having a slight ridge of bone that outlines each hole. If natural, this arrangement may enhance hearing.

All known skulls of *Chelonoidis* have arched palates except in *C. monensis*, which Williams (1950a) described as "...less arched dorsally." All living species have well developed vomerine pedestals and accompanying thin, knife-like septa, except for *C. alburyorum* that lacks this pedestal and sharp septum (Fig. 16). The *C. alburyorum* configuration results in a nearly flattened vomer and a diminished septum, which is expressed a partial, low-round ridge on the posterior aspect of the bone (Fig. 14). These features provide *C. alburyorum* with the greatest effective palatal surface among *Chelonoidis*. This configuration may be an adaptation for crushing fruits.

DISCUSSION

The Sawmill Sink tortoise fossils represent a distinct new species of *Chelonoidis* from the late Holocene of Abaco Island in the northern Bahamas. This is the first in a series of new tortoises that have been found in the Bahamian archipelago since 2005. Description of the additional new forms will follow as more material becomes available from inland blue holes.

Chelonoidis alburyorum is more similar to Neotropical and Caribbean groups of tortoises than to North American tortoises (as proposed by Meylan & Sterrer, 2000). Among living Neotropical (*Chelonoidis*) species, it shares more morphological features with the island-adapted *C. nigra* than with the mainland species *C. denticulata*, *C. carbonaria*, and *C. chilensis*. *Chelonoidis alburyorum* also is similar in a combina-

tion of characters to fossils from Mona and Hispaniola but differs sufficiently to be recognized as a separate taxon. The substantial differences between *C. alburyorum* and *C. cubensis* suggest that they are not closely related.

The shape of the shell for all known specimens of *Chelonoidis alburyorum* is consistent, with no indication of the saddleback condition that occurs in certain populations of *C. nigra* from the Galápagos Islands. On the posterior end of the carapace, however, a "caudal hump" at VER V tends to elongate the shell; its function, if there is one, is unclear although the additional space in females might provide opportunities for larger eggs or increased egg-carrying capacity.

The internal sculptures of the ENT are boldest in *C. nigra*, *C. cubensis*, and *C. alburyorum*, and weakest in *C. carbonaria* and *C. denticulata*. The ENT is not represented in *C. monensis* or the Hispaniolan material (Williams 1952, Franz and Woods 1983). Bramble (1971) found distinct ENT sculptures in the North American tortoises of the *Gopherus polyphemus* clade. He postulated that these structures facilitated buttressing actions as the acromial process of the scapula moves within the scapula-interclavicular joint. He thought that this arrangement could compensate for the resistance of the soil encountered during the power-stroke when gopher tortoises dig burrows with their front limbs. The role of these structures in Neotropical tortoises is unclear since none of these species is known to dig burrows. We suggest, however, that they operate as supportive structures associated with either some specialized locomotor function or posturing behavior where scapular bracing is an essential element. Possibilities could include the straight-legged behavior found in living Neotropical tortoises, or some undefined specialization associated with navigation over rugged, rocky terrain, such as the conditions found in The Bahamas (dog-toothed limestones) and the Galápagos (basaltic lava).

The brachycephalic condition in *Chelonoidis alburyorum* results from the expansion of the postotic chambers of the ears. Squamosal caps are missing. The second openings, posterior to the normal ear openings, penetrate through the squamosals into the postotic chambers on each side of the head. If natural, this arrangement might suggest the increased capacity for low-frequency sound reception. The need for such reception may be a direct response to intra-specific communications or to acoustical location of falling fruit.

The wide, highly vaulted palate and the reduced vomerine septum in *C. alburyorum* suggest some type of feeding specialization, possibly related to eating fruits. The fruits of mastic and satinleaf, found in the body cavi-

ties of two tortoises, are of an appropriate size to fit precisely into the palatal cavity of the T1 skull. The shortened gular and anterior lobe of the plastron may expedite the manipulation of small fruits lying on the ground.

At least two individuals in this study bear possible tooth marks that may have been produced by bites of Cuban crocodiles. T7 from Sawmill Sink has a series of deep scars that have partially healed (Steadman, et al. 2007: Fig. 4). A second specimen from The Fountain blue hole on Mayaguana shows a distinct row of bite wounds on the carapace with no sign of healing. The tooth row includes a line of four small holes and one large hole. The presence of bite wounds in two fossil tortoise specimens indicates that crocodiles may have attacked living tortoises or scavenged dead tortoises with some regularity. There are suggestions that Cuban crocodiles may be more terrestrial than other new world crocodiles (John Thorbjarnarson, pers. comm.). This opens the possibility that attacks on tortoises could have occurred on land, which expands the potential roles of crocodiles in The Bahamas as formidable terrestrial predators.

Within the Bahamian Archipelago, fossil tortoises are now known from 10 islands on seven island banks. They represent at least three species, two of which remain undescribed. This group of tortoises appears to represent a clade of thin-shelled species that is more closely related to each other than to other Caribbean fossil species, particularly *Chelonoidis cubensis*. The precise relationships, however, are unstudied.

The widespread occurrence of tortoises across the Bahamian Archipelago and the Caribbean area in general suggests a significant dispersal and subsequent radiation of these reptiles that probably involved multiple colonizations and island-hopping by ancestral stocks from South America during the mid to late Tertiary. These relationships will need to be explored using a phylogenetic approach when once island populations become better known.

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APPENDIX I. Shell measurements (in mm) for five modern *Chelonoidis carbonaria* specimens from the UF collection.

Character	UF48278	UF27384	UF33597	UF33596	UF5259
Sex	Male	Female	Female	Female	Female
Standard carapace length	247	242	253	189	226
Over-the-shell carapace length	339	317	317	247	287
Ento- plus hyoplastral length	89	85	77	71	83
Width of shell at midsection	155	155	153	121	129
Greatest height of shell	101	112	108	87	100
Minimum bridge length	107.3	118	113	96.4	112.7
Midline length of plastron	199	202	193	163	181
Greatest length of plastron	214	219	215	174	198
Anterior plastral lobe length	47.8	44.3	47.5	35	37.3
Posterior plastral lobe length	50.3	39.8	33.6	46.5	49.7
Combined lobe lengths	98.1	84.1	81.1	81.5	87
Nuchal plate length at midline	52.8	49.1	50.1	38.8	42.6
Nuchal plate width at shell margin	41.5	43.6	40	32.1	36.2
Greatest width of nuchal plate	56.3	62.6	57.4	49.6	57.7
Midline length of neural I	35.3	32.8	32.2	24.1	33.1
Width of neural I at transverse sulcus	27.8	24.3	21.8	18.2	25
Number of sides on neural I	6	4	4	6)	6)
Midline length of neural II	23	21.8	19.9	17.7	21.8
1 st width on neural II	38.7	33.3	31.6	30.7	33.8
2 nd width on neural II	na	36.6	36.2	na	Na
Number of sides of neural II	6	8	8	6)	6)
Midline length of neural III	22.7	22.5	24.5	18.2	21.7
Width on neural III at transverse sulcus	33.2	30.8	28.8	24	39.5
Number of sides on neural III	6	4	4	4	4
Midline length of neural IV	21.9	21.7	24.2	20.3	20.8
Greatest width on neural IV	39.2	38.8	36.8	30.1	35.2
Number of sides of neural IV	6	8	8	8	8
Midline length neural V	19.7	20.7	22.5	17.5	19.7
Width of neural V at transverse sulcus	32.6	31.5	27.5	23.2	28
Number of sides on neural V	6	5	4	4	4
Midline length neural VI	20	19	18	15.7	17.6
Greatest width of neural VI	35	34	33	25.8	31.2
Number of sides on neural VI	4	7	6	7	8
Number of sides on neural VII	6	4	6	5	4
Number of sides on neural VIII	4	6	6	6	6
Length of sulcus between suprapygal II & pygal	40	37.9	32.4	31.1	33.2

APPENDIX I. Continued.

Character	UF48278	UF27384	UF33597	UF33596	UF5259
Sex	Male	Female	Female	Female	Female
Width of pygal at shell margin	25.4	17.9	13	11.5	19.5
Epiplastron length at midline	20.9	18.5	28.7	15.6	17.1
Entoplastron length at midline	36.8	40.1	35.6	29.1	34.9
Entoplastron greatest width	42.6	46.4	44.1	30.5	37.3
Hyoplastron length at midline	44.8	45.4	44	40.6	45.2
Hypoplastron length at midline	62.8	63.5	58.4	53.3	59.8
Xiphiplastron length at midline	34.6	36.1	31.5	28.5	28.7
Distance between the entoplastron & humeral/pectoral sulcus	9.3	0	3.7	7.5	3.7
Length of nuchal midline sulcus	15	11.7	12.1	5	8.8
Midline length of vertebral scute I	57.4	57.2	54.6	45.5	49.5
Midline length of vertebral scute II	49.2	45.1	45.4	38.7	46.3
Midline length of vertebral scute III	46.5	45.4	46	38.9	42.7
Midline length of vertebral scute IV	53.4	51	52	40.5	47.5
Midline length of vertebral scute V	69.5	64.5	63	45.2	53.1
Greatest width of vertebral scute I	62.6	55.5	55.6	46.2	56.4
Greatest width of vertebral scute II	65.6	59.9	66.9	51.2	58
Greatest width of vertebral scute III	70.5	64.7	69.2	54.6	62.8
Greatest width of vertebral scute IV	66.8	60	61.5	50.1	52.6
Greatest width of vertebral scute V	85.4	76.9	80	62.3	64.7
Midline length of gular scute	30.2	26.8	25	22	26.2
Midline length of humeral scute	35.4	32.3	42.5	30.7	29.1
Midline length of pectoral scute	8.6	10.6	13.3	8.5	12.6
Midline length of abdominal scute	78.3	80	66.5	60.7	70.9
Midline length of femoral scute	46.7	45	43.3	39.5	40.4
Midline length of anal scute	11.7	8.1	4.8	6.7	4.8
Depth of anal notch	17.2	17.7	16.3	10	16

APPENDIX II. Shell measurements (in mm) for five modern *Chelonoidis denticulata* specimens from the UF collection.

Character	UF19242	UF23231	UF33661	UF61931	UF33670
Sex	Male	Female	Female	Male	Male
Standard carapace length	466	377	333	317	365
Over-the-shell carapace length	597	471	380	412	470
Ento- plus hyoplastral length	166	104	134	124	135
Width of shell at midsection	265	238	214	185	220
Greatest height of shell	187	163	146	123	143
Minimum bridge length	182	172	148	132	149
Midline length of plastron	331	312	285	272	Ca305
Greatest length of plastron	410	334	305	291	326
Anterior plastral lobe length	123	85	81	82	91
Posterior plastral lobe length	116	86	76	84	90
Combined lobe lengths	239	171	157	166	181
Nuchal plate length at midline	86.6	68	53.1	60.1	73.7
Nuchal plate width at shell margin	81.5	58.4	53.1	58.8	58.1
Greatest width of nuchal plate	94.1	79.1	75.8	72.3	80.9
Length of suture between nuchal plate & neural I	28.2	18	15.5	20.7	20.5
Midline length of neural I	55.9	50	36.2	34.7	40.7
Width of neural I at transverse sulcus	38.2	29.9	22.4	26.1	28.4
Number of sides on neural I	4	4	4	4	4
Midline length of neural II	40.7	36.2	27.8	27.9	30.9
1 st width on neural II	59.9	43.1	37.6	39	43.4
2 nd width on neural II	63.7	55.8	42	38.5	46
Number of sides of neural II	8	8	8	8	8
Midline length of neural III	39.5	36.3	29.7	27	29.5
Width on neural III at transverse sulcus	44.2	40.8	35	29.5	36.7
Number of sides on neural III	4	4	4	4	4
Midline length of neural IV	44.5	33.2	30.6	30.2	33.5
Greatest width on neural IV	63.7	57.5	48	43.4	50
Number of sides of neural IV	8	8	8	8	8
Midline length neural V	38	32	28.9	25.9	26.2
Width of neural V at transverse sulcus	44.6	40	35.2	33.2	38.1
Number of sides on neural V	4	4	4	4	4
Midline length of neural VI	35	27.6	25.7	24.3	27
Greatest width of neural VI	59.8	47.7	42.5	41.1	46.7
Number of sides on neural VI	6	6	8	6	6
Number of sides of neural VII	6	6	4	6	6

APPENDIX II. Continued.

Character	UF19242	UF23231	UF33661	UF61931	UF33670
Sex	Male	Female	Female	Male	Male
Number of sides on neural VIII	6	6	6	6	6
Length of sulcus between suprapygals II & pygal	56.5	42	46.2	44.5	43.2
Width of pygal at shell margin	31.9	26.6	32.1	27.4	27
Epiplastron length at midline	64.5	33.2	34.5	34.8	46.2
Entoplastron length at midline	72	63.3	60	52.1	57.1
Entoplastron greatest width	78.5	65.4	56.3	50.9	54
Hyoplastron length at midline	91.5	66	74.7	71.2	77.1
Hypoplastron length at midline	103.7	84.2	80.1	73.5	77.7
Xiphiplastron length at midline	ca 65	54.1	64.8	51.2	53.5
Distance between the entoplastron & humeral/pectoral sulcus	16.6	13.9	12.9	12.1	12.7
Length of nuchal midline sulcus	32.4	20.8	9.1	17.1	25
Midline length of vertebral scute I	85.2	72.7	62.8	62	71.6
Midline length of vertebral scute II	82.2	76.3	57	56.8	64.2
Midline length of vertebral scute III	84.6	71.1	61.6	57.3	64.2
Midline length of vertebral scute IV	105.4	80.7	69.7	74.5	78.1
Midline length of vertebral scute V	115.6	84.8	77.2	65.7	98
Greatest width of vertebral scute I	105.4	94.5	72.5	81.1	94.8
Greatest width of vertebral scute II	117.3	97.6	80.4	76.8	90.1
Greatest width of vertebral scute III	126.1	112.6	93.8	84.1	99.1
Greatest width of vertebral scute IV	111.3	89.1	78.6	81.3	88
Greatest width of vertebral scute V	ca 134.8	ca 99.1	ca 95.1	ca 97.7	ca 104.6
Midline length of gular scute	46.7	29.6	29.7	24.8	34.7
Midline length of humeral scute	105.7	79.4	77.4	75.2	79.4
Midline length of pectoral scute	19.2	27.9	19.7	18.9	18.7
Midline length of abdominal scute	127	109.2	100.1	93.6	97.2
Midline length of femoral scute	ca 75	62.9	54.4	53.2	62.8
Midline length of anal scute	na	13	13.8	16.5	16.5
Depth of anal notch	na	18	13	17	24.5

APPENDIX III. Shell measurements (in mm) for five modern *Chelonoidis chilensis* specimens from the UF collection.

Character	UF33603	UF33600	UF33604	UF33618	UF33617
Sex	Female	Female	Female	Female	Female
Standard carapace length	183	157	169	186	169
Over-the-shell carapace length	234	208	215	250	228
Ento-plus hyoplastral length	69	62	66	67	70
Width of shell at midsection	145	119	132	147	146
Greatest height of shell	94	75	85	101	94
Minimum bridge length	85.2	73.3	85	90	82.9
Midline length of plastron	157	134	152	159	149
Greatest length of plastron	166	145	161	169	162
Anterior plastral lobe length	42	38.9	38	38.7	42.8
Posterior plastral lobe length	44.4	42.7	45	43.4	48.6
Combined lobe lengths	86.4	81.6	83	82.1	91.4
Nuchal plate length at midline	31.1	26.9	27.6	29.3	30.1
Nuchal plate width at shell margin	28.1	30.4	28.2	33.4	29.6
Greatest width of nuchal plate	43.3	41.8	34.3	44.3	46.6
Midline length of neural I	27	22.5	24.3	26.3	23.7
Width of neural I at transverse sulcus	21.4	16.9	17.9	17.3	14.4
Number of sides on neural I	4	6	6	4	4
Midline length of neural II	19.2	14.7	15.3	19.9	18.4
1 st width on neural II	26.5	22.2	22.1	21.8	19.0
2 nd width on neural II	30.1	na	na	26.4	23.2
Number of sides of neural II	8	6	6	8	8
Midline length of neural III	23.3	17	21.3	25	18
Width on neural III at transverse sulcus	26.3	19.2	22.8	24.7	19.4
Number of sides on neural III	4	6	6	6	4
Midline length of neural IV	18.5	13.9	11.3	19.1	18.1
Greatest width on neural IV	30	20	23.2	26.9	24.4
Number of sides of neural IV	5	4	5	6	8
Midline length neural V	17.2	16.5	23.7	21.9	16.5
Width of neural V at transverse sulcus	26.5	19.2	19.7	24.6	29.2
Number of sides on neural V	4	6	4	6	4
Midline length of neural VI	11.5	17.9	16.3	15.7	14.4
Greatest width of neural VI	25.4	21.7	24.9	24	24.5
Number of sides on neural VI	6	8	6	6	7
Number of sides neural VII	6	(4)	6	(4)	4
Number of sides on neural VIII	6	6	5	6	6
Length of sulcus between suprapygal II & pygal	28.7	31.7	24.8	31.8	30.4

APPENDIX III. Continued.

Character	UF33603	UF33600	UF33604	UF33618	UF33617
Sex	Female	Female	Female	Female	Female
Width of pygal at shell margin	21.5	16.4	16.6	16.9	15.1
Epiplastron length at midline	22.4	19.8	18.5	17.6	14.5
Entoplastron length at midline	24.2	22.7	27.6	22	26.4
Entoplastron greatest width	27	22.7	31.6	26.4	29
Hyoplastron length at midline	44.2	36.4	38.3	51.5	40.2
Hypoplastron length at midline	44.8	33.2	42.9	42.7	45
Xiphiplastron length at midline	24.7	22.8	25.7	26.3	24.8
Distance between the entoplastron & humeral/pectoral sulcus	6.3	4.2	2.1	10.8	2
Length of nuchal midline sulcus	4.3	1.7	2.8	2	2.1
Midline length of vertebral scute I	42.4	37.4	36.1	41.4	41.3
Midline length of vertebral scute II	41.3	32.7	37	44.7	35.2
Midline length of vertebral scute III	39.7	32.2	38.7	42.6	36.6
Midline length of vertebral scute IV	42.7	35.8	36.7	48.1	42
Midline length of vertebral scute V	39.4	38.4	37.2	47.9	44
Greatest width of vertebral scute I	44	37.6	38.2	45	41.8
Greatest width of vertebral scute II	61.7	47.4	51.5	61.3	52.4
Greatest width of vertebral scute III	66.2	51.5	57.3	66	59.1
Greatest width of vertebral scute IV	55.6	48	51.7	59.3	52.8
Greatest width of vertebral scute V	49.1	43.7	41.9	55.8	55.7
Midline length of gular scute	20	18.9	21.3	18.7	17.2
Midline length of humeral scute	31.5	26.5	26.2	31.5	25.2
Midline length of pectoral scute	9.5	8.9	10.3	13.2	10.2
Midline length of abdominal scute	59.9	49.6	51.4	66.6	58.7
Midline length of femoral scute	26	16.3	29	23.8	27.7
Midline length of anal scute	13.1	11.4	10.4	5.6	8.2
Depth of anal notch	10	11	12	12	15

APPENDIX IV. Shell measurements (in mm) for five modern *Chelonoidis nigra* specimens (4 *C. n. ephippium* and one *C. n. vicina**) from United States National Museum collection. Na = data not available.

Character	USNM 51069	USNM1 102904	USNM1 222494	USNM1 65896*	USNM1 222492
Sex / age	Female	Male	Female	Subadult	Subadult
Standard carapace length	588	610	595	549	414
Over-the-shell carapace length	683	675	680	663	487
Width of shell at midsection	445	444	436	425	308
Greatest height of shell	289	297	243	265	199
Minimum bridge length	248	257	266	256	176
Midline length of plastron	491	498	515	436	359
Greatest length of plastron	506	515	533	452	366
Anterior plastral lobe length	139	138	142	102	99
Posterior plastral lobe length	121	123	115	92	92
Combined lobe lengths	260	261	257	194	191
Nuchal plate length at midline	80.5	80.7	90.0	na	59.4
Nuchal plate width at shell margin	130.2	124.3	125.0	na	82.4
Greatest width of nuchal plate	108.6	140	131	na	88.6
Length of suture between nuchal plate & neural I	38.9	39.9	39.9	na	na
Midline length of neural I	61.2	65.6	78.6	na	46.7
Width of neural I at transverse sulcus	62.1	65.6	70.7	50.6	43
Number of sides on neural I	4	4	4	n	4
Midline length of neural II	59.6	62.1	56.4	52.1	42.4
1 st width on neural II	91.4	88.9	103.5	78.2	56.4
2 nd width on neural II	102.1	87.7	98.8	na	63.8
Number of sides of neural II	8	8	8	6	8
Midline length of neural III	57.6	60.4	53.7	65.6	48.2
Width on neural III at transverse sulcus	82.0	75.6	67.0	68.4	60.0
Number of sides on neural III	4	6	na	6	4
Midline length of neural IV	62.1	61.7	na	53.5	42.4
Greatest width on neural IV	101.4	72.7	na	78.1	68.0
Number of sides of neural IV	8	6	na	6	6
Midline length neural V	55.2	53.0	na	76.1	36.5
Width of neural V at transverse sulcus	82.9	69.0	74.0	63.0	59.2
Number of sides on Neural V	4	4	6	Ab	6
Midline length of neural VI	41.9	35.7	40.0	Ab	30.5
Greatest width of neural VI	90.0	55.8	69.8	Ab	51.4
Number of sides on neural VI	8	6	6	Ab	6
Number of sides on neural VII	6	6	6	Ab	6
Number of sides on neural VIII	6	6	6	6	6

APPENDIX IV. Continued.

Character	USNM 51069	USNM1 102904	USNM1 222494	USNM1 65896*	USNM1 222492
Sex / age	Female	Male	Female	Subadult	Subadult
Length of sulcus between suprapygal II & pygal	79.0	72.5	na	58.6	59.9
Width of pygal at shell margin	48.2	33.7	na	na	28.1
Epiplastron length at midline	36.5	40.4	43.6	30.2	26.2
Entoplastron length at midline	91.7	92.6	97.5	77.8	64.2
Entoplastron greatest width	93.7	100.4	106.5	97.9	71.4
Hyoplastron length at midline	151.0	150.0	153.0	128.6	100.0
Hypoplastron length at midline	152.0	140.0	145.0	133.1	120.0
Xiphiplastron length at midline	72.5	88.0	85.0	64.2	58.0
Distance between the entoplastron & humeral/pectoral sulcus	34.6	39.6	35.0	17.6	19.0
Length of nuchal midline sulcus	10.8	9.0	13.6	12.7	8.0
Midline length of vertebral scute I	98.3	113.7	116.8	112.0	79.7
Midline length of vertebral scute II	117.0	113.7	119.1	124.2	89.1
Midline length of vertebral scute III	122.2	119.0	113.6	121.2	86.1
Midline length of vertebral scute IV	133.0	128.5	118.6	104.2	86.6
Midline length of vertebral scute V	135.2	129.8	na	105.6	86.7
Greatest width of vertebral scute I	128.3	144	155	169	99
Greatest width of vertebral scute II	175.9	167	192	168.4	126.4
Greatest width of vertebral scute III	197.0	161	187.5	177	128.5
Greatest width of vertebral scute IV	173.0	142	150	145	114.6
Greatest width of vertebral scute V	175.8	162.5	na	150	121.6
Midline length of gular scute	48.2	43.6	60	36.4	40
Midline length of humeral scute	109.2	122.4	118	83.4	68
Midline length of pectoral scute	17.4	25.0	37	28.9	28
Midline length of abdominal scute	203.0	190	180	190	135
Midline length of femoral scute	71.0	82	90	55	58
Midline length of anal scute	47.5	43	45	45	35
Depth of anal notch	na	na	15.1	14.5	6.9
Width of anal notch	na	na	76.6	76.7	50.5
Gular width at sulcus	90.8	93.1	92.8	83.2	61.3
Gular width at lobe base	225.0	230	250	140	170

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Snelson, F.F. Jr., T.J. Krabbenhoft, and J.M. Quattro. *Elassoma gilberti*, a New Species of Pygmy Sunfish (Elassomatidae) from Florida and Georgia. Bull. Florida Museum Nat. Hist. 48(4): 119-144. Price \$7.00

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