

NEW TURTLES (CHELONIA) FROM THE LATE EOCENE THROUGH LATE MIOCENE OF THE PANAMA CANAL BASIN

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ABSTRACT—Four distinct fossil turtle assemblages (Chelonia) are recognized from the Panama Canal Basin. The oldest, from the late Eocene–early Oligocene Gatuncillo Formation, is dominated by podocnemidid pleurodires. The early Miocene Culebra Formation includes both podocnemidids and trionychids. The early to middle Miocene Cucaracha Formation includes taxa classified in Geoemydidae (including *Rhinoclemmys panamaensis* n. sp.), Kinosternidae (represented by *Staurotypus moschus* n. sp.), large testudinids, trionychids, and podocnemidids, and finally, the late Miocene Gatun Formation records cheloniid sea turtles. These fossils include the oldest known representatives of *Rhinoclemmys*, the oldest record of kinosternids in Central America with a more extensive southern paleodistribution for *Staurotypus* and staurotypines in general, early occurrences of giant tortoises in the Neotropics, the oldest occurrence of soft-shell turtles in the tropics, the oldest late Eocene–early Oligocene Neotropical occurrences of podocnemidids. The Panamanian fossil turtles represent clades that are primarily endemic to North America, showing their very early arrival into the Neotropics prior to the complete emergence of the Isthmus of Panama, as well as their first contact with Caribbean–South American pleurodires by the early Miocene.

INTRODUCTION

EXTANT TURTLES from North and Central America are exclusively represented by cryptodires, whereas in South America pleurodires are dominant and cryptodires less diverse. This modern distribution of turtles in the New World is the result of a complex and poorly documented biogeographical history resulting from endemism, diversification, interchange and mixing of lineages from different geographic sources, all these events potentially influenced by geologic history.

The most recent geological event with profound implications in the dispersal and interchange of biota between North–Central America and South America, also causing the isolation between Caribbean and Pacific marine faunas, was the formation of the Isthmus of Panama about 4 Myr ago (Barley et al., 2010; Coates et al., 2004; Coates and Obando, 1996; Herrera et al., 2008; Webb, 1985). The emergence of the Isthmus of Panama allowed for the dispersal of some cryptodires from North to South America, including members of the Kinosternidae, Chelydridae, Emydidae, and Geoemydidae (Pritchard, 1984). Molecular data recognizes at least three different dispersal events of the Geoemydidae (Batauridae) from North to South America through Panama after the emergence of the isthmus (Le and McCord, 2008). In contrast, the arrival to South America by members of the Trionychidae and Testudinidae (including giant tortoises) may have taken place from Florida through the Antilles (Head et al., 2006; Pritchard, 1984).

In the early Miocene (around 20 Myr) North–Central America was separated from South America by a narrow strait (Kirby et al., 2008; Montes et al., in press) (Fig. 1.1). During the beginning of the middle Miocene (around 15 Myr) the Culebra strait was closed, expanding the Central American Peninsula farther to the east. However, the Atrato seaway still separated the peninsula from South America (Kirby et al., 2008) (Fig. 1.2). The opening and closing of narrow straits at the easternmost tip of the Central American Peninsula persisted until the rise of eastern Panama and final closure

of the Atrato Seaway by the Pliocene (4 Myr) that connected South with Central America (Kirby et al., 2008) (Fig. 1.3).

Recent fieldwork by geologists and paleontologists from the Florida Museum of Natural History–University of Florida, the Smithsonian Tropical Research Institute, and the Panama Canal Authority was conducted in order to relocate previously collected sites (Whitmore and Stewart, 1965) and to prospect for new fossil localities. The later has been facilitated by the recent excavations associated with the widening of the Panama Canal resulting a once-in-a-century opportunity to explore fresh exposures of fossiliferous rocks. The result is that many new mammal, crocodile, snake, turtle, fish, crab, mollusk, and plant fossils have been recovered. One of the primary conclusions coming from the early–middle Miocene mammalian fossil record is that all of the recovered taxa have exclusive affinities with taxa from North America (MacFadden, 2006; MacFadden, 2009; MacFadden et al., 2010).

Previously the known fossil record of turtles from southern Central America has been sparse, based on fragmentary specimens that include: 1) *Geochelone costarricensis* from the Oligocene–Miocene of Costa Rica (Coates, 1999; Segura, 1944); 2) carapace pieces of *Rhinoclemmys* sp. and shells of *Geochelone* sp. from the late Miocene of Honduras (D. Webb and Perrigo, 1984); 3) isolated costal bones of a trionychid from the Pliocene of Costa Rica (Laurito et al., 2005); 4) *Rhinoclemmys nicoyana* from the late Pleistocene Costa Rica (Acuña, 1996); and 5) undescribed Miocene fossil turtles from outcrops along the Panama Canal (MacFadden, 2006; Whitmore and Stewart, 1965).

Here we describe fossil turtles initially reported by Whitmore and Stewart (1965) and MacFadden (2006) as well as new specimens recently collected along the Panama Canal area and the Panama Colon Highway (Fig. 2). The fossils are from the: 1) late Eocene–early Oligocene Gatuncillo Formation (Montes et al., in press); 2) early Miocene Culebra and Cucaracha formations cropping out along the Gaillard Cut (Kirby et al., 2008; Montes et al., in press); and 3) late Miocene Gatun Formation (Coates, 1999).

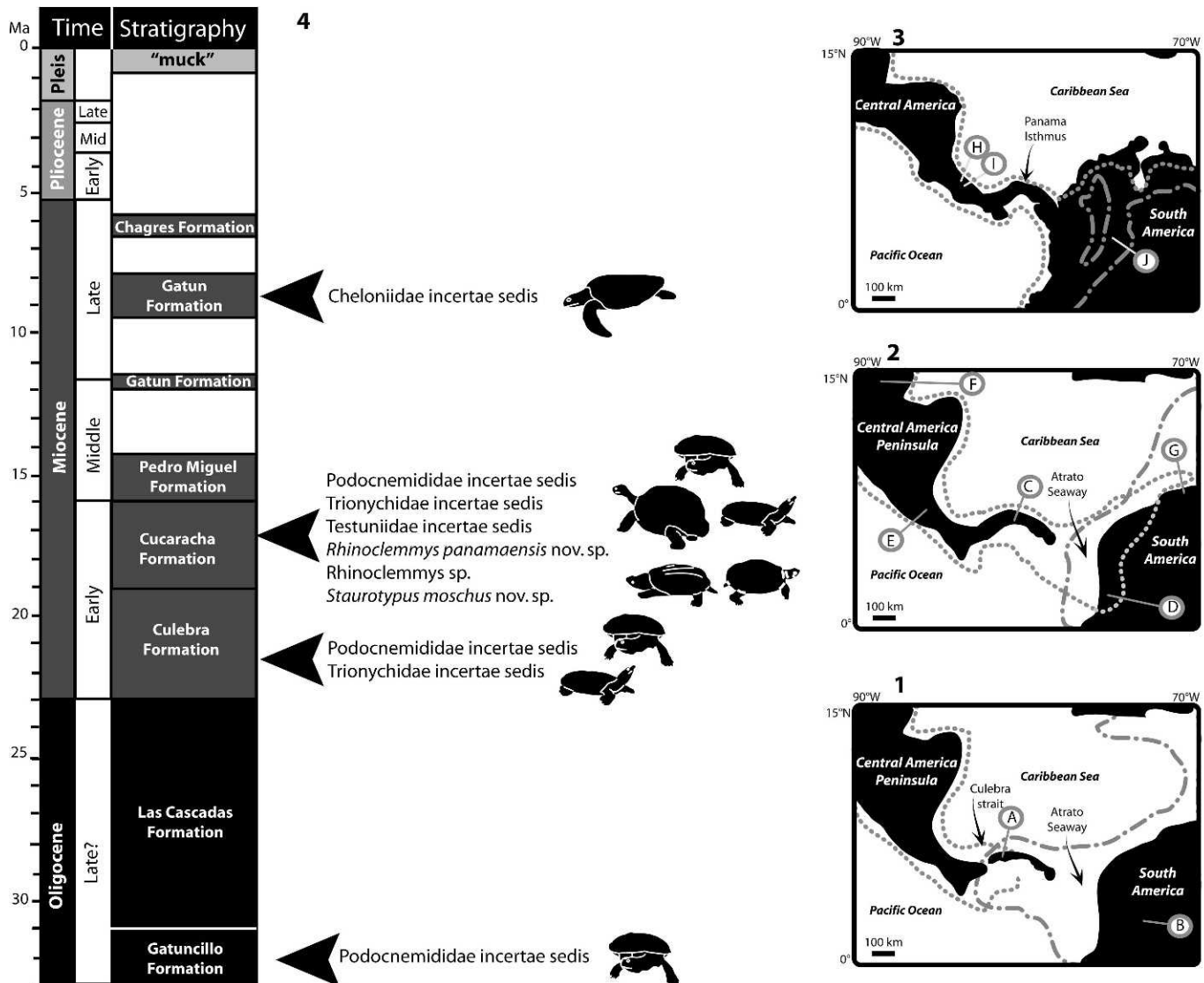


FIGURE 1—Early Miocene to Present paleogeographical reconstructions of Central America, modified from Kirby et al. (2008). Numbers represent localities with fossil turtles. 1, early Miocene, hypothetical distribution of North American cryptodires (trionychids) and Caribbean–South American pleurodires (podocnemidids); 2, middle-late Miocene arrival of cryptodires (trionychids and testudinids) into South America; 3, Pliocene–Present arrival of kinosternids and geoemydids into South America, and complete retreat of trionychids toward North-Central America and podocnemidids into more fluvial environments of South America; 4, geologic history of the Panama Canal Basin modified from Kirby et al., 2008, showing the fossil record content for each formation. Past (hypothetical) and modern distribution for pleurodires is shown by the gray dash-gap-dash line enclosing the land areas and costal margins, and for cryptodires is shown by the gray dash-dash line. A, Panama Canal Basin; podocnemidids, trionychids; B, Pubenza Locality, Colombia; podocnemidids ‘unpubl. data’ Cadena; C, Panama Canal Basin; trionychids, testudinids, geoemydids, and kinosternids; D, La Venta, Colombia; podocnemidids, testudinids, (Wood, 1997); E, Costa Rica; geoemydids (Segura, 1944); F, Honduras; geoemydids and testudinids (Web & Perrigo, 1984); G, Urumaco, Venezuela; geoemydids and trionychids (Sanchez-Villagra & Scheyer, 2010); H, Costa Rica; trionychids (Laurito et al., 2005); I, Costa Rica; geoemydids (Acuña and Laurito, 1996); J, Pubenza locality, Colombia; kinosternids (Cadena et al., 2007). Past (hypothetical) and modern distribution for pleurodires is shown by the gray dash-gap-dash line enclosing the land areas and costal margins, and for cryptodires is shown by the gray dash-dash line.

The available geochronology for these lithostratigraphic units includes: 1) Sr⁸⁷/Sr⁸⁶ chemostratigraphy for the Culebra Formation (Kirby et al., 2008); 2) magmatic U/Pb dates (19.3 ± 0.4 Ma) calculated for the lowermost part of the Culebra Formation (Montes et al., in press); 3) biostratigraphy for the Gatuncillo (Montes et al., in press); and 4) the proposed ages for the late Miocene Gatun Formation (Coates, 1999).

SYSTEMATIC PALEONTOLOGY

Institutional abbreviations.—AMNH, American Museum of Natural History, Division of Vertebrate Paleontology, New York, U.S.A.; CRI, Peter Pritchard’s collection at the Chelonian Research Institute, Oviedo, Florida, U.S.A.; UMNH, The University of Utah, Utah Museum of Natural

History, Salt Lake City, U.S.A.; UF, University of Florida, Florida Museum of Natural History Vertebrate Paleontology Collection, Gainesville, U.S.A.; UF (H), University of Florida, Florida Museum of Natural History Herpetology Collection, Gainesville, U.S.A.; USNM, Smithsonian National Museum of Natural History, Paleobiology, Washington, U.S.A.

- TESTUDINES (Batsch, 1788)
- CRYPTODIRA (Cope, 1868)
- GEOEMYDIDAE (Theobald, 1868)
- RHINOCLEMMYS (Fitzinger, 1836)

Included species.—*R. punctularia punctularia* (Daudin, 1801), *R. punctularia flammigera* (Paolillo, 1985), *R. annulata* (Gray, 1860), *R. aereolata* (Duméril et al., 1851), *R. diademata*

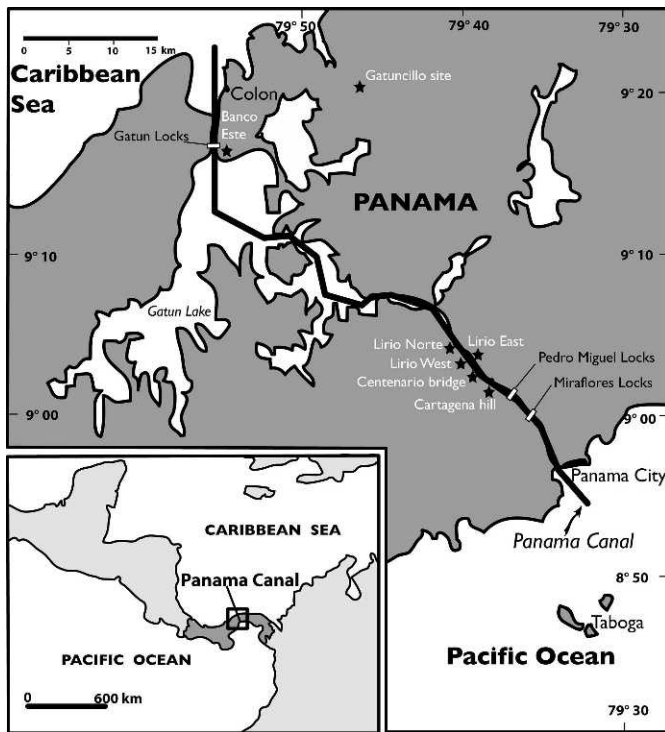


FIGURE 2—Map of the Panama Canal Basin. Star symbols indicate early Miocene fossil localities from the Culebra and Cucaracha Formations (Lirio East, Lirio West, Lirio Norte, Centenario Bridge, Cartagena Hill), one late Miocene site from the Gatun Formation (Banco Este), and one from the Oligocene, Gatuncillo Formation (Gatuncillo site).

(Mertens, 1954), *R. funerea* (Cope, 1875), *R. melanosterna* (Gray, 1861), *R. nasuta* (Boulenger, 1902), *R. pulcherrima pulcherrima* (Gray, 1855), *R. pulcherrima incisa* (Bocourt, 1868), *R. pulcherrima manni* (Dunn, 1930), *R. pulcherrima rogerbarbouri* (Ernst, 1978), *R. rubida rubida* (Cope, 1870), *R. rubida perixantha* (Mosimann and Rabb, 1953), and *R. panamaensis* n. sp.

RHINOCLEMMYS PANAMAENSIS new species

Figure 3.1–3.5

Holotype.—UF 237887, articulated shell, missing only the posterior carapace and both xiphiplastra.

Referred material.—UF 257068 (Fig. 3.5), neural 3, UF 257066 (right epiplastron); UF 257067 (left epiplastron).

Etymology.—Named for its provenance, the country of Panama.

Occurrence.—Recovered from a sandstone in the upper part of the early to middle Miocene, Cucaracha Formation located just under the west side of the Centenario Bridge, in the Panama Canal Basin (MacFadden et al., 2010; more detailed locality information available at the Division of Vertebrate Paleontology, Florida Museum of Natural History).

Diagnosis.—Differs from all species of *Rhinoclemmys* in its large adult size (estimated carapace length of between 38 to 41 cm); elongate carapace and plastron; dorsum of carapace smooth and acarinate to only faintly keeled medially; anterior peripherals 1–3 relatively flat with little to no step along the visceral marginal scale sulci; and an anteriorly wide gular scute.

Comparative description.—The type specimen of *Rhinoclemmys panamaensis* n. sp. is a partial articulated shell that is 30.5 cm long (from the anterior margin of the shell to the right hypo-xiphiplastral suture) by 25.4 cm wide. Recovered

elements include: the nuchal, neurals 1–4, paired costals 1–4 and partial costal 5, paired peripherals 1–6 and right peripheral 7, paired epiplastra, the entoplastron, paired hyoplastra, and paired partial hypoplastra. The shell is rectangularly ovoid in shape, with the anterior margins of the carapace and plastron straight and smooth. The shell is flattened, distorted by fractures and crushing, particularly along the midline of the plastron. The plastral forelobe is almost rectangular in shape, similar to that seen in other geoemydids including other species of *Rhinoclemmys*.

Rhinoclemmys panamaensis n. sp. is the largest known member of the genus and is morphologically most similar to extant *R. funerea*. It is recognized as a geoemydid by the presence of inguinal and axillary musk duct foramina (Character 36; Claude and Tong, 2004) with a discernible axillary pore on the ventral side of the left peripheral 3. It is further classified in *Rhinoclemmys* based on the following shared characters: an almost smooth transition from the dorsal margin of the gular scale to the visceral surface of the epiplastron; presence of a very small axillary scale; nuchal with a strong posteromedial concavity on the ventral surface; visceral gular margin very narrow at the midline, gradually widening or flaring posteriorly and overlapping or nearly overlapping the humeral along the margin of the epiplastron; moderately keeled nuchal with narrow and elongate semi-triangular cervical scale; nuchal with very broad sutural contact with neural 1 (Carr, 1991; Hutchinson, 2006).

Carapace.—The specimen lacks distinct dorsolateral keels along the costals as in other *Rhinoclemmys* species and *Echmatemys* which is the typical condition in these two New World genera (Claude and Tong, 2004). Whereas *R. panamaensis* lacks distinct lateral carination on the carapace in the form of thickened bony ridges, it does possess a faintly discernible medial keel restricted to the nuchal and anterior neural 1. It is possible that a keel was present along the posterior-most neurals as in modern *Rhinoclemmys* species, however the rear portion of the fossil carapace is not preserved. The faint anterior medial keel (or hump) exhibited in UF 237887 is similar to the condition observed in *R. funerea*.

Nuchal.—The nuchal bone is wider than long with a shallow embayment along the anterior margin. In this way, it resembles that of other extant species of *Rhinoclemmys*, as well as other Miocene aged nuchals referred to *Rhinoclemmys* sp. from Panama (UF 237892) and Honduras (UF 46671; Webb and Perrigo, 1984). The cervical scale is trapezoidal in shape and narrower than wide. In contrast, the Eocene geoemydid *Bridgeremys pusilla* Hutchison, 2006 has a wider than long cervical, and primitive geoemydids such as *Palaeoemys testudiformis* and *Echmatemys septaria* have a small squared cervical. Posteriorly on the nuchal, there is a very broad sutural contact with neural 1 typical of other *Rhinoclemmys* species.

Neurals.—Neural 1 of *R. panamaensis* is oval in shape, broadly contacts the nuchal and does not contact costal set 2. In other *Rhinoclemmys* where the neural 1 contacts costal set 2, the shape tends to be hexagonal. Neural 2 of *R. panamaensis* is octagonal and contacts costal set 1 by way of shortened anterolateral sides. This character is shared with *R. funerea* and some *R. punctularia* (e.g., CRI 03190, CRI 0796, CRI 1813, CRI 3706) (UMNH 11440, 11445 sensu (Hutchinson, 2006; personal observation) in which at least one of the anterolateral sides contacts at least one of the first costals. All other *Rhinoclemmys* tend to have a hexagonal neural 2 that is widest posteriorly, and lacks contact with costal set 1. Contact

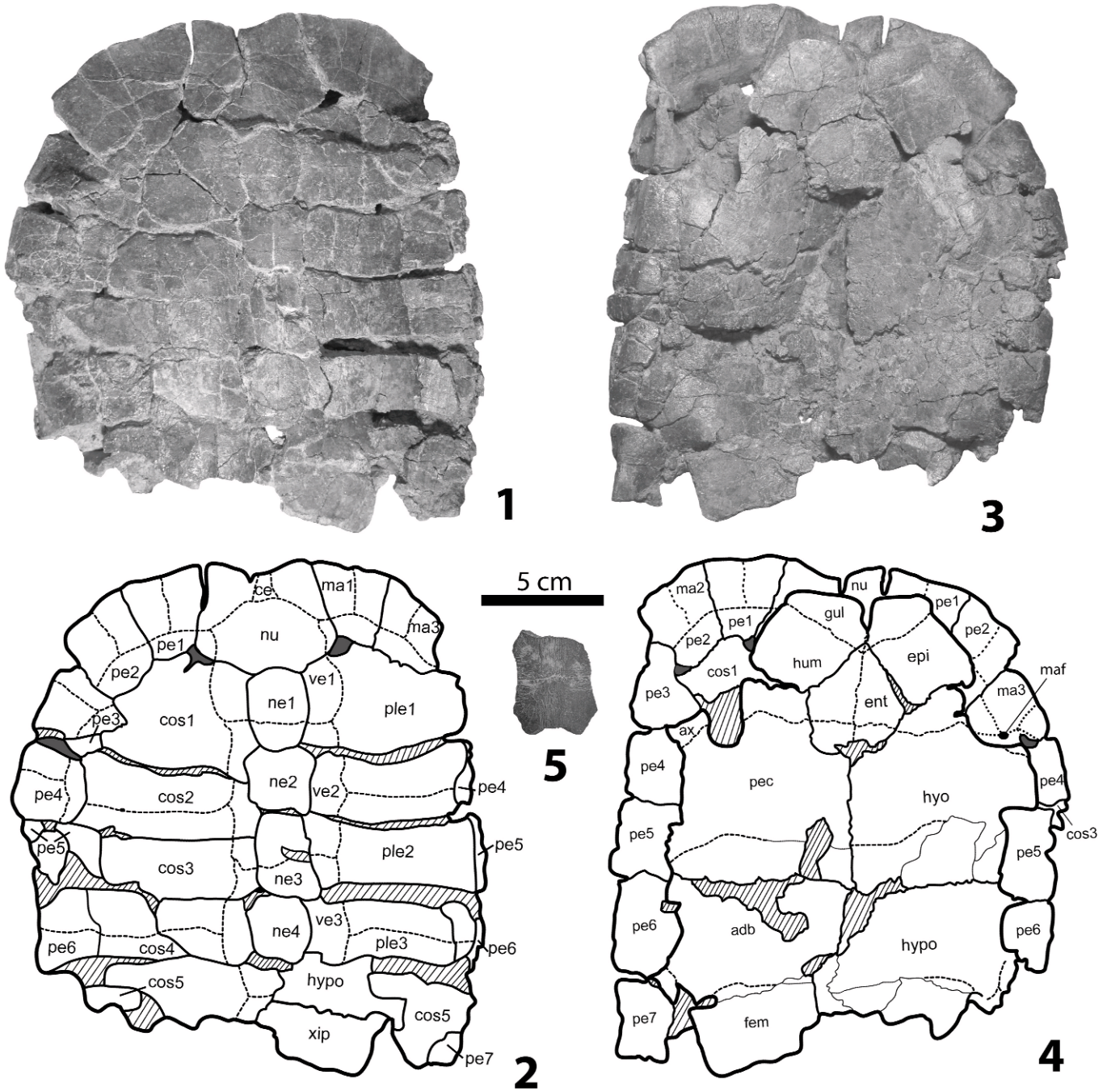


FIGURE 3—*Rhinoclemmys panamaensis* holotype, UF 237887. 1, 2, carapace in dorsal view; 3, 4, plastron and carapace in ventral view; 5, dorsal view, *R. panamaensis*, UF 257068, neural 3. Abbreviations: abd=abdominal scute; ce=cervical scute; cos=costal; ent=entoplastron; epi=epiplastron; fem=femoral scute; gul=gular scute; hum=humeral scute; hypo=hyoplastron; hyp=hyoplastron; intg=intergular scute; ma=marginal scute; ne=neural; pec=pectoral scute; pe=peripheral; pl=pleural; ve=vertebral scute.

of neural 2 with costal set 1 is considered primitive and shared with *Bridgeremys pusilla* (Hutchinson, 2006), *Echmatemys septaria* (Hay, 1892), *Palaeoemys testudiniformis*, and *P. hessiaca* (Claude and Tong, 2004). Neural 3 of *R. panamaensis* is nearly rectangular in shape but is distorted due to crushing.

Costals.—Costals 1–5 of *R. panamaensis* are preserved on both sides of the carapace, and the right costal 5 only partially preserved. Vertebral scales 1–3 are slightly longer than wide, and vertebral 2 is the longest. Presence of longer than wide vertebral scales is primitive and seen in the fossils *Palaeoemys testudiniformis* and *Echmatemys septaria*. Vertebrals that are

as long as wide or wider than long are typical for most derived geoemydids. Pleural scales 1–2 are preserved on both sides of the carapace, as well as the anterior-most portion of the right pleural 3. Contact between pleural 2 and marginal 4 has been suggested as derived for geoemydids (Claude and Tong, 2004); however after examination of a considerable number of specimens for eight of the nine extant species of *Rhinoclemmys* (see Appendix 1) we conclude that this condition is highly variable and in most of the cases marginal 4 only contacts pleural 1. This is also the condition in *R. panamaensis* and the primitive geoemydids *Palaeoemys testudiniformis* and *Bridger-*

emys pusilla. The marginal scales 1–7 are discernible on the left side of the carapace, whereas on the right side only marginal 1–3 are clearly delimited.

Peripherals.—Peripherals 1–6 are preserved on the left side of the carapace, and peripherals 1–7 on the right. On the ventral surface, the transition or slope between scaled and unscaled parts of peripheral 1–2 is moderate and almost smooth, as is the condition for all species of *Rhinoclemmys* (Hutchinson, 2006). On the ventral side of peripheral 3, the anterior musk duct pore is situated along the axillary scale sulcus just proximal to the marginal 3–4 sulcus.

Plastron (epiplastron).—The epiplastron, is overall similar to that of *Rhinoclemmys* and other geoemydids. The medial contact between the epiplastra is very short, and their lateral margins are only slightly convex to relatively straight as in the primitive geoemydid *Palaeoemys testudiniformis*. Typically geoemydids have slightly convex lateral margins on the epiplastra. *Rhinoclemmys panamaensis* has a triangular shaped gular scute with its posterior tip overriding a very small area on the anterior portion of the entoplastron. The degree of gular overlap on the entoplastron is highly variable within geoemydids, and can range from being restricted to the epiplastra, to considerably overlapping the anterior portion of the entoplastron. On the dorsal surface of the epiplastra of UF 237887 (Fig. 4.1), the transition from the most posterolateral margin of the gular to the visceral surface is marked by an almost smooth step, and the medial contact between the gulars is very short as is *R. nassuta* and *R. melanosterna*. The dorsal humeral scale overlap is also more reduced than is typical for other geoemydids.

An epiplastron with straight anterior and lateral edges, and without a distinct notch at the contact between the gular and humeral scales, is primitive and seen in the early Eocene *Palaeoemys testudiniformis* and *Paleoemys hessiaca*. *Bridgeremys pusilla* and *Echmatemys septaria* from the middle Eocene show a derived epiplastron with slightly convex lateral edges and a faint tuberosity along the distal margin of the gulars. In these taxa the dorsal surface the gular and humeral scales is very wide, and the gulars are squared with their posterior margins straight and perpendicular to the midline near the entoplastron. *Rhinoclemmys panamaensis* (Fig. 4.1) possesses an epiplastron with straight lateral edges (plesiomorphic); however, the notch at the contact between the gular and humeral is well defined as in all other derived geoemydids. Extant species of *Rhinoclemmys* display a considerable variety of shapes and scale arrangements on the anterior plastral lobe with a marked increase in ornamentation and distinction between the gular and the humeral scales, particularly on the dorsal surface (Fig. 4). For instance, *R. annulata* and *R. areolata* have a rectangular gular scale that is wider than long with the posterior edge straight and perpendicular to the midline of the plastron. This is similar to *Bridgeremys pusilla* and *Echmatemys septaria*; however, in these taxa the gular is slightly longer than wide. *R. diademata*, *R. funerea*, *R. punctularia*, and *R. pulcherrima* all have triangular gular scales with short medial contact. A diagnostic character for *R. pulcherrima* is the presence of a series of narrow ridges on the dorsal surface of the humeral scale being parallel to the gular-humeral sulcus. In *R. nassuta* the diagnostic character is a dorsally concave gular scale, for *R. punctularia* gulars that are restricted to the epiplastron and not overlapping onto the entoplastron as in other species. Epiplastron comparisons for extant species of *Rhinoclemmys* and *R. panamaensis* are illustrated in Figure 4, showing the arrangement of scales in dorsal view.

Plastron (entoplastron).—The entoplastron of *R. panamaensis* is bell-shaped, slightly longer than wide, with straight anterior sides and convex posterior sides typical of other geoemydids. The humeral-pectoral sulcus crosses the posterior portion of the entoplastron and the anterior hyoplastra as in most geoemydids. This sulcus overlaps the posteromedial portion of the epiplastra in *R. diademata* (Carr, 1991) and occasionally in *R. funerea* and *R. punctularia*.

Plastron (hyo-hyoplastra).—The medial contact between the hyoplastra is shorter than the contact between the hyoplastra. The axillary and inguinal buttresses are well developed (despite being slightly crushed), and both the anterior and posterior musk duct foramina are discernible on the left side of the plastron. The presence of paired axillary and inguinal musk duct foramina is considered synapomorphic for all turtles (Hirayama, 1984; Le and McCord, 2008).

The pectoral-abdominal sulcus is anterior to the hyo-hyoplastral suture as in other geoemydids. Conversely, in *Bridgeremys pusilla* this sulcus is medially very close to the hyo-hyoplastral suture. A very small axillary scale is present at the most anterolateral corner of both hyoplastra, in contrast to *Bridgeremys pusilla*, *Echmatemys septaria* and *Palaeoemys* sp., which lack this scale. As in all species of *Rhinoclemmys* the axillary is enclosed by the pectoral scale.

RHINOCLEMMYS sp.

Here we include other fossil material, most of them isolated bones that lack of the diagnostic characters defined above for *R. panamaensis*, but they share enough morphological similarities to be considered as *Rhinoclemmys*.

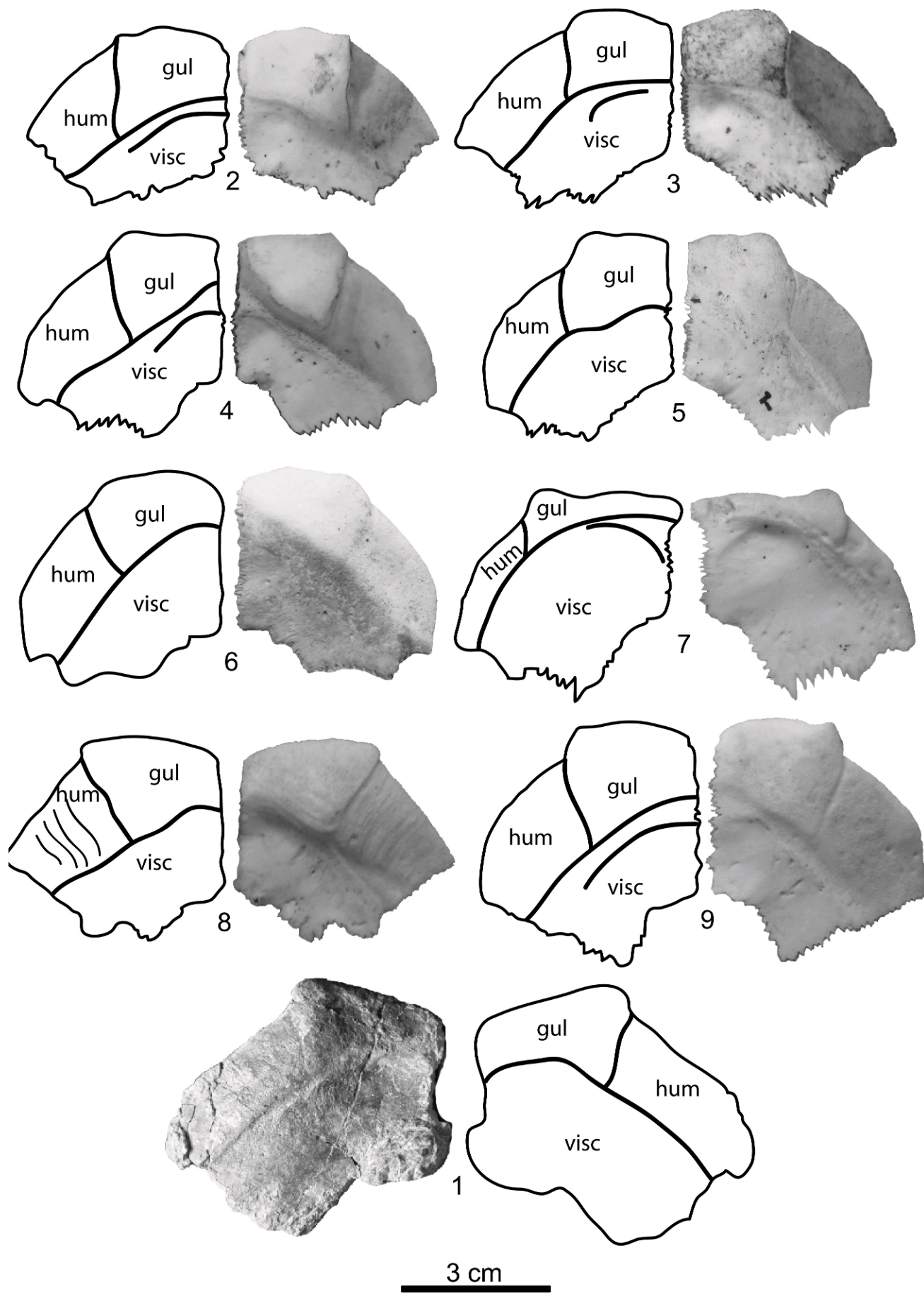
Referred material.—UF 242075, USNM PAL171020A, USNM PAL171020C, USNM PAL171021, UF 237888, UF 237889, UF 237892, UF 237895, UF237897, UF237995.

Occurrence.—The UF specimens are from the same locality and age as for *Rhinoclemmys panamaensis*. Additionally, USNM PAL171020 (A–C) and USNM PAL171021 were collected by Whitmore and Stewart at the Culebra Reach, Station 1998 + 00, 600 feet W of center line of Panama Canal, Cucaracha Formation, early to middle Miocene in age (Kirby et al., 2008).

Description and remarks.—UF 242075 (Fig. 5.1, 5.2) pygal. This specimen possesses a small medial notch along the margin, and is longer than wide. It resembles juvenile specimens of *Rhinoclemmys funerea* and *Rhinoclemmys areolata* (Gray, 1860), e.g., UF(H) 54199 (Fig. 5.3, 5.4).

USNM PAL171021 (Fig. 5.5, 5.6) right costal 1; UF 237888, left costal 1; and UF 237889, left costal 1. These specimens represent different individuals of similar size, approximately two times smaller than the costal 1 in the holotype of *Rhinoclemmys panamaensis*. A distinct sulcus between vertebrals 1 and 2, and between these vertebrals and pleural 1 is present on the dorsal surface of these specimens. On the ventral and distal surfaces of the costal, the axillary buttress scar is preserved and well developed as in other geoemydids.

UF 237892 (Fig. 5.7, 5.8), nuchal. This specimen has a very narrow cervical scale on the dorsal surface, accompanied by thickened bone in this area. The sulcus between marginal 1 and vertebral 1 is visible at the anterior-most portion of the nuchal. There is a small portion of pleural 1 that contacts vertebral 1 along the lateral sutures. Ventrally, the visceral sulcal margin is adjacent to a deep medial concavity. In most aspects UF 237892 and UF 46671 (Fig. 4.9) from the late



Miocene of Honduras (Webb and Perrigo, 1984) resemble the nuchals of *Rhinoclemmys* spp.

UF 237881 (Fig. 5.10), neural 5. This specimen has well-discerned intervertebral sulci, and resemble other species of *Rhinoclemmys* spp.

USNM PAL171020A (Fig. 5.11, 5.12), left xiphiplastron. This specimen possesses a rounded posterior tip. The femoral-anal sulcus is strongly incised on the ventral surface and the anal scale overrides almost 60% of the bone. On the dorsal surface, the visceral sulcus of the femoral and anal scales is marked by a shallow groove that runs almost parallel to the lateral margin of the xiphiplastron. USNM PAL171020A resembles the xiphiplastra of *Rhinoclemmys* spp.

USNM PAL171020C (Fig. 5.13, 5.14), right xiphiplastron. This specimen resembles USNM PAL171020A in many aspects, with the exception of the posterior tip of the element having a wide shallow embayment, in all aspects is similar to the xiphiplastron of *Rhinoclemmys* spp.

UF 237895 (Fig. 5.15, 5.16), left epiplastron; UF 237895 (Fig. 5.17, 5.18), right epiplastron. Both specimens resemble the epiplastra of *Rhinoclemmys diademata*, *R. funerea*, *R. punctularia*, and *R. pulcherrima* in both dorsal and ventral views, having the same arrangement of scales and contacts between them.

UF 237795 (Fig. 5.19–5.21), left dentary. This specimen is the only turtle cranial element recovered from the Panama Canal Basin. It is 2.8 cm long which is much larger than that of *R. funerea* (1.5 to 2 cm long average) and other living species of *Rhinoclemmys* (1 to 1.5 cm long average). Due to its large size, this specimen may be attributable to *R. panamaensis*. In dorsal view the lingual and labial ridges are almost parallel, and rounded at the symphysis as in most living species of *Rhinoclemmys*. In lateral view, the labial ridge is slightly higher than the lingual as in all living species of *Rhinoclemmys*. The sulcus cartilaginis meckelii ends at the symphysis in a sinuous path, in contrast to living species in which this sulcus is nearly straight from the posterior to the symphysis. The sulcus cartilaginis meckelii is very wide, similar to that of *R. funerea*. This sulcus is narrower in other living species of *Rhinoclemmys*. The foramen alveolare inferius is clearly visible on UF 237795.

KINOSTERNIDAE (Hay, 1892)

STAUROTYPUS (Wagler, 1830)

STAUROTYPUS MOSCHUS new species

Figure 6.1–6.3

Holotype.—UF 242076, left peripheral 2.

Occurrence.—Same locality and age as for *Rhinoclemmys panamaensis*.

Etymology.—From Latin *moschus* for “musk” or “musky” in reference to the well-developed anterior musk duct groove present in this species.

Diagnosis.—Presence of a well-developed deeply incised anterior musk duct groove that runs parallel with and closely adjacent to the visceral scale margin for marginals 1 and 2 (differs from *S. triporcatius* and *S. salvinii* which possess a very faintly incised anterior musk duct groove that is further from the marginal 1–2 sulcus); terminus for the anterior musk duct groove situated anteriorly on peripheral 2 or on the peripheral

1–2 suture (differs from *S. triporcatius* and *S. salvinii* in which the anterior musk duct terminus lies on peripheral 1); marginal scales 1 and 2 relatively narrow to the height of the peripheral in dorsal aspect; costiform process of the nuchal with slight contact to the anterior-most portion of peripheral 2 at the peripheral 1–2 suture.

Description and comparisons.—UF 242076 (Fig. 6.1–6.3) is from an adult individual with fully-formed sutures, comparable in size to extant members of the genus *Staurotypus* examined here with a carapace length between 24 and 27 cm. On the dorsal surface, marginals 1–2 are moderately bulbous and narrow, with a strong notch at the intermarginal sulcus along the lateral margin of the peripheral. Such a notch is absent to only slightly-developed in *S. salvinii* and *S. triporcatius*. The outer rim of the marginals is notably thick and squared, with a distinct lip (or crest) along the dorsal edge. The outer marginal rim is typically much thinner and tapered in that of modern *Staurotypus*. Arguably, the most significant feature on the element is the presence of the deeply incised musk duct on the visceral face and the atypical position of its terminal point along the peripheral 1–2 suture. The presence of an anterior musk duct groove is a synapomorphy for Kinosternidae and generally spans from peripheral 4 to its terminus well into peripheral 1 in *Staurotypus* (Hutchinson, 1991).

Staurotypus moschus n. sp. is the most southern-occurring staurotypine yet known. Its extant congeners are *S. salvinii* from the Pacific lowlands of Southern Mexico to Guatemala and *S. triporcatius* from the base of the Yucatan Peninsula (Bonin et al., 2006; Iverson, 1985). Interestingly, these three species each exhibit different degrees of development of the anterior musk duct groove that appear to represent a morphocline, with *S. moschus* being the most deeply incised, *S. salvinii* being only moderately to weakly so, and *S. triporcatius* very weakly developed. This character has been coded as “weakly incised” for the genus *Staurotypus* in previous phylogenetic analyses (Hutchinson, 1991). A weakly incised musk duct groove has been interpreted as primitive due to its absence in early kinosternoids (Hutchinson, 1991). The antiquity of *S. moschus* and its possession of a seemingly derived deeply incised musk duct groove could provide evidence that a weakly developed musk duct in the extant taxa *S. salvinii* and *S. triporcatius* represents a secondary character state reversal. Alternatively, extant *Staurotypus* could represent a more basal lineage than *S. moschus*. The distance of this groove from the visceral marginal sulcus represents a morphocline, with the groove being closest to the marginal sulcus in *S. moschus*, moderately close in *S. salvinii*, and farthest from the sulcus in *S. triporcatius*. For reasons discussed here, including depth and distance of the musk duct from the ventral marginal sulcus, *S. moschus* is tentatively interpreted here as having its closest affinities with *S. salvinii*.

A small pit that would receive the distal-most tip of the costiform process is just visible on the visceral face of UF 242076, at the peripheral 1–2 suture, indicating that the costiform process would have extended across the entire visceral face of peripheral 1. Just posterior to this pit, there is a slight swelling of the element, also present in *S. salvinii* and *S. triporcatius*. However, this pit is more substantial in the latter

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FIGURE 4—Epiplastra of species of *Rhinoclemmys* in dorsal view. 1, *R. panamaensis* UF 237887; 2, *R. annulata* CRI 3638; 3, *R. areolata* CRI 8318; 4, *R. diademata* CRI 1516; 5, *R. funerea* CRI 1730; 6, *R. melanosterna* CRI 4198; 7, *R. nasuta* CRI 2638; 8, *R. pulcherrima* CRI 1839; 9, *R. punctularia* CRI 2702. Abbreviations: gul=gular scute; hum=humeral scute; visc=visceral surface.

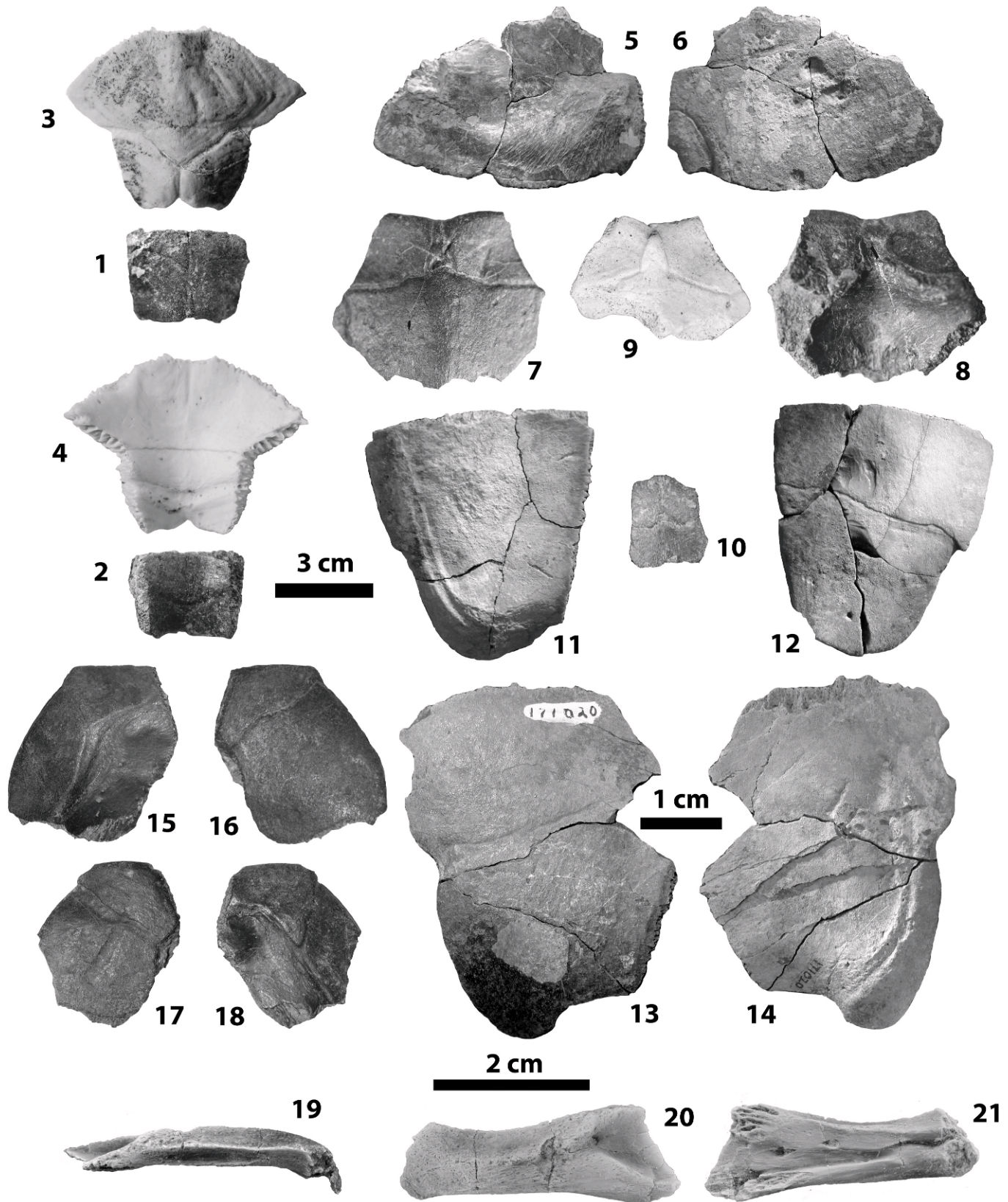


FIGURE 5—*Rhinoclemmys* sp., UF 242075, most posterior portion of the pygal. 1, dorsal view; 2, ventral view, *Rhinoclemmys areolata* UF(H) 54199 complete pygal; 3, dorsal view; 4, ventral view, *Rhinoclemmys* sp. USNM PAL 171021, right costal 1; 5, ventral view; 6, dorsal view, *Rhinoclemmys* sp., UF 237892, nuchal bone; 7, dorsal view; 8, ventral view, *Rhinoclemmys* sp., UF 46671, nuchal bone referred in Web and Perrigo (1984), from late Miocene of Honduras; 9, dorsal view, *Rhinoclemmys* sp., UF 237881, neural 5; 10, dorsal view, *Rhinoclemmys* sp., USMN PAL171020A, left xiphiplastron. 11, Dorsal view, 12, ventral view, *Rhinoclemmys* sp., USMN PAL171020C, right xiphiplastron; 13, ventral view; 14, dorsal view, *R. panamaensis*, UF257066, left epiplastron; 15, dorsal view; 16, ventral view, *R. panamaensis*, UF257067, right epiplastron; 17, ventral view; 18, dorsal view, *R. panamaensis*, UF 257195, left dentary; 19, dorsal view; 20, lateral view; 21, medial view. Scale bar=3 cm for 1–12, 14–18; 1 cm for 13, 14; 2 cm for 19–21.

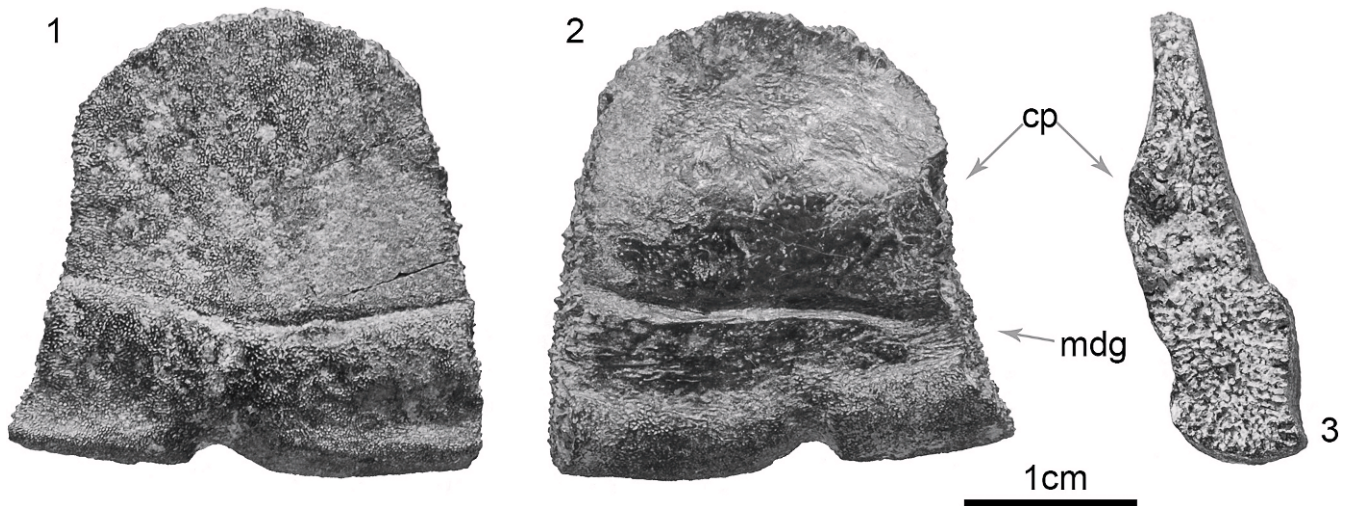


FIGURE 6—*Staurotypos moschus* holotype, UF 242076, left peripheral 2. 1, dorsal view; 2, ventral view; 3, anterior sutural view. Abbreviations: cp=pit that accepts the costiform process; mdg=anterior musk duct groove.

two taxa, with the costiform process usually more intrusive on peripheral 2 (Hutchinson, 1991; Fig. 5).

TESTUDINIDAE (Gray, 1825)
INCERTAE SEDIS

Referred material.—USNM V23180, USNM PAL171017, USNM PAL171020, USNM V23146, UF 242091.

Occurrence.—All USNM specimens were collected by Whitmore and Stewart at the Culebra Reach, Station 1998 + 00, 600 feet W of center line of the Panama Canal, Cucaracha Formation. The age for the Cucaracha Formation is early to middle Miocene sensu (Kirby et al., 2008).

Description and remarks.—USNM V23180 (Fig. 7.1, 7.2), right coracoid. This specimen is 19 cm long by 14 cm wide (maximum values) and missing a portion of the posterolateral margin and most of the dorsal and ventral margins of the proximal articular area. The medial edge is thinner than the lateral, and the blade is relatively short, with slightly rounded and flared distal margin. Proximally, the most central part of the glenoid surface is preserved, being slightly concave for articulation with the humerus. The sutural contact with the scapula is not preserved.

USNM PAL171017 (Fig. 7.3, 7.4), complete right ulna. This specimen measures 13 cm long by 4 cm wide (maximum values). The olecranon process is rounded and well developed. The proximal articular surface is curved and the bicipital tubercle is poorly preserved. Proximally, the ulna is convex where it articulates with the humerus, and the most dorsolateral margin is missing.

USNM PAL171017 and USNM V23180 resemble the ulna and the coracoid of giant tortoises, such as members of the Galapagos Island complex *Chelonoidis elephantopus* USNM 59867 (Fig. 7.5–7.8). These elements could belong to the Caribbean/Central-South American genus *Chelonoidis*, or perhaps represent another extinct giant tortoise clade such as *Hesperotestudo* (or *Caudochelys*).

USNM V23146 (Fig. 7.9), osteoderm. This specimen is highly curved and elongate, typical of osteoderms found on the distal forelimbs, hind-quarters, or posterior pedes in modern tortoises.

USNM PAL171020 (Fig. 7.10, 7.11), right xiphiplastron. This element is relatively small (5 cm long by 4 cm wide, maximum values). Ventrally, it possesses a very small anal

scale, which is trapezoidal in shape and short medially. On the dorsal surface the transition from the margins of the femoral and anal scales to the visceral surface is strongly marked by a deep concavity. USNM PAL171020 resembles the xiphiplastron of *Chelonoidis*.

UF 242091 (Fig. 7.12–7.14), right epiplastron. This specimen is 6.8 cm long by 5.9 cm wide. Dorsally it possesses a broad gular margin, with a deep step posteriorly. The gular-humeral margins are very thick, being thickest at the posterior gular. The gular is highly convex in both dorsal and ventral aspects. Ventrally, the gular-humeral sulcus terminates at the epi-entoplastral suture, indicating that the posteromedially terminus of the gulars would have been on the anterior portion of the entoplastron. In these features it resembles *Hesperotestudo* specimens examined.

CHELONIIDAE (Gray, 1825)
INCERTAE SEDIS

Referred material.—UF 244433 (Fig. 8.1, 8.4), right costal 4.

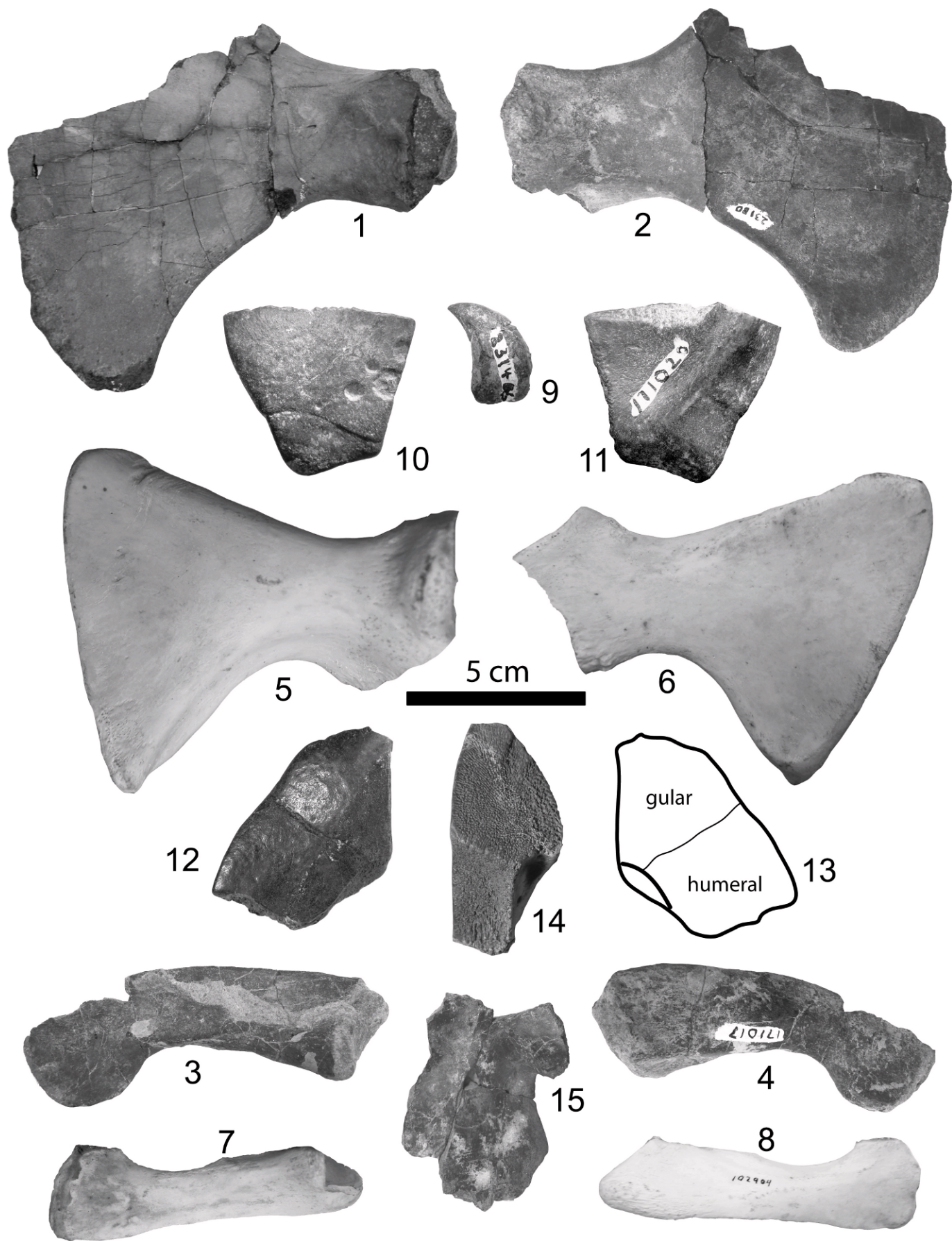
Occurrence.—Recovered from the lower part of the middle-late Miocene Gatun Formation (Coates, 1999). The locality is located on the Eastern side of the Gatun Locks, area of Colon, Northern area of the Panama Canal Basin (more detailed locality information available at the Division of Vertebrate Paleontology, Florida Museum of Natural History).

Description and remarks.—This specimen is 35 cm long by 19 cm wide). Dorsally, the sulci between pleural 2–3 and between these and vertebral 3 are discernible. In many aspects this costal resembles the costal bones of cheloniids, particularly of *Caretta caretta* (Fig. 8.5, 8.6), one of the most abundant modern sea turtles in the neotropics.

TRIONYCHIDAE (Baur, 1893)
INCERTAE SEDIS

Referred material.—UF 242108 (Fig. 8.7), right costal 1; UF 242088 (Fig. 8.8), costal; UF 242106 (Fig. 8.9), costal.

Occurrence.—UF 242088 is from the same locality and age as for *Rhinoclemmys panamaensis*, Cucaracha Formation. UF 242108 and UF 242106 were collected at the Lirio Norte site, west margin of the Panama Canal, upper member of the Culebra Formation, early Miocene (Fig. 2; more detailed



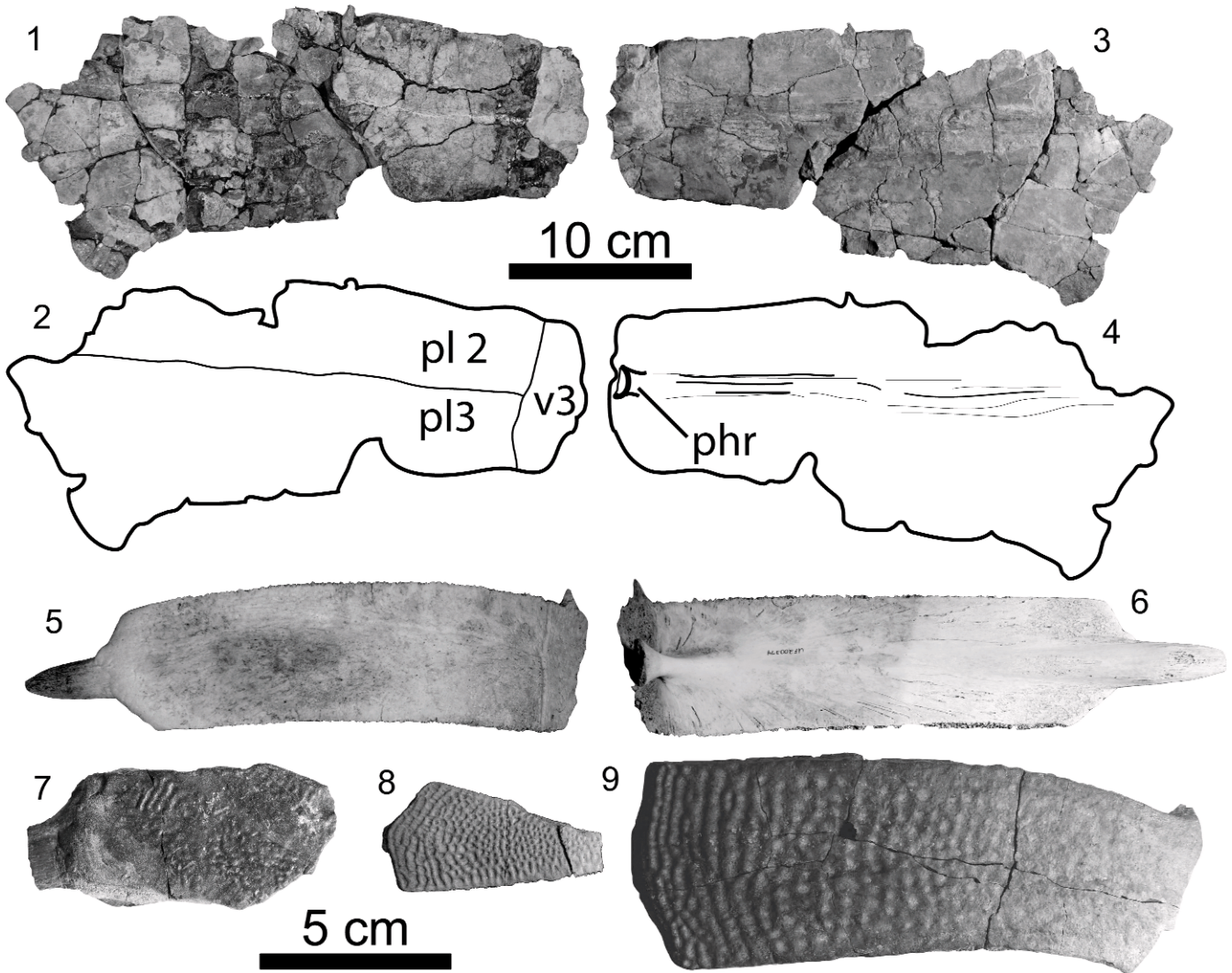


FIGURE 8—Cheloniidae incertae sedis, UF 24443, right costal. 1, 2, dorsal view; 3, 4, ventral view, *Caretta caretta*, UF 200374, right costal 4; 5, dorsal view; 6, ventral view, Trionychidae incertae sedis, UF 212108, left costal 1; 7, dorsal view; 8, dorsal view, UF 242088, costal bone; 9, dorsal view, UF 242106, costal bone. Scale bar=10 cm for 1–6, 5 cm for 7, 8. Abbreviations: pl=pleural scute; phr=proximal head of the rib; v=vertebral scute.

locality information available at the Division of Vertebrate Paleontology, Florida Museum of Natural History)

Description and remarks.—All of the costals exhibit ornamentation consisting of ridges and large pits typical of trionychids or soft shell turtles. The nature of the dorsal pitting on the fossils shows similarities to the genus *Apalone*. *Apalone* is the only extant North-Central American trionychid (Meylan, 1987) and is absent from South America today.

PLEURODIRA (Cope, 1874)
PELOMEDUSOIDES (Cope, 1868)
PODOCNEMIDIDAE (Cope, 1868)
INCERTAE SEDIS

Referred material.—UF 242276, UF 242170, UF 244763, anterior plastral lobe; UF 242174, right xiphiplastron; UF

242160; right costal 6; UF 242150, left costal 2; UF 242165, right side of a pelvic girdle; UF 242171, distal and proximal portions of a right humerus; UF 242097, proximal portion of a left femur; UF 242111, right peripheral 2; UF 242158, left peripheral 8; UF 242168, neural 3 or 5?; UF 242161, right partial xiphiplastron. UF 257070, right epiplastron, UF 242168, left peripheral.

Occurrence.—UF 242097 and UF 242170 were collected at the Lirio East site (Fig. 2), east margin of the Panama Canal, conglomeratic sandstones, Culebra Formation, early Miocene. UF 242161 was collected at the Gatuncillo site, Gatuncillo Formation, middle to late Eocene (Graham, 1985). UF 257070, was collected at Lirio West, UF 242168 was collected at the lower segment of Cucaracha Formation, Centenario Bridge site. All other UF specimens were collected at the Lirio

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FIGURE 7—Testudinidae incertae sedis, USNM V23180, right coracoid. 1, ventral view; 2, dorsal view, USNM PAL 171017, right ulna; 3, ventral view; 4, dorsal view, *Chelonoidis elephantopus*, USMN 59867, right coracoids; 5, dorsal view; 6, ventral view, *Ch. Elephantopus*, USMN 59867, right ulna; 7, dorsal view; 8, ventral view, USNM V23146, osteoderm; 9, lateral view, USNM PAL 171020, right xiphiplastron; 10, ventral view; 11, dorsal view, UF 257065, right epiplastron; 12, 13, dorsal view; 14, medial sutural view, UF 257069, right hypoplastron; 15, dorsal view.

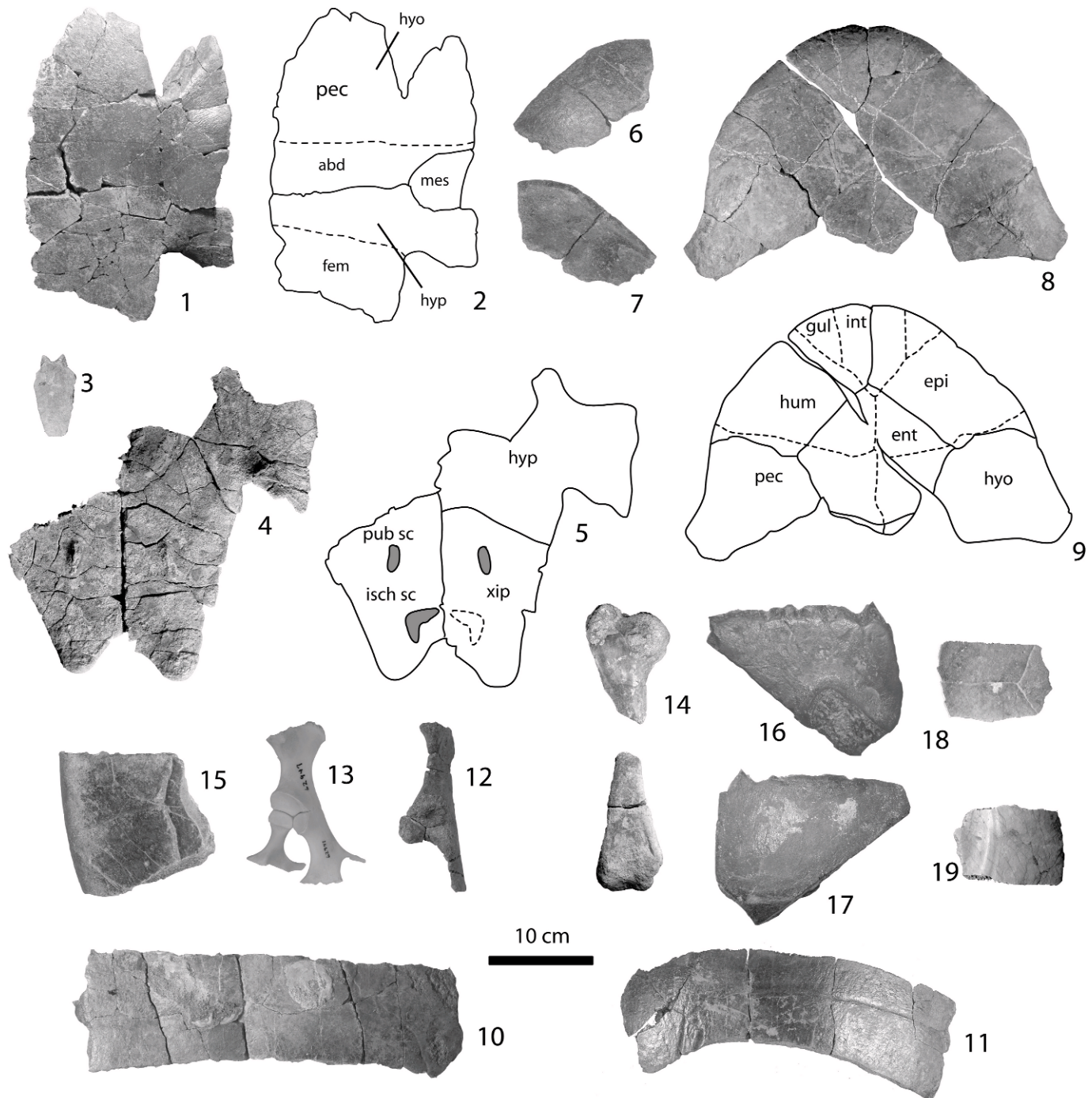


FIGURE 9—Podocnemididae incertae sedis, UF 242176, left articulated hyoplastron, hypoplastron and mesoplastron. 1, 2, ventral view, UF 242170, neural 2; 3, dorsal view, UF 242170, left and right xiphiplastra, together with the right hypoplastron; 4, 5, dorsal view, UF 257070, right epiplastron; 6, ventral view; 7, dorsal view, UF 244763, anterior plastral lobe; 8, 9, ventral view, UF 242160, right costal 6; 10, dorsal view, UF 342150, left costal 2; 11, dorsal view, UF 242165, right side of a pelvic girdle; 12, lateral view, *Podocnemis expansa*, AMNH 62942, right side of the pelvic girdle; 13, lateral view, UF 242171, distal and proximal ends of a right humerus; 14, lateral view, UF 242158, left peripheral 8; 15, dorsal view, UF 242161, right partial xiphiplastron; 16, dorsal view; 17, ventral view, UF 242168, left peripheral; 18, dorsal view; 19, ventral view. Abbreviations: abd=abdominal scute; ent=entoplastron; epi=epiplastron; fem=femoral scute; gul=gular scute; hum=humeral scute; hyo=hyoplastron; hyp=hypoplastron; int=intergular scute; isch sc=ischium scar; mes=mesoplastron; pec=pectoral scute; pub sc=pubic scar.

Norte site, west margin of Panama Canal, from conglomerate channels belonging to the Culebra Formation (more detailed locality information available at the Division of Vertebrate Paleontology, Florida Museum of Natural History).

Description and remarks.—UF 24217 (Fig. 9.1, 9.2), articulated left hyoplastron, hypoplastron and mesoplastron. The mesoplastron is almost circular in shape and laterally

positioned between the hyoplastron and hypoplastron, as in all other pelomedusoids (Gaffney et al., 2006). On the ventral surface the pectoral scales contact the epiplastra as in almost all other podocnemidids (Gaffney et al., 2011), variable in *Peltocephalus dumerilianus* and *Podocnemis sextuberculata* (Cadena et al., in press). Also, the pectoral-abdominal sulcus is anterior to the mesoplastron, which is typical but not

exclusive of podocnemidids. The abdominal-femoral sulcus ends laterally at the hypoplastral notch.

UF 242170 (Fig. 9.3–9.5), associated left and right xiphiplastron, right hypoplastron, neural 2, costal 3 or 5?, and at least ten undifferentiated fragments of costals. It is difficult to discern any scute sulci on the ventral plastron. The open U-shaped anal notch and concave outline of the mesoplastron at the anterolateral margin of the hypoplastron are the most diagnostic features ventrally. Dorsally, both xiphiplastra preserve the pubic and ischial scars, indicating a strongly sutured pelvis to the plastron, a synapomorphy for Pleurodira (Gaffney and Jenkins, 2010). The pubic scar is oval-shaped, oriented almost parallel to the medial margin of the xiphiplastron. The ischial scar is triangular in outline and ends medially at an acute point very close to the sutural contact between both xiphiplastra typical of podocnemidids. Neural 2 is hexagonal and elongate with short anterolateral sides and lacking a vertebral sulcus. There are two lateral horn-like projections at the most anteroventral margin where it articulates with neural 1. The presence of neural bones in UF 242170 excludes it from being related to *Bairdemys venezuelensis* a late Miocene Caribbean-Tropical South American podocnemoid that lacks the entire neural bone series (Scheyer et al., 2008).

UF 257070 (Fig. 9.6, 9.7), right epiplastron. On the dorsal surface, the gular scale is small and triangular, as for most podocnemidids. UF 244763 (Fig. 9.8, 9.9) is a complete anterior plastral lobe that is as long as wide, as in all other podocnemidids. In contrast, bothremydids possess a forelobe that is much wider than long. The entoplastron is diamond-shaped and located anterior to the bridge as in other podocnemidids. This differs from bothremydids in which the most posterior tip of the entoplastron generally reaches the level of the bridge. The gular scale is triangular and only overlaps the epiplastron, whereas the intergular is very wide and overlaps the most anterior corner of the entoplastron. The humeral-pectoral sulcus in UF 244763 is situated anterior to the epi-hyoplastral suture and crosses the entoplastron at its maximum width as in all other podocnemidids (Gaffney et al., 2011) except *Peltocephalus dumerilianus* and occasionally in *Podocnemis sextuberculata* (Cadena et al., in press). In the latter two taxa this sulcus is posterior to the epi-hyoplastral suture, and crosses the entoplastron in its posterior region. In contrast, most bothremydids have a humeral-pectoral sulcus that is situated well-posterior to the epiplastron-hyoplastron suture, slightly crossing or touching the most posterior margin of the entoplastron. The long anterior plastral lobe of UF 244763 differs from *Bairdemys venezuelensis*, which has a shorter anterior plastral lobe (Gaffney et al., 2006, fig. 275).

UF 242160 (Fig. 9.10), right costal 6. This specimen is moderately curved dorso-ventrally. Dorsally, the sulcus between pleural 3 and 4 is visible, as well as the sulcus between vertebral 4 and pleural 3 and 4.

UF 242150 (Fig. 9.11) left costal 2. The anterior and posterior margins are almost parallel, with a short posterolateral side, and well preserved sulci between pleurals 1 and 2, and vertebral 2 and pleurals 1 and 2. UF 242160 and UF 242150 were found associated, and presumably belong to the same individual.

UF 242165 (Fig. 9.12), right side of a pelvic girdle, including a complete ilium, pubis, and the most distal portion of the ischium. The acetabulum capsule is almost oval with sutural contacts between the ilium, pubis, and ischium typical to that of all pleurodires. It is particularly similar to the pelvic girdle

of the genus *Podocnemis*, e.g., *P. expansa* AMNH 62947 (Fig. 9.13).

UF 242171 (Fig. 9.14), partial right humerus. Only the distal and proximal portions are preserved, with the central portion missing. Proximally, the lateral process is missing and the medial process is large and posteroproximally projected. The articular hemisphere is rounded and lacks a shoulder, a synapomorphy for pleurodires (Gaffney, 1990). The distal portion has a rounded and slightly convex capitulum for articulation with the ulna and radius, and a distinct ectepicondylar foramen on the anterodistal margin, characteristic of all turtle humeri.

UF 242097, proximal left femur. Dorsally, the acetabular head is oval and slightly elongate and inclined clockwise with respect to the longitudinal axis of the bone. The major and minor trochanters are almost at the same horizontal plane with prominent lateral projections. Ventrally, the interthrocanteric fossa is very shallow with a long scar on its posterior edge. In all aspects UF 242097 resembles the femur of podocnemidids.

Other isolated carapace elements include: UF 242111, right peripheral 2; UF 242158 (Fig. 9.15), peripheral 8 (10 cm long \times 8 cm wide, maximum values); and UF 242168 neural 3 or 5?, in all aspects resembling podocnemidids.

UF 242161 (Fig. 9.16, 9.17), partial right xiphiplastron (anterolateral-most portion). The anterior-most part of the sutural scar for the ilium is well-discerned on the dorsal surface. Ventrally, the posterior-most portion of the femoral-anal sulcus is preserved, in all features resembling the xiphiplastron of podocnemidids.

UF 242168 (Fig. 9.18, 9.19), left peripheral. This specimen exhibits a well-defined visceral marginal step similar to all other podocnemidids.

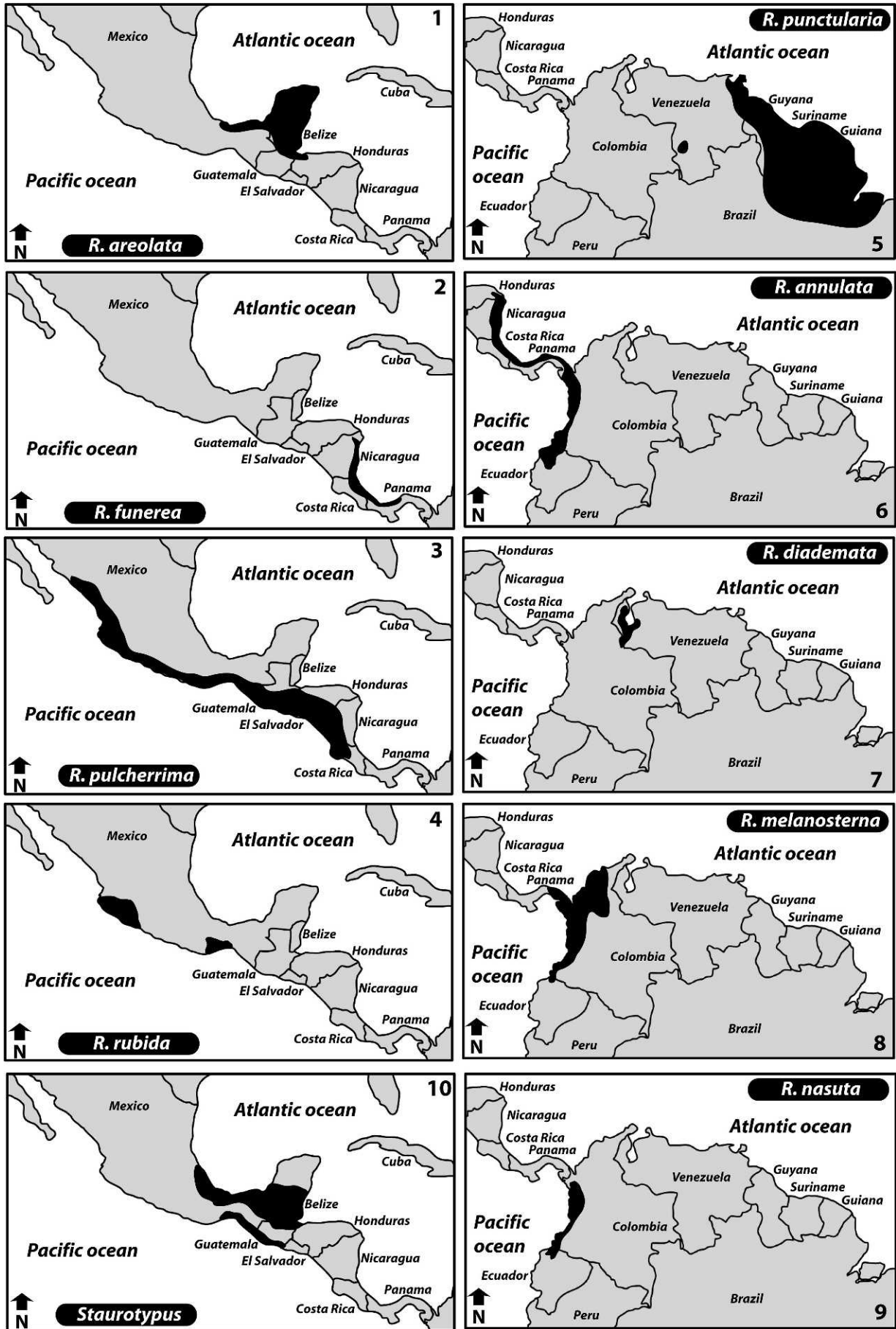
DISCUSSION

The turtle record, in contrast to mammals from the same localities (MacFadden, 2006; MacFadden et al., 2010), shows that during the early Miocene lineages of both North-Central American cryptodires and Caribbean-South America pleurodires were present in the Panamanian isthmus, previous to its complete emergence during the early Pliocene.

Four stratigraphically distinct fossil turtle assemblages are recognized from Panama that lend insight into the evolution of the group in southern Central America: 1) the late Eocene–early Oligocene fossils from Gatuncillo Formation; 2) the early Miocene fossils from Culebra Formation; 3) the early to middle Miocene fossils from Cucaracha Formation; and 4) the late Miocene fossils from Gatun Formation.

Assemblage 1 (late Eocene–early Oligocene).—The occurrence of podocnemidids, from the late Eocene–early Oligocene Gatuncillo Formation together with the Paleocene record of podocnemidids from Colombia (Cadena et al., 2010; Cadena et al., in press) and the Oligocene record from South Carolina (Weems, 2009), indicates a very wide distribution for podocnemidids in the Paleogene neotropics, particularly in the Caribbean and its coastal regions. It also shows the earliest northern migration of South American fresh-water turtles across the Panamanian seaway.

Assemblage 2 (early Miocene).—Turtles from the early Miocene Culebra Formation are represented by cryptodires (trionychids) and pleurodires (podocnemidids), inhabiting deltaic or estuarine environments, a paleodeposition suggested for the upper segment of the Culebra Formation (Kirby et al., 2008; Montes et al., in press) Most of the fossils from the Culebra Formation are complete but disarticulated shell elements, with very few non-shell elements, and abundant



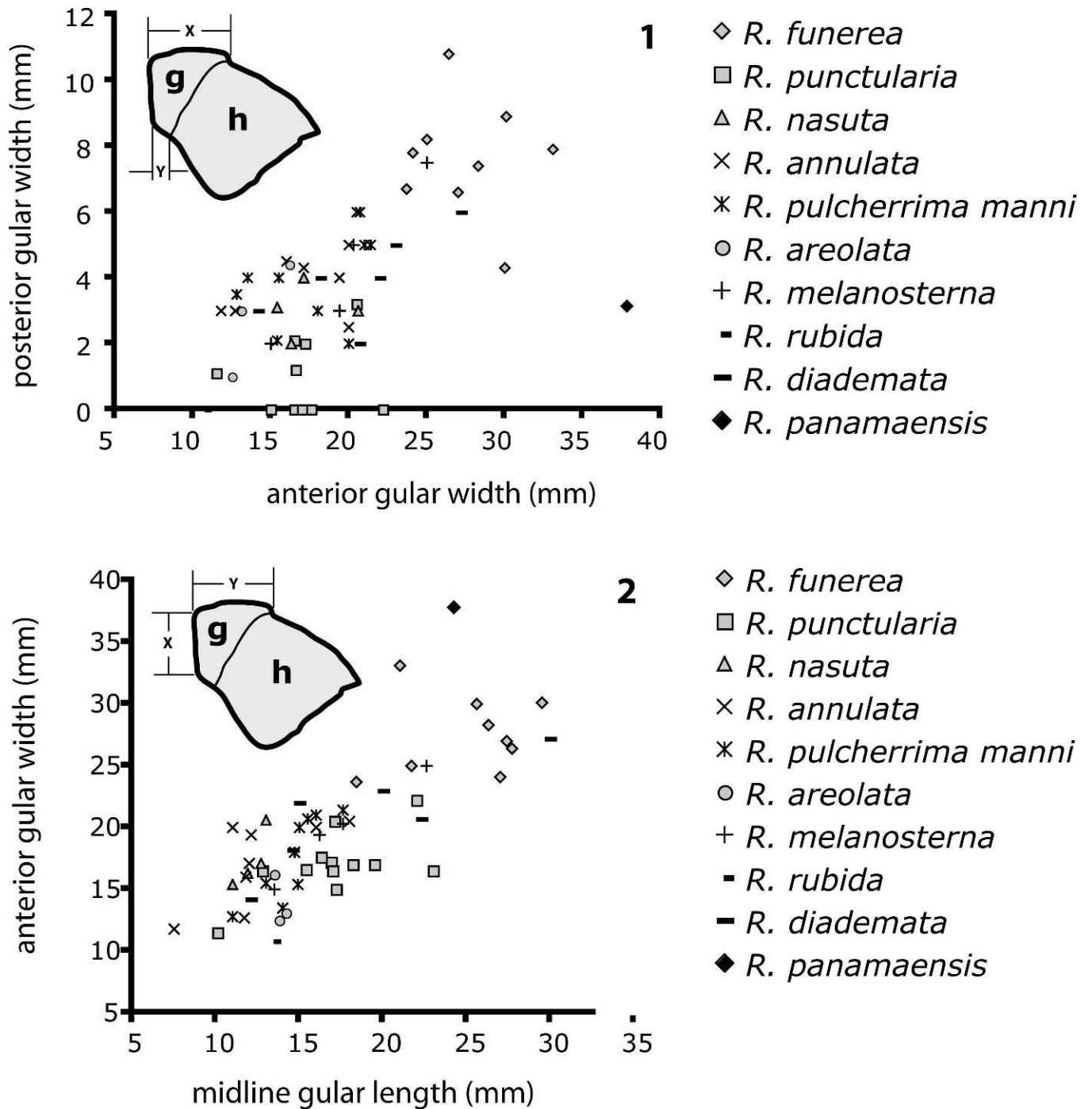


FIGURE 11—Gular scute measurements for species of *Rhinoclemmys* (see specimens examined in Appendix 2). *Rhinoclemmys panamaensis* has the widest anterior gular in the genus *Rhinoclemmys*. 1, anterior gular width (X) versus posterior gular (Y) width; 2, midline gular length (X) versus anterior gular width (Y). All measurements in mm. Abbreviations: g=gular scute; h=humeral scute.

evidence of bioerosion produced by mollusks. This suggests that turtle bones were exposed to pre-burial transport by streams. This assemblage is the earliest evidence of interaction between North American trionychids and Caribbean-South American podocnemidids in the Neotropics.

New World trionychids are represented by only one genus, *Apalone*, which is restricted today to temperate–subtropical regions of North America (Bonin et al., 2006). The early Miocene occurrence of trionychids from the Panama Canal basin represents the southernmost record for this family in the

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FIGURE 10—Geographical distributions for extant species of *Rhinoclemmys* and *Staurotypos*, after Iverson 1992. 1, *R. areolata*; 2, *R. funerea*; 3, *R. pulcherrima*; 4, *R. rubida*; 5, *R. punctularia*; 6, *R. annulata*; 7, *R. diademata*; 8, *R. melanosterna*; 9, *R. nasuta*; 10, the genus *Staurotypos*.

New World, and together with the record from the Castillo Formation (late Miocene) in North-western Venezuela (Sanchez-Villagra et al., 2004) represents the earliest arrival of trionychids to the tropics of Central and South America, even being able to cross the Panamanian seaway before its final closure. The record suggests that trionychids inhabited a much wider range in the Americas including tropical climates.

Podocnemidids from Culebra Formation indicate their continuous occurrence at the most eastern tip of Central America Peninsula after the Paleogene. Exhibiting large size of the shell, which we estimate to have been approximately 100 cm long at the midline, based on the size of some isolated elements including the costals UF 242160 (Fig. 9.10) and UF 242150 (Fig. 9.11), and the peripheral UF 242158 (Fig. 9.15), which are slightly larger than the largest size reported for modern *Podocnemis* specimens, which is 80 cm in *P. expansa* (Valenzuela, 2001).

Assemblage 3 (early to middle Miocene).—Represented primarily by cryptodires, including a trionychid (present in both the Culebra and Cucaracha formations), and kinosternid, and perhaps multiple species of geoemydid, testudinid, and podocnemidid. Many of these lineages first occur in Panama at the lower segment of Cucaracha Formation. This formation has been interpreted as a paleodeltaic plain (Kirby et al., 2008). In contrast to the turtles from the Culebra Formation, the turtles from the Cucaracha Formation are represented by more complete and articulated specimens, e.g., the holotype of *Rhinoclemmys panamaensis* n. sp., indicating relatively little pre-burial transport.

The occurrence of *Rhinoclemmys panamaensis* and *Rhinoclemmys* sp. during the early to middle Miocene in the Panama Canal basin not only represent the earliest record of geoemydids in Central America but also support the hypothesis suggested by Le and McCord (2008), based on molecular data, of an initial dispersal event of the lineage that contains *R. nasuta* from Central to South America during the early Miocene. The strong morphological similarities between *R. panamaensis* and *R. funerea* suggest that the fossil species was probably largely aquatic.

Closely related to geoemydids are testudinids (Lourenco et al., 2012). It has been suggested that land tortoises arrived to Central and South America by passive flotation from North America and the Antilles during the Miocene (Pritchard, 1984), favored by their adaptations for over-water dispersal (Meylan and Sterrer, 2000). The fossil testudinids described here are, together with the Oligocene?–Miocene record of *Geochelone costarricensis* described by Segura (1944), the earliest records of land tortoises from Central America. Some of the fossil material described here is slightly larger than modern giant tortoise material, including *Chelonoidis elephantopus* USNM 59867 from the Galapagos Islands and *Dipsoschelys gigantea* USNM 222495 from the Aldabran Islands, and indicates the presence of one of the giant tortoise lineages (perhaps of the *Chelonoidis* or *Hesperotestudo* groups) in Central America during the early Miocene.

The family Kinosternidae is endemic to North America, with the oldest fossils being from northern Mexico (Brinkman and Rodriguez De La Rosa, 2006) and the northwestern United States (Hutchison, 1991). The occurrence of *Staurotypus moschus* in Panama represents the oldest record of kinosternids in Central America. It also indicates a significant former southeastern range extension for the genus and for the subfamily Staurotypinae as a whole. Today, this subfamily comprises only the extant taxa *Staurotypus triporcatus*, *Staurotypus salvinii*, and *Claudius angustatus*, all with relatively

small ranges in middle Central America. Staurotypines have been hypothesized as the most primitive living kinosternids (Hutchison and Bramble, 1981) yet almost nothing is known about their fossil record. Pleistocene fossils from the Rio de la Pasion, Guatemala (AMNH 13989, 24176, 24177, 24179) probably represents *Staurotypus* (JRB, personal observation).

Assemblage 4 (late Miocene).—Represented by a sea turtle (Cheloniidae), from the marine deposits of the Gatun Formation, which likely represented a shallow marine strait that connected the Pacific Ocean and the Caribbean Sea during the late Miocene (Coates and Obando, 1996).

ACKNOWLEDGMENTS

Funding for this project came from National Science Foundation grants OISE 0638810, EAR 0642528, and EAR 0824299, PIRE 0966884 (OISE, EAR, DRL), the Smithsonian Institution, the Panama Canal Authority, M. Tupper, SENACYT, R. Perez SA, the Florida Museum of Natural History Miss Lucy Dickinson Fellowship. Thanks go to the Authority of the Panama Canal for access to the Panama Canal areas. Thanks for access to collections to K. de Querioz, J. Jacobs (Smithsonian National Museum of Natural History, Washington, U.S.A.); E. Gaffney and C. Mehling, (Fossil Amphibians, Reptiles, and Birds Collections, Division of Paleontology, American Museum of Natural History, New York, U.S.A.); P. Pritchard (Chelonian Research Institute, Oviedo, Florida U.S.A.); R. Rowe (Utah Museum of Natural History, Salt Lake City, Utah U.S.A.), K. Krysko (Florida Museum of Natural History, Herpetology collection, Gainesville, Florida U.S.A.), R. Hulbert, Jr. (Florida Museum of Natural History, Vertebrate Paleontology collection, Gainesville, Florida U.S.A.). Special thanks to N. Cannarozzi (who found *Rhinoclemmys panamaensis* holotype), S. Moron, A. Gomez, L. Grawe, and all other paleontologists and geologists working at the Panama Canal Basin.

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ACCEPTED 13 JANUARY 2012

APPENDIX 1—Specimens studied by direct examination.

Institutional Abbreviations

AMNH, American Museum of Natural History, Division of Vertebrate Paleontology, New York, USA

CRI, Peter Pritchard's collections at Chelonian Research Institute, Oviedo, Florida, USA

ICN, Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá, Colombia

UMNH, The University of Utah, Utah Museum of Natural History, Salt Lake City, USA

UF, University of Florida, Florida Museum of Natural History Vertebrate Paleontology Collections, Gainesville, USA

UF (H), University of Florida, Florida Museum of Natural History Herpetology Collections, Gainesville, USA

USNM, Smithsonian National Museum of Natural History, Paleobiology, Washington, USA

Rhinoclemmys

R. annulata: CRI 2962, CRI 0049, CRI 0048, CRI 3638, CRI 1132, CRI 2774, CRI 1222, CRI 2773, UMNH 10241, UMNH 11393, USNM 7252, USNM 8217, USNM 562917. *R. areolata*: CRI 8318, CRI 2775, CRI 2963, UMNH 6480, UF(H) 54199, USNM 46002, USNM 46299, USNM

59934. *R. diademata*: CRI 1339, CRI 3656, CRI 3826, CRI 1517, CRI 1476, CRI 1516. *R. funerea*: CRI 4380, CRI 2961, CRI 5494, CRI 4579, CRI 0348, CRI 4578, CRI 5250, CRI 7699, CRI 1730, UMNH 3050, UMNH 8274, UMNH 8277, USNM 59934, USNM 8218, USNM 8273, USNM 8270. *R. melanosterna*: CRI 2441, CRI 2434, CRI 2433, CRI 4198. *R. nasuta*: CRI 2443, CRI 2638, CRI 2448, CRI 2442. *R. pulcherrima*: CRI 2155, CRI 1839, CRI 1433, CRI 1090, CRI 7597, CRI 1444, CRI 2895, CRI 6625, CRI 1478, UMNH 11516, UMNH 11517, USNM 46308, USNM 46309, USNM 46310, USNM 102889, USNM 104626. *R. punctularia*: CRI 2877, CRI 2871, CRI 3706, CRI 2514, CRI 0345, CRI 4581, CRI 3191, UMNH 9982, UMNH 11440, USNM 28978, USNM 85022, USNM 86861, USNM 65108. *R. rubida*: CRI 1234, USNM 45615, USNM 222433.

Staurotypus

S. triporcatus: CRI 1488, CRI 0166, CRI 1105, CRI 0157, CRI 0167, CRI 0161. *S. salvini*: CRI 1104, CRI 3622, CRI 1142.

Chelonoidis

C. abingdoni: USMN 222479. *C. carbonaria*: ICN 7619, ICN 7644, ICN 1733. *C. elephantopus*: USMN 015192, USMN 59867, USMN 284682, USMN 284685, USMN 284693, USMN 284694. *C. gigantea*: USMN 222495, USMN 107644.

APPENDIX 2—Rhinoclemmys measurements, Peter Pritchard Collection, Oviedo, FL, July 2009.

Species	Epiplastron measurements (mm)			Sex
	Midline gular width	Anterior gular width	Posterior gular width	
Rhinoclemmys funerea CRI 4380	29.5	30.1	8.9	F
Rhinoclemmys funerea CRI 2961	26.3	28.3	7.4	M
Rhinoclemmys funerea CRI 5494	25.6	30	4.3	F
Rhinoclemmys funerea CRI 4579	18.4	23.7	6.7	F
Rhinoclemmys funerea CRI 0348	27.4	27	6.6	F
Rhinoclemmys funerea CRI 4578	27	24.1	7.8	F
Rhinoclemmys funerea CRI 5250	21	33.1	7.9	F
Rhinoclemmys funerea CRI 7699	21.7	25	8.2	F
Rhinoclemmys funerea CRI 1730	27.7	26.4	10.8	M
Rhinoclemmys punctularia CRI 2877	23	16.5	0	F
Rhinoclemmys punctularia CRI 2871	16.9	17.2	2	F
Rhinoclemmys punctularia CRI 3706	22	22.2	0	F
Rhinoclemmys punctularia CRI 2514	17.1	20.5	3.2	F
Rhinoclemmys punctularia CRI 0345	12.8	16.5	2.1	F
Rhinoclemmys punctularia CRI 4581	16.3	17.6	0	F
Rhinoclemmys punctularia CRI 3191	18.2	17	0	F
Rhinoclemmys punctularia CRI 0296	17	16.5	0	F
Rhinoclemmys punctularia CRI 0796	19.5	17	0	F
Rhinoclemmys punctularia CRI 1813	17.2	15	0	F
Rhinoclemmys punctularia CRI 2702	15.4	16.6	1.2	F
Rhinoclemmys punctularia CRI 5481	10.1	11.5	1.1	F
Rhinoclemmys nasuta CRI 2443	11.9	16.3	2	F
Rhinoclemmys nasuta CRI 2638	13	20.6	3	M
Rhinoclemmys nasuta CRI 2448	12.7	17.1	4	M
Rhinoclemmys nasuta CRI 2442	11	15.4	3.1	F
Rhinoclemmys annulata CRI 2962	18	20.5	6	M
Rhinoclemmys annulata CRI 0049	11.8	16	4.5	F
Rhinoclemmys annulata CRI 0048	12	17.1	4.3	M
Rhinoclemmys annulata CRI 3638	11	11	5	F
Rhinoclemmys annulata CRI 1132	11.7	12.7	3	M
Rhinoclemmys annulata CRI 2774	12.1	19.4	4	M
Rhinoclemmys annulata CRI 1222	16	20	2.5	F
Rhinoclemmys annulata CRI 2773	7.5	11.8	3	F
Rhinoclemmys pulcherrima manni CRI 2155	15	20	2	M
Rhinoclemmys pulcherrima manni CRI 1839	16	21	5	M
Rhinoclemmys pulcherrima manni CRI 1483	17.6	21.4	5	F
Rhinoclemmys pulcherrima manni CRI 1090	11	12.8	3.5	F
Rhinoclemmys pulcherrima manni CRI 7597	13	15.5	4	M
Rhinoclemmys pulcherrima manni CRI 1444	15.5	20.7	6	F
Rhinoclemmys pulcherrima manni CRI 2895	14	13.5	4	M
Rhinoclemmys pulcherrima manni CRI 6625	14.7	18	3	M
Rhinoclemmys pulcherrima manni CRI 1478	14.9	15.4	2.1	F
Rhinoclemmys areolata CRI 8318	13.5	16.2	4.4	F
Rhinoclemmys areolata CRI 2775	14.2	13.1	3	F
Rhinoclemmys areolata CRI 2963	13.8	12.5	1	M
Rhinoclemmys melanosterna CRI 2441	22.6	25	7.5	F
Rhinoclemmys melanosterna CRI 4198	17.6	20.3	5	F
Rhinoclemmys melanosterna CRI 2434	16.2	19.4	3	F

APPENDIX 2—Continued.

Species	Epiplastron measurements (mm)			Sex
	Midline gular width	Anterior gular width	Posterior gular width	
Rhinoclemmys melanosterna CRI 2433	13.5	15	2	F
Rhinoclemmys rubida CRI 1234	13.5	10.8	0	F
Rhinoclemmys diademata CRI 1339	30	27.2	6	F
Rhinoclemmys diademata CRI 3656	22.3	20.7	2	F
Rhinoclemmys diademata CRI 3826	14.6	18.2	4	F
Rhinoclemmys diademata CRI 1517	15	22	4	F
Rhinoclemmys diademata CRI 1476	12.1	14.2	3	F
Rhinoclemmys diademata CRI 1516	20	23	5	F
Rhinoclemmys panamaensis	24.22	37.83	3.14	