

Contributions

from the Museum of Paleontology, University of Michigan

VOL. 33, NO. 2, PP. 29-64

NOVEMBER 2, 2020

NEW SPECIMENS OF THE LATE EOCENE TURTLE *CORDICHELYS* (PLEURODIRA: PODOCNEMIDIDAE) FROM WADI AL HITAN AND QASR EL- SAGHA IN THE FAYUM PROVINCE OF EGYPT

BY

MICHAEL D. CHERNEY¹, JEFFREY A. WILSON MANTILLA¹, IYAD ZALMOUT²,
MOHAMMED SAMEH M. ANTAR³, AND PHILIP D. GINGERICH¹

Abstract — Podocnemidid turtles in the subtribe Stereogenyina are diagnosed by a unique, partially developed secondary palate that consists of a pair of lateral flanges, each formed by the maxilla and palatine, separated by a midline cleft. Two monospecific stereogenyine genera, *Stereogenys* and *Cordichelys*, overlap temporally and spatially in the upper Eocene deposits of the Fayum Depression in Egypt. The taxonomic history of these genera is complicated and intertwined, and the two species (*St. cromeri* and *C. antiqua*) may be more closely related than their long history of generic separation suggests. Here we describe two new specimens of *Cordichelys*—a skull and shell from the lower Priabonian Birket Qarun Formation and a complete skull from the overlying middle Priabonian of the Qasr el-Sagha Formation. We also attribute to *Cordichelys* a mandible that previously had been tentatively identified as *Stereogenys*. These specimens along with previously described *Cordichelys* materials reveal substantial morphological variation within the currently monotypic genus. Presence of *Cordichelys* in the Birket Qarun Formation corroborates previous interpretations of a marine habitat for these turtles. Meanwhile, the reconstructed shell of the new Birket Qarun specimen reveals moderate doming and an ovoid outline that contrast with previous interpretations of its shape as “flat” and “cordiform.”

INTRODUCTION

The shallow marine sediments of the Birket Qarun and Qasr el-Sagha deposits formed during the late Eocene, when the Tethys Sea covered large sections of northern Africa, including what is now the Fayum Depression of Egypt (Fig. 1). The Fayum locality Wadi Al Hitan (“Valley of Whales”) has a dense record of vertebrates from the Birket Qarun Formation, including archaic whales, sea cows, fishes, and turtles (Gingerich, 1992). The Qasr el-Sagha beds north of Birket Qarun (e.g., Andrews, 1906) are also heavily sampled, and in addition to marine vertebrates, they produce terrestrial vertebrate remains, including those of *Moeritherium*

(Andrews, 1901) and *Arsinoitherium* (Beadnell, 1902).

Abundant, well-preserved archaic whale remains from Fayum deposits have facilitated our understanding of the evolutionary transition of whales from the terrestrial to the marine realms (e.g., Gingerich and Smith, 1990; Gingerich et al., 1990; Gingerich and Uhen, 1996). However, the turtle remains from these formations have received significantly less attention and are still poorly understood. Among them are members of the subtribe Stereogenyina (Gaffney et al., 2011), previously referred to as the *Shweboemys*-group turtles (Broin, 1988). Although similar to other podocnemidids in many respects, these pleurodires had an autapomorphic palatal structure that consisted of a

¹Museum of Paleontology and Department of Earth and Environmental Sciences, University of Michigan, 1105 N. University Avenue, Ann Arbor MI 48109-1085, U.S.A. (mcherney@umich.edu, wilsonja@umich.edu, gingeric@umich.edu)

²Saudi Geological Survey, Sedimentary Rocks and Palaeontology Department, Jeddah, Saudi Arabia (izalmount@ksu.edu.sa)

³Egyptian Environmental Affairs Agency, Wadi Al Hitan World Heritage Site, Fayum, Egypt (wrpashark@yahoo.com)

pair of medially projecting lateral flanges, each formed jointly by the maxilla and palatine. This partial secondary palate was likely an adaptation to a durophagous diet (Andrews, 1906; Wood, 1971; Ferreira et al., 2015). *Stereogenyina* has no living members, but extinct species span most of the Cenozoic from both sides of the Atlantic and in Asia. A Mesozoic occurrence was reported from India (Jain, 1977, 1986), but this taxon is of doubtful assignment to *Stereogenyina* (Gaffney et al., 2011) and has been excluded here. *Stereogenyina* has been positively identified from the Eocene of Egypt (Andrews, 1901, 1903; Wood, 1971; Gaffney et al., 2011); the Oligocene of South Carolina (Weems, 2009; Weems and Knight, 2013); the Miocene of Egypt (Dacqué, 1912; Gaffney et al., 2011), India (Prasad, 1974), Pakistan (Wood, 1970), Puerto Rico (Gaffney and Wood, 2002), and Venezuela (Wood and Díaz de Gamero, 1971; Sánchez-Villagra and Winkler, 2006; Gaffney et al., 2008; Ferreira et al., 2015); and the Pliocene or Pleistocene of Burma (Swinton, 1939) (Fig. 2). Thus, the Fayum deposits of Egypt have produced the two oldest known stereogenyines, *Stereogenys* (Andrews, 1901) and *Cordichelys* (Gaffney et al., 2011), which also record the earliest definitive appearance of the partial secondary palate that characterizes the group.

The present investigation examines new material and consults the previous literature to review the Egyptian genera *Stereogenys* and *Cordichelys*. The new material includes a skull and shell from the lower Priabonian Birket Qarun Formation and a complete skull from the overlying middle Priabonian Qasr el-Sagha Formation.

INSTITUTIONAL ABBREVIATIONS

AMU-CURS	— Alcaldía del Municipio Urumaco, Colección Urumaco Rodolfo Sánchez, Venezuela
CGM	— Egyptian Geological Museum, Cairo, Egypt
EEAA	— Egyptian Environmental Affairs Agency, Cairo, Egypt
MCNC	— Museo de Ciencias Naturales de Caracas, Caracas, Venezuela
MUVP	— Mansoura University Vertebrate Paleontology, Mansoura City, Egypt
NHMUK	— Natural History Museum, London, U.K.
SCSM	— South Carolina State Museum, Columbia, U.S.A.
UMMP	— University of Michigan Museum of Paleontology, Ann Arbor, U.S.A.

YPM — Yale Peabody Museum, New
Haven, U.S.A.

COMPARATIVE MATERIALS

Comparative materials examined include *Cordichelys antiqua* (Gaffney et al., 2011), a nearly complete skull, carapace, and plastron (YPM 7457); *Stereogenys cromeri* (Andrews, 1901), a nearly complete skull and lower jaws (holotype, CGM 10027); *St. cromeri*, a nearly complete skull (referred material, CGM 10031); an unidentified carapace and plastron collected by Beadnell in 1903 (CGM 8718); and *Erymnochelys madagascariensis*, a complete dry skeleton (YPM HERR.010884).

METHODS

Collection

The skull of CGM 42191 was found exposed on the surface of a mild slope among a scattering of shell fragments. The superficially exposed fragments were collected and the location mapped with GPS coordinates. The next day, workers sifted through the surrounding sediment to retrieve all the remaining fragments.

The skull-only specimen, MUVP498, was discovered isolated and partially exposed on the surface. It was brought back to camp after its location was mapped with GPS coordinates.

The lower jaw, UMMP 97531, previously documented by Gaffney et al. (2011), was found isolated on the surface and its precise location was mapped with GPS coordinates.

Measurements

All reported measurements were taken directly from fossil specimens. Transverse measurements that were not possible due to incompleteness of the specimen were estimated by doubling the measurement from the midline and are listed in brackets. All other estimated measurements of incomplete elements are marked with an asterisk. Measurements across curved surfaces reflect the straight-line measurement between its two extremes unless otherwise noted.

Stereophotography

Stereophotos were taken with a 6–8 degree spread using a camera mount attached to the end of an arm set to pivot on an axis through the focal point on the specimen. The camera was positioned approximately 70

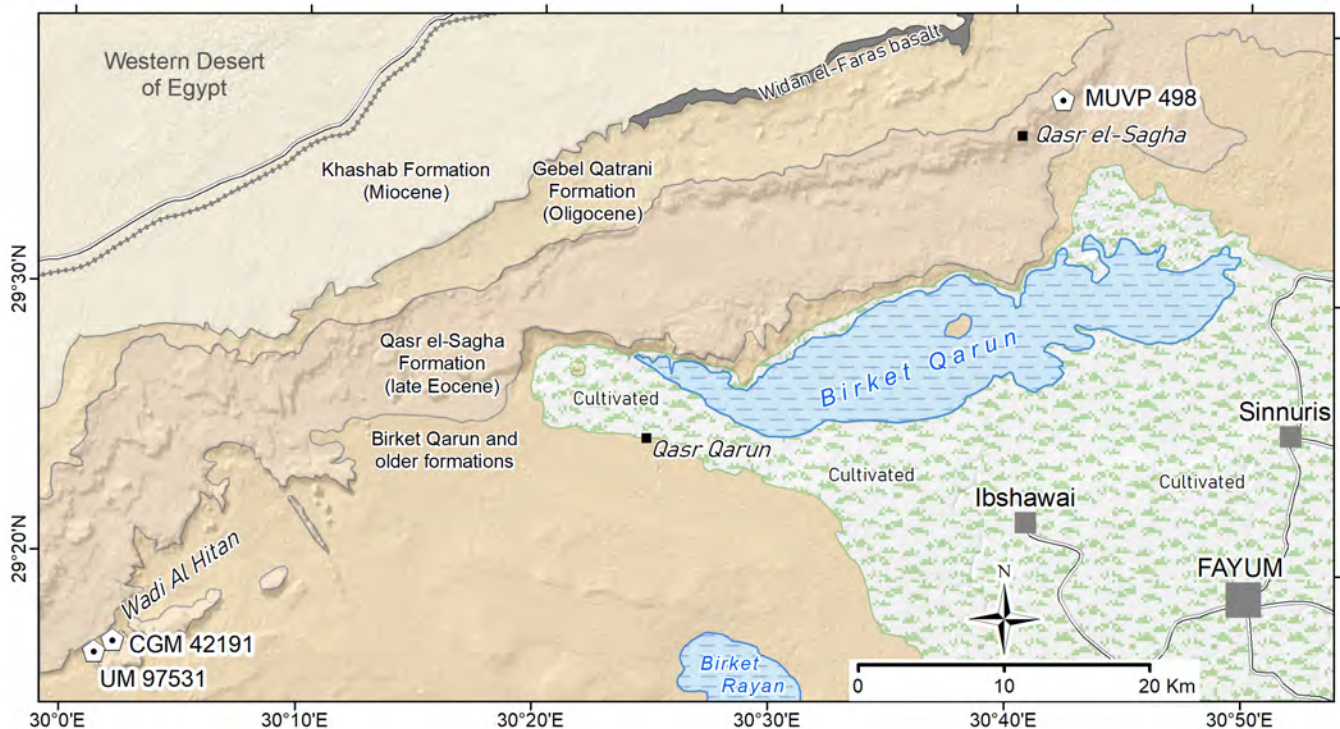


FIGURE 1 — Geological map of desert escarpments north and west of Fayum in the western desert of Egypt showing localities yielding the late Eocene turtle specimens described here. Specimens were found in exposures of the Birket Qarun Formation in Wadi Al Hitan (CGM 42191, UM 97531) and the Qasr el-Sagha Formation north of lake Birket Qarun (MUVP 498).

cm from the specimen, and photos were shot with a 50 mm macro lens at 10-megapixel resolution. The focal point was set approximately 1/3 of the way back from the top of the object to optimize three-dimensionality for the primary focus of each stereo image.

Illustrations

Line drawings were created in Adobe Illustrator by tracing lines over photographs. First-hand observations of the fossil material assisted interpretation of the photographs. We referred to Gaffney et al. (2006) for representational style. Dashed lines represent reconstructed missing bone, dotted lines represent scute sulci, hashed regions delineate exposed internal bone surface, and stippling represents matrix.

Fossil Preparation

Shell fragments of CGM 42191 were rearticulated with cyanoacrylate where a positive association between fractured edges could be identified. When assembly of several pieces contained empty spaces

for which no fragments fit, we filled the spaces with a paste epoxy to stabilize the reconstruction. Isolated elements were not reconstructed and when preparation was complete, numerous fragments remained for which we could not find a definite association. The associated skull was discovered nearly intact with the right temporal fossa, nasal cavity, and orbits filled with matrix. This provided an internal mold that guided the reassembly of fragments that had been disarticulated from the dorsal surface of the skull. A mold and cast of the skull have been deposited in the UMMP collections. To reconstruct the pelvis, we sculpted directly onto the bone, molded and cast the reconstructions, and then removed the sculpted portions from the original fossil material.

For the skull of MUVP 498, air-scribe preparation was used to remove the matrix and to clean a layer of gypsum from the surface of the bone. No reconstruction was required. A mold and cast of the specimen have been deposited in the UMMP collections.

Lower jaw UMMP 97531 was consolidated with polyvinyl acetate but did not require any matrix removal or reconstruction.

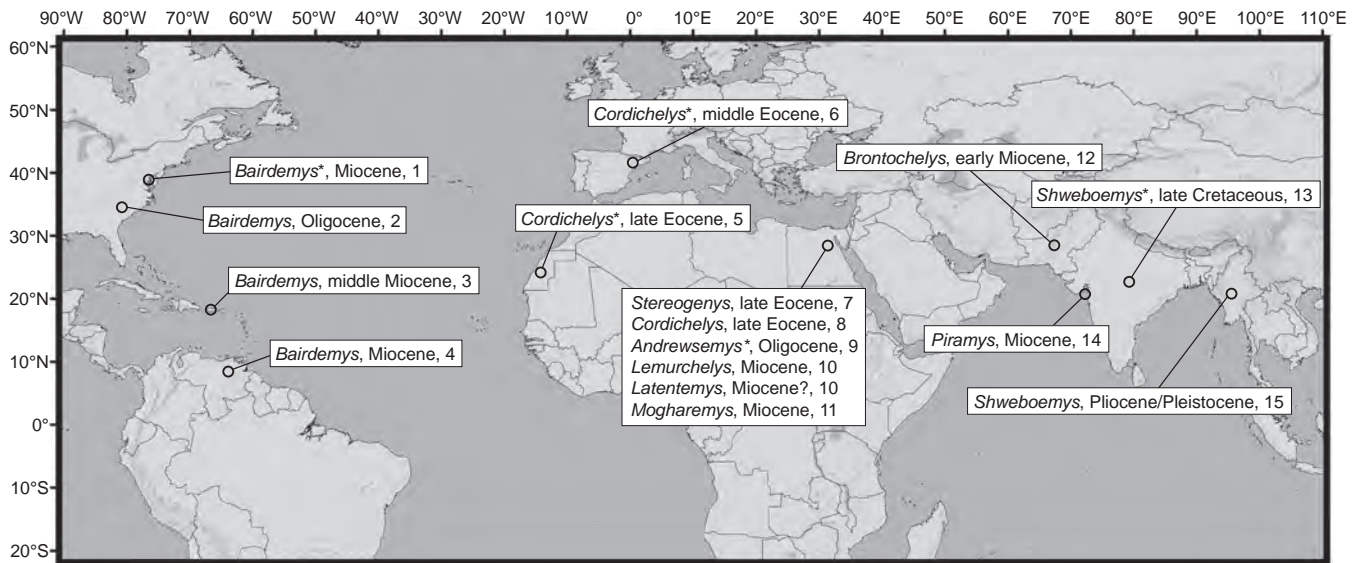


FIGURE 2 — Global distribution of Stereogenyina. Asterisks designate shell specimens we consider tentatively assigned to Stereogenyina. **1**, Collins and Lynn (1936), Weems and Knight (2013); **2**, Weems (2009), Weems and Knight (2013); **3**, Gaffney and Wood (2002); **4**, Wood and Díaz de Gamero (1971), Sánchez-Villagra and Winkler (2006), Gaffney et al. (2008), Ferreira et al. (2015); **5**, Zouhri et al. (2018); **6**, Broin et al. (2018); **7**, Andrews (1901); **8**, Andrews (1903), Wood (1971), Gaffney et al. (2011); **9**, Pérez-García (2019); **10**, Gaffney et al. (2011); **11**, Dacqué (1912), Gaffney et al. (2011); **12**, Wood (1970), Gaffney et al. (2011); **13**, Jain (1977, 1986); **14**, Prasad (1974), Ferreira et al. (2018); **15**, Swinton (1939).

SYSTEMATIC PALEONTOLOGY

TESTUDINES Linnaeus 1758
 PLEURODIRA Cope 1864
 PODOCNEMIDIDAE Cope 1868
Cordichelys Gaffney et al., 2011

Type species.— ‘*Podocnemis*’ *antiqua* Andrews, 1903.

Included species.— *Cordichelys antiqua*.

Specimens referred herein.— CGM 42191, a partial skull, mostly complete shell, and partial pelves (Figs. 3–8); MUV 498, a nearly complete skull (Fig. 9–10), YPM 7457, a complete skull and shell (Figs. 11–13), and UMMP 97531, a nearly complete lower jaw (Fig. 14).

Emended diagnosis (modified from Gaffney et al., 2011).— *Cordichelys* is a podocnemidid of the Tribe Stereogenyini that has in common with all other members of the Subtribe Stereogenyina a well-developed secondary palate consisting of medially projecting expansions of the maxillae and palatines with a cleft separating them at the midline. *Cordichelys* is known from the skull, shell, and pelves and is diagnosed by a shallow interorbital depression, a large ventral process of the postorbital in the septum orbitotemporale that contacts a moderate dorsal extension of the palatine preventing jugal-pterygoid contact, and a eustachian

tube confluent with the fenestra postoticum. It differs from *Lemurchelys*, *Shweboemys*, and *Stereogenys* in possessing arched, rather than straight, medial edges of the palatal cleft in ventral view. It differs from *Bairdemys* in possessing a low, rather than high, ventral convexity on the triturating surface of the secondary palate, an open, rather than closed, antrum postoticum (shared with *Latentemys*), and frontal and prefrontal that in profile are flat, rather than rounded (shared with *Shweboemys*). It differs from *Stereogenys* in possessing a less well-developed secondary palate, shorter prefrontals that contribute less to the dorsal margin of the orbit, an interorbital depression in the prefrontals, and a less extensive dorsal extension of the palatine that does not contact the parietal. If the lower jaw UMMP 97531 described below indeed pertains to *Cordichelys*, then additionally it can be differentiated by a heart-shaped triturating surface that is less expanded than in *Stereogenys*, but more expanded than in *Bairdemys*. It further differs from *Stereogenys* in having an evenly curved anterolateral outline in dorsal view, a median ridge running across the triturating surface with depressions on either side of it, and a more emarginated posterior margin of the triturating surface.

Our emendment of the diagnosis eliminates two important features listed by Gaffney et al. (2011: 49) as diagnostic: the ‘cordiform’ carapace for which the genus was named and the minimal contact of the pterygoids

at the midline. Three-dimensional reconstruction of the nearly complete shell described below (CGM 42191) suggests that the cordiform or heart-shaped outline of the Yale carapace (YPM 7457) probably resulted from taphonomic crushing of a carapace that was

arched more anteriorly than posteriorly, an observation first made by Andrews (1906: 289). It may later be shown that this particular form of arching, together with the anterior emargination and posterior tapering of the shell are diagnostic of *Cordichelys* even if the

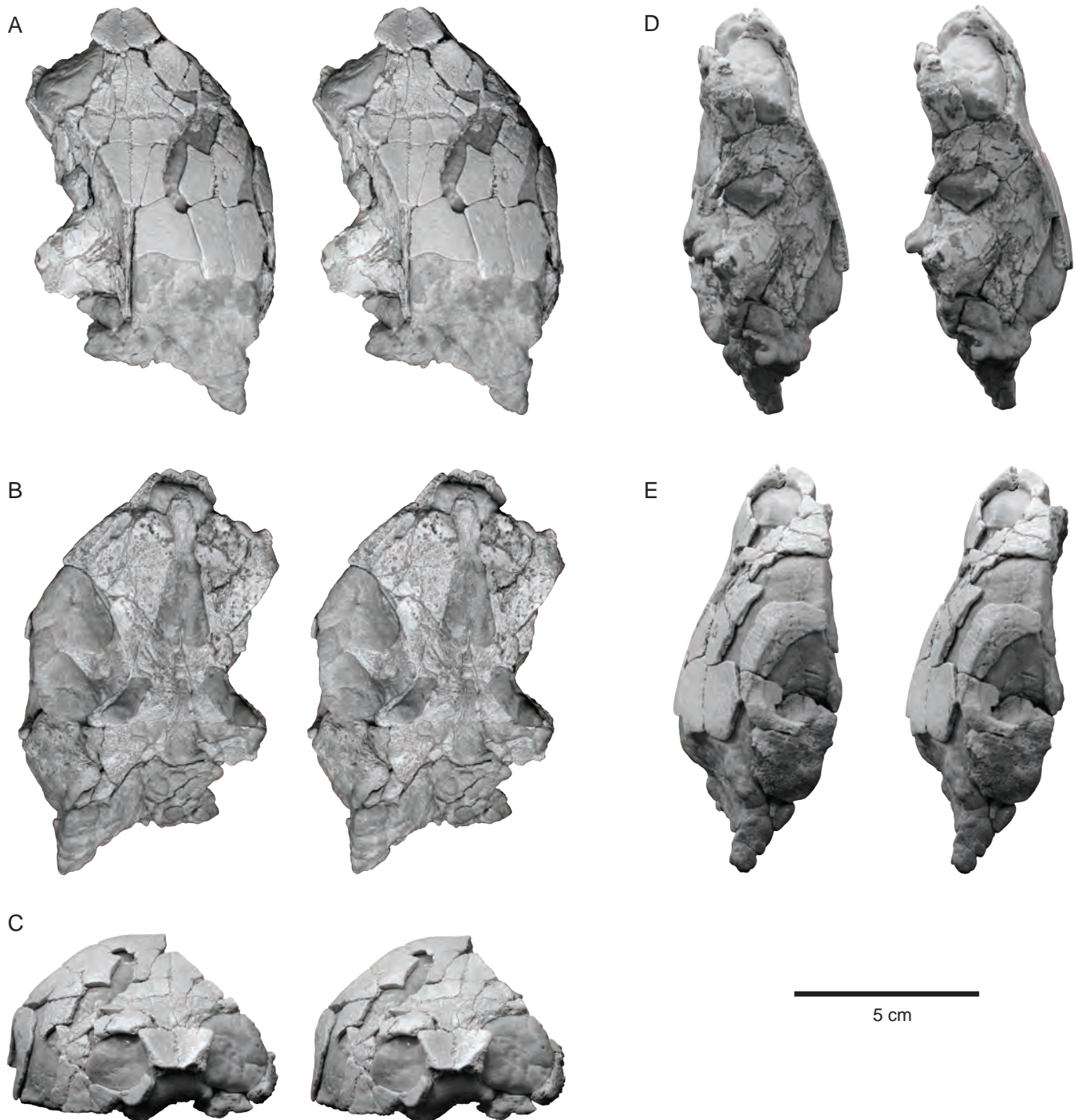


FIGURE 3 — *Cordichelys* aff. *antiqua* (CGM 42191). Stereophotographs of skull in dorsal (A), ventral (B), anterior (C), left lateral (D), and right lateral (E) views.

apparent ‘cordiform’ outline is a taphonomic artifact. However, these features remain ambiguous because there is currently no shell described for the other Egyptian stereogenyine taxon, *Stereogenys cromeri*. Our observations on the Yale specimen (YPM 7457) confirm the original description of Wood (1971: 153), which stated that the pterygoids do not contact one another on the midline (contra Gaffney et al., 2011: 49). In the three *Cordichelys* skulls considered below, contact between the basisphenoid and palatines appears to prevent median contact of the pterygoids. Although the possibility of taphonomic loss of delicate medial processes of the pterygoid cannot be eliminated, any midline contact would be minimal. We were not able to inspect the other cranial material currently referred to *Cordichelys antiqua*, such as the two partial skulls in the NHMUK collections originally identified by Andrews (1906) as *Stereogenys*. These specimens consist of posterior portions of the skull with obscure sutures (Wood, 1971), and so we doubt they would offer a more reliable assessment of this character.

Our emendment of the diagnosis based on inclusion of the new specimens described here also removes several features that Gaffney et al. (2011) listed as differentiating *Cordichelys* from *Stereogenys*. These include the wider angle at the front of *Stereogenys* skull, which we regard as the result of deformation. Both the holotypic skull (CGM 10027) and another nearly complete skull (CGM 10031) are taphonomically flattened, resulting in substantial alteration of the angle at the front of the skull. Evidence for this distortion is present in the articulated holotypic skull and lower jaws, which are separated by nearly two centimeters at the quadrate-articular joint. Other features Gaffney et al. (2011) listed as distinguishing *Cordichelys* and *Stereogenys* are present in one of the referred specimens (MUV 498), which in most other aspects matches *Cordichelys*. These include differences in the jugal contribution to the orbital rim, the anterior extent of the basisphenoid, and the shape of the snout.

Emended distribution (modified from Gaffney et al., 2011).— *Cordichelys* has been recorded from the upper Eocene of Egypt, both in the lower Priabonian beds of the Birket Qarun Formation and the middle Priabonian beds of the Qasr el-Sagha Formation. Originally attributed to the Qasr el-Sagha Formation, inclusion of specimens collected by UM (CGM 42191, UM 97531) and revision of the provenance for the Yale specimen (YPM 7457) extend the stratigraphic distribution of *Cordichelys* into the Birket Qarun Formation. Shell material from the late Eocene Samlat Formation of Morocco (Zouhri et al., 2018) and the middle Eocene Taveret Limestone Formation in Spain (Broin et al., 2018) have been referred to *Cordichelys*, but we refrain

from including these specimens within the genus pending discovery of diagnostic material (e.g., cranial remains).

Comments.— Attribution of the new specimens to the currently monotypic genus *Cordichelys* implies a greater degree of intraspecific variation than previously hypothesized (see Cherney, 2011; Cherney et al., 2011). We choose this conservative taxonomy over the alternative approach, in which the differences are interpreted to reflect genus- or species-level distinctions, due to the already considerable historical complexity of Egyptian stereogenyine taxonomy, absence of the *Cordichelys* holotype at CGM, and lack of anatomical overlap in key *Cordichelys* specimens. Specimens described here partially resolve associations between skull and shell morphotypes in *Cordichelys*, but a robust taxonomic revision would require additional skull-and-shell specimens. Turtle remains are common in the Fayum, and so we think it is only a matter of time before these issues are resolved with adequate specimens to provide a solid foundation for taxonomic revision.

Cordichelys aff. *antiqua* (CGM 42191)
(Figs. 3–8; Table 1)

Locality.— Wadi Al Hitan, western Fayum Province, Egypt, WGS-84 GPS coordinates N29.278524, E30.037326 (Fig. 1).

Formation and age.— Birket Qarun Formation, upper Eocene (lower Priabonian) according to Gingerich (1992).

Material.— A partial skull (Figs. 3, 4), mostly complete shell (Figs. 5–7), and partial pelves (Fig. 8). A cast of the skull of CGM 42191 has been deposited in the University of Michigan Museum of Paleontology collection (UMMP 13995). This specimen possesses the diagnostic partial secondary palate formed by flanges extending from the maxillae and palatines. It differs from other *Cordichelys* specimens described here (YPM 7457 and MUV 498) in various ways. In contrast to YPM 7457 it has a relatively wide midline cleft between the palatal flanges, a moderate dorsal projection of the palatine that meets the ventral projection of the postorbital on the posterior side of the septum orbitotemporale. It differs from MUV 498 in having flat frontals (in lateral view) that create a depression immediately anterior to the dorsally expanded parietal region that lacks the midline depression present in YPM 7457, and contrasts with both YPM 7457 and MUV 498 in having a posteriorly tapered squamosal that has a dorsoventral ridge along its posterior edge but lacks a concave lateral surface. Its shell is distinct from that of YPM 7457 in having a nuchal about 1.5 times wider

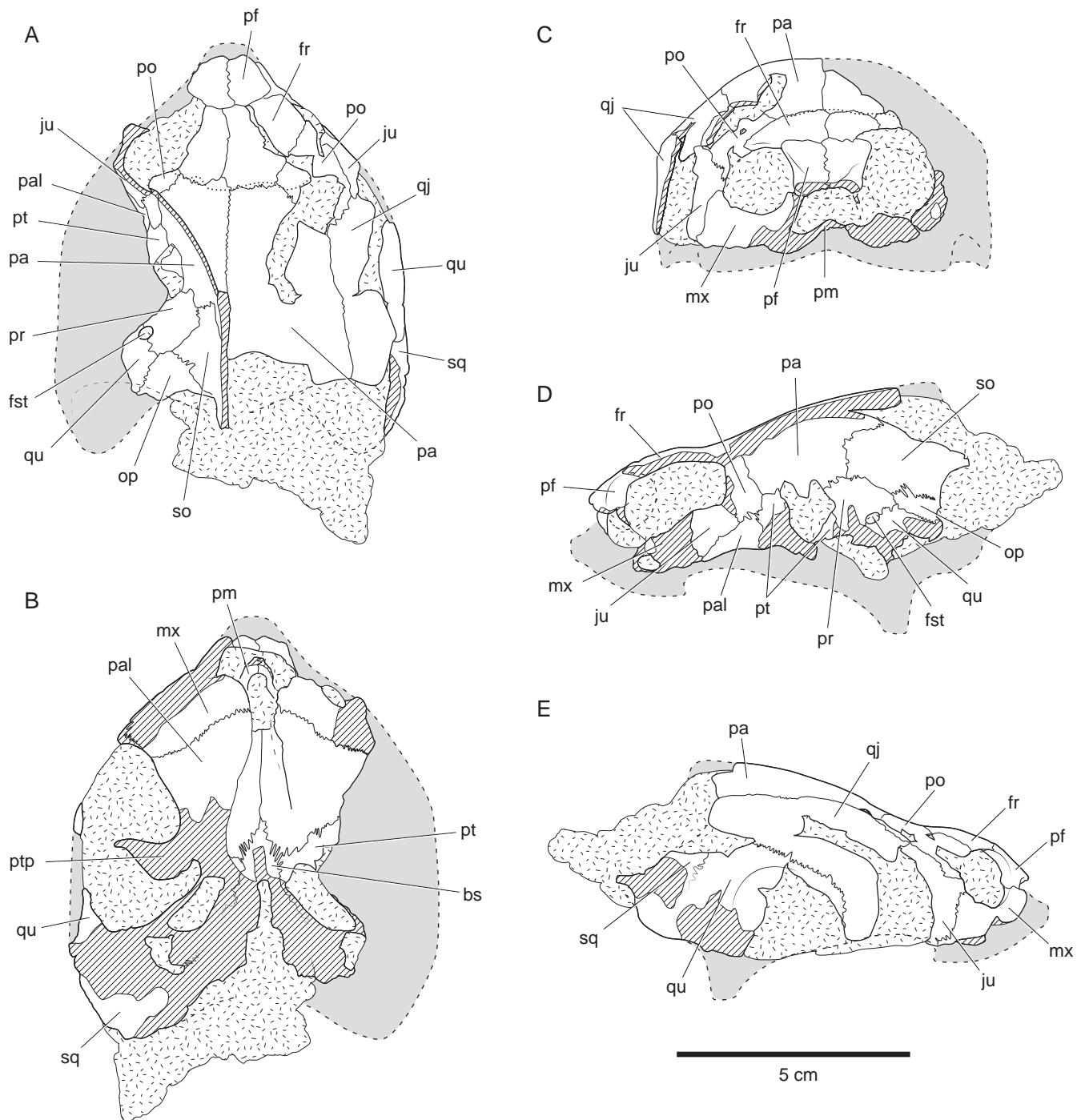


FIGURE 4 — *Cordichelys* aff. *antiqua* (CGM 42191). Line drawings of skull in dorsal (A), ventral (B), anterior (C), left lateral (D), and right lateral (E) views. Abbreviations: *bs*, basisphenoid; *fr*, frontal; *fst*, foramen stapedio-temporale; *ju*, jugal; *mx*, maxilla; *op*, opisthotic; *pa*, parietal; *pal*, palatine; *pf*, prefrontal; *pm*, premaxilla; *po*, postorbital; *pr*, prootic; *pt*, pterygoid; *ptp*, processus trochlearis pterygoidei; *qj*, quadratojugal; *qu*, quadrate; *so*, supraoccipital; *sq*, squamosal.

than long, a pygal nearly as wide as the suprapygal, a deep U-shaped anal notch bounded laterally by round-tipped xiphiplastral projections, and first marginal scutes that meet at the midline.

When Wood (1971) referred '*P.*' *antiqua* to *Shweboemys* (as *Sh. antiqua*), he also included '*Podocnemis stromeri*,' '*P. stromeri* var. *major*,' and the previously undescribed Yale specimen YPM 7457.

TABLE 1 — Measurements of three turtle specimens described herein. Square brackets indicate estimates made by doubling the complete dimension preserved on one side; asterisks indicate estimates based on reconstruction of incomplete surfaces.

<i>Feature</i>	<i>mm</i>
CGM 42191	
Cranium, width at widest point	[77]
Cranium, maximum length in dorsal midline	75*
Cranium, distance from tip of trochlear process of the pterygoid to the midline	30
Carapace, length	269
Carapace, width	[208]
Nuchal, width	51
Nuchal, length	36
Neural row (1–6), length	140
Suprapygal, length	38
Suprapygal, width	41
Plastron, length	235*
Plastron, anteroposterior length of anterior lobe	44*
Plastron, width at anterior margin of the bridge	[110]
Mesoplastron, anteroposterior length	30
Mesoplastron, width	34
Xiphiplastron, width at widest point	94
Xiphiplastron, length (from tips of protrusions to anteriormost point)	79
Xiphiplastral notch depth	22
Pelvis, height (based on complete of right ilium and complete of left pubis)	60*
MUVP 498	
Cranium, maximum width	49
Cranium, maximum length in dorsal midline	57
Cranium, width between ends of the trochlear process of the pterygoid	39
Cranium, distance between outer edges of quadrate–mandibular articulation	45
UM 97531/ZV 161	
Total anteroposterior length	65
Length of symphysis	35
Extreme width of expanded triturating surface	56
Extreme width at articulating surfaces	[69]

This taxonomic decision accommodated a significant amount of intraspecific variation in shell characters, including differences in proportions of the plastron, shape of the xiphiplastral projections and notch, and relative proportions of the nuchal, pygal, suprapygal, mesoplastron, and entoplastron. The new material we describe here (CGM 42191) closely matches descriptions and illustrations of the shell-only holotype

of *Cordichelys antiqua* (CGM 10038); we can identify no significant differences in osteology or soft tissue structures (i.e., scute sulci) that distinguish these two specimens. In contrast, YPM 7457, referred to the species by Wood (1970), differs from the holotype of *C. antiqua* in several features of the carapace and plastron.

CGM 42191 was collected from an exposure of the Birket Qarun Formation in Wadi Al Hitan. The skull

is filled with sedimentary matrix that forms an internal mold of the temporal fossa, orbits, and nasal passages on its right side. This internal mold provided a contoured surface onto which we refit several associated bone fragments. The skull is nearly complete, lacking only the basioccipital and exoccipital. The posterior bones of the cranium are significantly eroded and, in some cases, unobservable because they are enclosed in matrix. The cranial scute sulci are almost completely indiscernible, with exception of one short sulcus overlying the parietal-frontal suture. The ventral surface of the skull is partially eroded, and the left temporal roof is missing, exposing the medial surface of the temporal fossa on one side.

The carapace was reconstructed from many fragments and represents about 60% of its total surface area. The entire anteroposterior length of the carapace is preserved as a series of interconnected elements, and its transverse breadth is preserved on one side. With these two dimensions preserved, as well as a representation of all major carapacial elements, we were able to reconstruct the entire carapace (Fig. 5). The plastron includes the complete left and part of the right epiplastron, most of the entoplastron, a complete right hyoplastron, both mesoplastra, and both xiphiplastra (Fig. 6). This represents about 60% of the surface area of the plastron. A complete bridge connection between the anterior carapace and hyoplastron on the left side enables both an estimate of the cross-sectional profile of the shell (Fig. 7), as well as a reliable spatial association between the anterior plastron and the rest of the shell. Although the hypoplastra are missing, the total length of the plastron can be confidently estimated because the xiphiplastron can be positioned in relation to the rest of the shell through its pelvic connection to the carapace. The pelvic scars on the plastron are well defined, whereas on the carapace they are present but significantly eroded. Most of the sutures and scute sulci are clearly visible on the shell. Parts of both right and left pelvises are preserved, which nearly completely preserve the ilium, pubis, and shape and size of the acetabulum (Fig. 8). Most of the ischium is missing.

Cranium

In dorsal view, the skull is broad posteriorly and gently curves anteriorly to form a slightly protruding, but blunt rostrum. The anterolaterally oriented, ovoid orbits are located near the external nares and may be partially exposed dorsally, although due to the condition of the one reconstructed orbit it is difficult to say with certainty. There are no nasals. The dorsally expanded parietal region slopes into the flat frontals creating a transverse depression in the posterior half of the frontals.

The temporal fossa is covered primarily by the parietal and quadratojugal, which in combination produce a moderately emarginated posterior edge between the supraoccipital and squamosal. The prefrontals display a shallow midline depression. The palate possesses an expanded triturating surface formed by medially expanded flanges of the maxillae and palatines, with the palatines making up the majority of the surface. These palatal flanges do not extend as far back as the trochlear process, have curved medial edges, and are separated by a moderate cleft.

Parietal.— The reconstructed fragments of the right parietal preserve most of its dorsal outline, whereas the absence of the dorsal surface of the skull on the left side allows observation of the parietal contribution to the medial surface of the temporal fossa. On its dorsal surface, the parietal contacts the frontal and postorbital anteriorly, the quadratojugal laterally, and the opposite parietal on the midline. On the medial surface of the temporal fossa, the parietal contacts the supraoccipital posteriorly, the prootic and pterygoid ventrally, and the postorbital anteriorly.

In dorsal view, the parietal resembles a rectangle with anterolateral corner removed. It is slightly convex both anteroposteriorly and transversely. The parietal contacts the frontal along a short, transversely oriented suture. At the lateral edge of its contact with the frontal, the parietal contacts the postorbital along a suture angled ca. 45 degrees from the midline. The parietal contacts the quadratojugal along a suture nearly parallel to the midline that extends from the posterolateral end of its contact with the postorbital to the posterior margin of the temporal roof. The parietal contacts its opposite along the midline, but the posterior portion of this contact is not preserved, and it is unknown if it contacts any part of the supraoccipital in its dorsal surface.

This ventromedial portion of the parietal is roughly trapezoidal but has a posterodorsal projection of unknown length that limits the dorsal extent of the supraoccipital. The parietal extends ventrally to meet the prootic and pterygoid along its ventral edge. The parietal meets the ventral extension of the postorbital along a straight anteriorly leaning suture that extends from the anterodorsal corner of the pterygoid to the dorsal surface of the skull.

Frontal.— The dorsal surface of the right frontal is nearly complete, but any contribution the frontal makes to the nasal cavity and internal surface of the orbit is obscured by matrix infill. In dorsal view, the frontal contacts the parietal posteriorly, the postorbital laterally, the prefrontal anteriorly, and the opposite frontal medially. The frontal contacts the parietal along a transverse suture and the postorbital along a suture that extends anterolaterally to the orbital margin. It

contacts the prefrontal along a transverse suture, which terminates laterally at the orbital rim. The frontal meets its opposite in a gently arched suture that is offset left of the midline. This creates a distinct 'step' between parietal, frontal, and prefrontal sutures. The frontal participates in the orbital rim for approximately the middle third of the dorsal side of the orbit. The flat frontal floors a depression between the sloped parietals and prefrontals.

Prefrontal.— Both prefrontals are nearly complete, lacking only their anterior edge. Matrix in the orbits prevents observation of their contribution to the internal surface of the orbits and nasal cavity. The prefrontal contacts the frontal posteriorly and the maxilla anterolaterally. The prefrontal contacts the frontal along a transverse suture that extends from the midline to the orbital margin. Its contact with the maxilla is not well preserved.

Dorsally, the prefrontal is roughly rectangular in outline, with its anterior edge shorter than its posterior edge, giving it a slight taper toward the anterior margin. Its dorsal surface is flat but slopes ventrally from posterior to anterior and from lateral to medial. The slope along the transverse axis creates a shallow, V-shaped trough between the orbits. The prefrontal forms the dorsal half of the anterior third of the orbital margin.

Quadratojugal.— Most of the exterior surface and outline of the quadratojugal is preserved on the right side, but the posterolateral corner, the anterolateral portion, and most of the ventral margin are missing. The quadratojugal contacts the parietal medially, the postorbital anteriorly, and the quadrate posterolaterally. Its contacts with the squamosal and jugal cannot be observed on this specimen.

The quadratojugal contacts the parietal along a suture that extends from the posterior edge of the temporal roof to the postorbital anteriorly. Its contact with the postorbital is parallel to the frontal-postorbital suture, being angled ca. 30 degrees to the midline. Its lateral edge contacts the quadrate in a curved suture that from anterior to posterior first travels dorsally along the anterior margin of the quadrate and then curves around the cavum tympani toward the posterior margin of the temporal roof. The quadratojugal and parietal form the majority of the temporal roof. The quadratojugal separates the quadrate from the parietal dorsally and the postorbital and jugal anteriorly. It is roughly L-shaped with its posterior leg tapered slightly. It contacts both the posterior and ventral margins of the temporal roof.

Quadrate.— The quadrate is only partially preserved. The right quadrate consists of some of the lateral and ventral surfaces, though much of it, including the mandibular articulation and most of the cavum tympani,

is missing. On the left side, the participation of the quadrate in the ventral surface of the temporal fossa is exposed and partially preserved. On its lateral surface, the quadrate contacts the quadratojugal anteriorly and dorsally and the squamosal posteriorly. On the ventral surface of the temporal fossa, it contacts the opisthotic posteromedially and the prootic anteromedially.

The contribution of the quadrate to the lateral portion of the temporal roof is bounded by its contact with the quadratojugal, which prevents it from contacting the jugal anteriorly and the parietal dorsomedially. The suture joining the quadrate and squamosal is only partially visible and cannot be described precisely. Its ventral contacts with the pterygoid, basisphenoid, basioccipital, and exoccipital are not well defined. The quadrate contacts the opisthotic and prootic medially. Brief contact between the opisthotic and prootic prevents the quadrate from contacting the supraoccipital. The foramen stapedio-temporale is preserved along the quadrate-prootic suture.

Squamosal.— The right squamosal is partially preserved, but its lateral surface is eroded, obscuring most of the quadrate-squamosal suture. Its medial and posterior surfaces are contained in matrix. The overall shape of the squamosal is not preserved, but a soft dorsoventral ridge forms its posterior edge. The lateral surface of the squamosal is flat from its posterior ridge to the posterolateral edge of the quadrate.

Jugal.— The right jugal is partially preserved and shows the contacts with the postorbital and maxilla. The left jugal is missing its lateral surface but preserves its contribution to the septum orbitotemporale. Its lateral portion contacts the postorbital dorsally and the maxilla anteriorly. Its contact with the quadratojugal is not preserved. On the septum orbitotemporale, it contacts the postorbital medially and the palatine ventrally.

On the lateral surface, the jugal contacts the postorbital along a straight suture roughly parallel to the parietal-postorbital suture that extends from the quadratojugal to the orbital margin. The jugal contacts the maxilla along a roughly dorsoventral suture that travels slightly posteriorly from the orbital rim to the ventral surface of the maxilla. The jugal provides a small section of the posterior margin of the orbit. Not enough of the surface is present to determine its shape. On the anteromedial surface of the temporal fossa, the jugal contacts the palatine at its ventral margin. It also appears to contact the ventral extension of the postorbital at its posterior margin. However, spalling and fractures in this area make it difficult to precisely trace these sutures.

Postorbital.— Although much of the dorsal surface of the right postorbital is missing, enough of the bordering sutures are visible that its general shape is

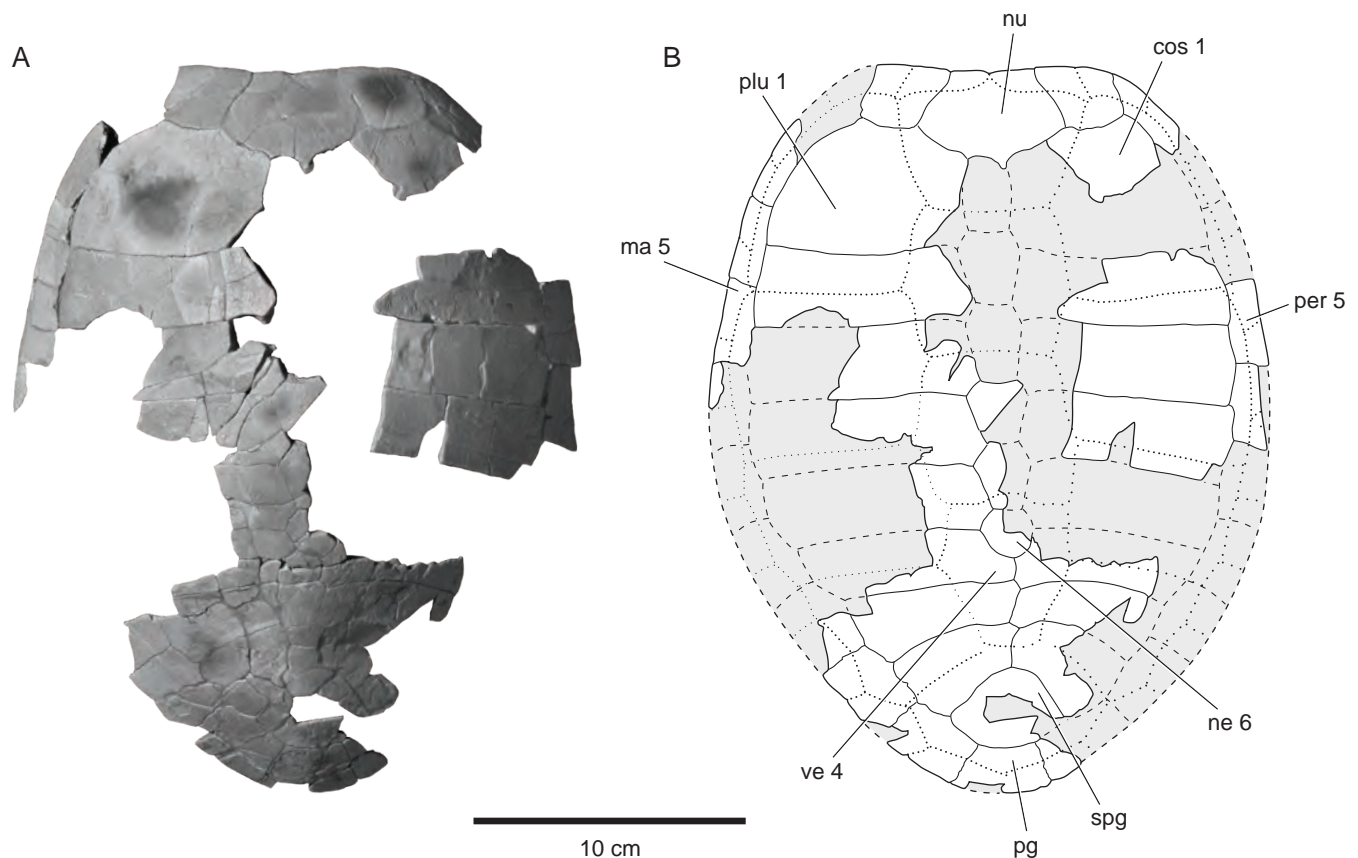


FIGURE 5 — *Cordichelys* aff. *antiqua* (CGM 42191). Photograph (A) and line drawing reconstruction (B) of carapace in dorsal view. Dashed lines represent the reconstructed outline of the carapace and sutures between bones; dotted lines represent scute sulci. Reconstructed sulci are marked by more widely spaced dots. Scute labels are on the left side of B, bone labels are on the right. Abbreviations: *cos*, costal; *ma*, marginal; *ne*, neural; *nu*, nuchal; *per*, peripheral; *pg*, pygal; *plu*, pleural scute; *spg*, suprapygal; *ve*, vertebral scute.

apparent. The ventral extension of the postorbital into the septum orbitotemporale is visible on the left side of the skull where the temporal roof is missing. On the dorsal surface, the postorbital contacts the parietal posteromedially, the quadratojugal posterolaterally, the jugal anterolaterally, and the frontal anteromedially. On the septum orbitotemporale, the postorbital contacts the jugal laterally, the parietal and pterygoid medially, and the palatine ventrally.

The postorbital-parietal suture travels posteriorly at ca. 45 degrees from the midline. It contacts the quadratojugal in a suture that, mirroring the postorbital-parietal suture, extends anteriorly at a slightly less than 45 degrees from the midline until it meets with the jugal. It contacts the jugal along a straight suture that is roughly parallel to the midline and extends from the quadratojugal to the orbital rim. It contacts the frontal along a straight suture that travels anteriorly at ca. 30 degrees from the midline. These four contacts are of roughly equal lengths. The surface contour of the postorbital is gently saddle-shaped, being dorsally

concave along the anteroposterior axis and dorsally convex on the transverse axis. It contributes the posterodorsal third of the orbital margin.

Maxilla.— Both maxillae are partially preserved. The more complete right maxilla shows its ventral surface, as well as its lateral surface just below the orbit. The lingual ridge is missing. On the exterior surface of the skull, the maxilla contacts the jugal posteriorly and the prefrontal anterodorsally, but its contact with the premaxilla cannot be observed. On the palate, it contacts the palatine posteriorly and the premaxilla briefly at its anteromedial corner.

The maxilla contacts the jugal along a suture that extends from the posterior edge of the orbit to the ventral margin of the temporal fossa. It contacts the palatine along a gently S-shaped suture that is anteromedially convex and laterally concave. This suture travels posteriorly at an angle ca. 25 degrees from the medial edge of the maxilla and palatine to near the anterior margin of the temporal fossa. Too little of the premaxilla is present to evaluate its contact with the

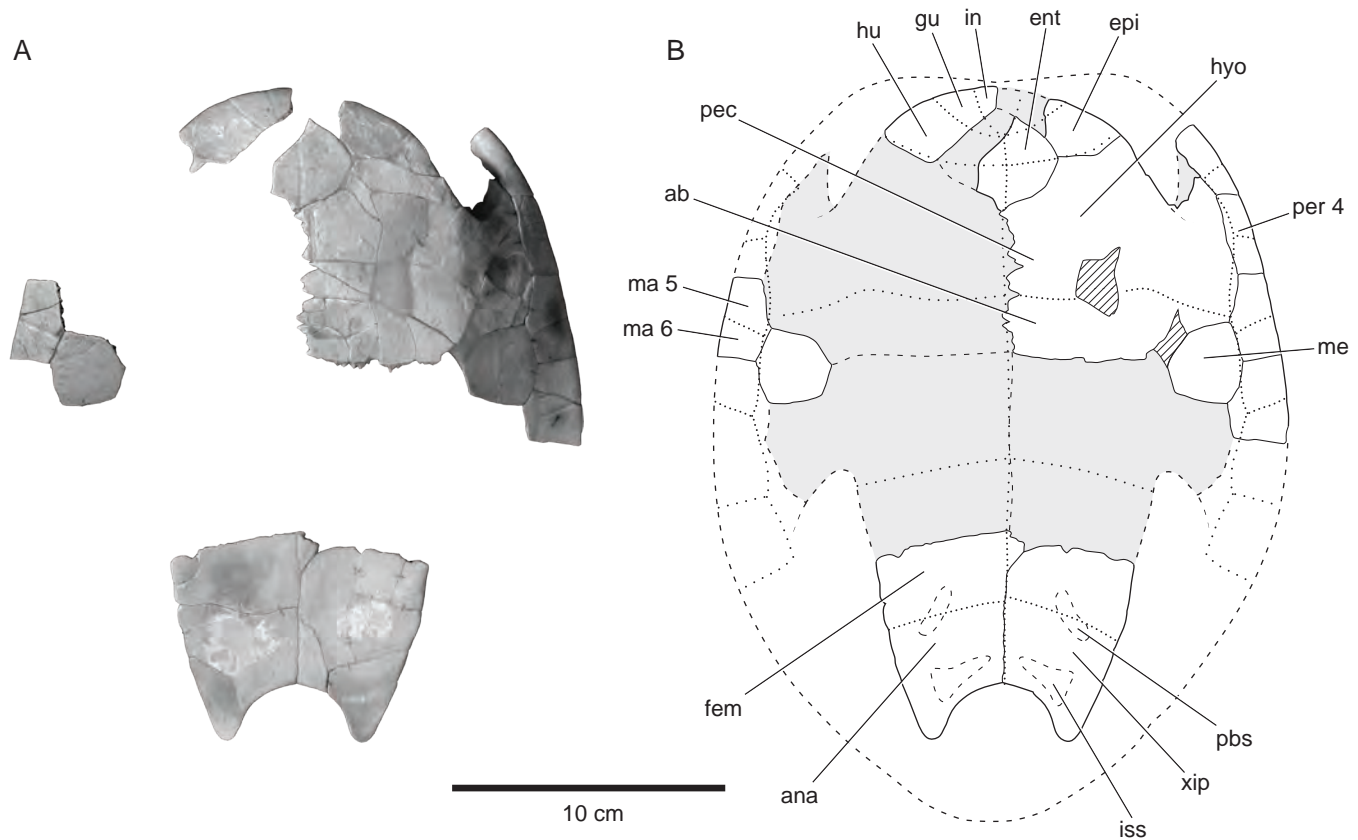


FIGURE 6—*Cordichelys* aff. *antiqua* (CGM 42191). Photograph (A) and line drawing reconstruction (B) of plastron in ventral view. Relative position of the separated xiphoplastron is based on articulation of pelvis with pelvic scars on carapace and xiphoplastron. Dashed lines represent the reconstructed outline and sutures. Dotted lines represent scute sulci; reconstructed sulci are marked by more widely spaced dots. The pelvic scars from the dorsal surface of the plastron are projected on the ventral surface. Scute labels are on the left side of B, bone labels are on the right. Abbreviations: *ab*, abdominal scute; *ana*, anal scute; *ent*, entoplastron; *epi*, epiplastron; *fem*, femoral scute; *gu*, gular scute; *hu*, humeral scute; *hyo*, hyoplastron; *in*, intergular scute; *iss*, ischial scar; *ma*, marginal; *me*, mesoplastron; *pbs*, pubic scar; *pec*, pectoral scute; *per*, peripheral; *xip*, xiphoplastron.

maxilla. The maxilla also contacts the prefrontal at the middle of the anterior edge of the orbit. Matrix filling the orbit and nasal passages prohibits observation of the extent of this maxilla-prefrontal contact along these internal surfaces.

Laterally, the maxilla forms the entire ventral portion of the orbital rim, and with a slightly laterally convex curve it provides most of the anterior tapering of the skull outline in dorsal view. Ventrally, the maxilla forms the anterior portion of an expanded flange that creates a wide triturating surface and partially encloses the nasal cavity, likely displacing the internal nares posterior to the palatines. The ventral surface of the maxilla is slightly concave along its transverse axis.

Premaxilla.— Only the posterior edge of the premaxilla is preserved in the specimen, and it is mostly buried in matrix. A small portion of its contact with the maxilla is preserved on the right side, where it meets

the anteromedial corner of the maxilla. It also meets the opposing premaxilla in a straight midline suture. Not enough of either premaxilla is sufficiently preserved to describe its shape or contributions to the floor of the nasal aperture and triturating surface of the palate.

Palatine.— The majority of both palatines is preserved. The right palatine more completely displays the ventral surface. The left palatine shows its dorsal extension into the medial surface of the temporal fossa. In ventral view, the palatine contacts the maxilla anteriorly, the pterygoid posterolaterally, and the basisphenoid medially. On the medial surface of the temporal fossa, it contacts the jugal and postorbital dorsally and the pterygoid posteriorly.

The palatine contacts the maxilla along a mildly serpentine suture, which is anteriorly convex for its medial half and concave laterally. It contacts the pterygoid along a stepped suture that angles ca. 30

degrees anteriorly from its medial contact with the basisphenoid to the margin of the temporal fossa where it bends dorsally and continues to where it meets the ventral extension of the postorbital on the medial surface of the temporal fossa. The palatines contact each other except for at their posterior margin where an anterior projection of the basisphenoid separates them. The palatine contacts the ventral extensions of the jugal and postorbital along a suture that angles dorsally from the anterolateral corner of the palatine to the pterygoid.

The palatine makes the primary contribution to the palatal flange. The medial edge of the palatine starts to diverge from the midline after the anterior quarter of its anteroposterior length. The expanded region of the palatine is slightly concave. The dorsomedial surface of the palatines, where they contact at the midline, forms the anterior portion of the braincase floor.

Pterygoid.— The right pterygoid preserves the size and shape of the trochlear process, but it is missing its ventral surface. The dorsal extension of the pterygoid into the temporal fossa is exposed on the left side. On the basicranium, the pterygoid contacts the palatine anteriorly and the quadrate posteriorly, though this latter contact is not well represented. On the medial surface of the temporal fossa, the pterygoid contacts the prootic posteriorly, the parietal dorsally, and the palatine and postorbital anteriorly. It does not contact the jugal.

The pterygoid contacts the palatine along a stepped suture that slants posteriorly from the margin of the temporal fossa just anterior of the trochlear process to the basisphenoid. It contacts a suture that forms the side of the triangular basisphenoid. The pterygoid contacts the palatine and postorbital along a dorsoventral suture, is bounded dorsally by its contact with the ventral extension of the parietal parallel to the dorsal surface of the skull, and contacts the prootic at a partially preserved suture along its posterior edge.

The trochlear process extends laterally from the medial wall of the temporal fossa more than half the distance to the lateral surface of the skull. The pterygoids are separated by an anterior projection of the basisphenoid and do not appear meet each other at the midline. The pterygoid is separated from the jugal by the contact of a dorsal projection of the palatine and a ventral extension of the postorbital.

Basisphenoid.— The basisphenoid is poorly preserved, and only its anterior and lateral sutures are observable. The basisphenoid is roughly triangular in ventral outline, and it is situated between the pterygoids, preventing them from contacting at the midline. Its anterior point extends between the posterior corners of the palatines as well. Its posterior contacts are ambiguous due to surface erosion that obscures the sutures.

Supraoccipital.— The supraoccipital is partially preserved on the left side but is buried in matrix in the right temporal fossa. The posterodorsal portion of the supraoccipital, including the posterior projection and its contributions to the occiput, is missing. In the medial wall of the temporal fossa, it contacts the parietal both anteriorly and dorsally, and it contacts the prootic and opisthotic ventrally.

The supraoccipital contacts the parietal along an L-shaped suture that travels dorsally and then bends posteriorly to travel parallel to the contour of the skull roof. Its contacts with the prootic and opisthotic lie along an erratic anteroposterior suture. Other than preserving its substantial contribution to the medial wall of the temporal fossa, the supraoccipital is not sufficiently represented to enable a detailed description of its shape and significance.

Opisthotic.— The opisthotic is exposed and partially preserved on the left side, where the temporal fossa is not filled with matrix. It is bounded by a medial contact with the supraoccipital, a brief anterior contact with the prootic, and a lateral contact with the quadrate. The posterior portion of the opisthotic is missing, and any contact with the exoccipital or squamosal is not observable.

Prootic.— The prootic is present and exposed on the left side, but it is poorly preserved and possesses little diagnostic value. It is bounded dorsally by contact with the ventral extension of the parietal along a suture that runs parallel to the skull roof. Posterodorsally, it contacts the supraoccipital along a suture that runs posterolaterally from its contact with the parietal. It contacts the pterygoid anteriorly, but fracturing and the presence of matrix obscure the details of this margin. Posteriorly, it has a small contact with the opisthotic, and posterolaterally it contacts the quadrate. The foramen stapedio-temporale is located on the quadrate-prootic suture.

Shell

The dorsal surface of the shell follows a continuous curve in lateral view from its anterior margin all the way to the posterior edge of the pygal. The ventral surface is nearly flat in this view, with a slight dorsal curvature at both the anterior and posterior ends. The carapace extends beyond the anterior and posterior ends of the plastron. The length of the posterior overhang of the carapace is about twice its anterior overhang. In anterior profile, the carapace is moderately domed, and the plastron is flat. The bridge between them angles ca. 35 degrees dorsally from the ventral surface.

The carapace is roughly ovoid in dorsal view, with the anterior end gently squared off and the posterior

end slightly pointed. The anterior border has a slight emargination at the nuchal. The carapace is transversely widest at the posterior end of the bridge, based on projections from the intact sections of the outline. Anterior to the middle of the bridge, the dorsal outline of the carapace tapers gradually. Posteriorly, it tapers more abruptly, forming the mildly pointed tail end. The carapace is composed of the nuchal, six neurals, eight costals, 11 peripherals on each side (22 total), the pygal, and the suprapygal. The first costal is anteroposteriorly elongate compared to the other seven. The first five costals contact neurals medially, but costals 6–8 meet at the midline between neural 6 and the suprapygal. The pygal and suprapygal have nearly the same transverse dimension, but the anteroposterior axis of the suprapygal is roughly 15 percent longer than that of the pygal.

Sulci for twelve marginal scutes line the perimeter of the carapace, completely enclosing the vertebral and pleural scutes. There are sulci for four pleural scutes generally covering the costals and five vertebral scutes along the midline.

The plastron has a broad, short anterior lobe that has an evenly rounded anterior margin. The posterior lobe of the plastron is evenly tapered with flat lateral edges. It possesses a deep U-shaped anal notch and is approximately twice as long as the anterior lobe. However, because the hypoplastra are missing, the posterior lobe is incomplete. Its length can only be estimated through comparison to related species. The midline sutures of the xiphiplastron and hyoplastron are nearly identical in length. The medial axis of the entoplastron is about 2/3 that length, whereas the midline contact of the epiplastra is very short, only about 1/5 the length of the hyoplastron midline suture. Based on the relative position of the xiphiplastron, which we determined by its pelvic connection to the carapace, the midline contact of the hypoplastra appears to be the longest, ca. 25 percent larger than the midline sutures of the xiphiplastra and hyoplastra. The mesoplastron is moderately sized, with its transverse and anteroposterior axes nearly equal in length, being about 1/2 the length of the midline suture between the hypoplastra.

The scute sulci are only partially preserved on the plastron, but enough are present to reconstruct the general pattern. A broad, short intergular scute is encompassed laterally by the gular scutes that curve anteriorly and appear to nearly meet medially. The humeral scutes also appear to curve anteriorly and meet each other at the midline for at least most of their medial margin. The abdominal scute overlays the mesoplastron except for the lateral tip of the mesoplastron, which is covered by marginal 6. The anal scute covers only

the posterior 2/3 of the total anteroposterior length of the xiphiplastron. The lengths of the abdominal and femoral scutes are not preserved.

Nuchal.— The nuchal is completely preserved and retains well-defined sulci of the first marginal scutes. It contacts peripheral 1 along a roughly straight suture that slants medially from the edge of costal 1 to the anterior rim of the shell. It contacts neural 1 along the middle 1/3 of its posterior margin in an anteriorly convex suture. Lateral to the neural contact and posterior to the peripheral contact, the nuchal contacts costal 1 along a slightly convex edge that slants anteriorly from the anterior corner of the neural. The nuchal is about 1.5 times greater in its transverse dimension than in its midline length. It has a concave anterior edge that produces the emargination of the anterior carapace. Well-defined sulci of the first marginals show a slight contact between them.

Pygal.— The pygal is preserved with well-defined edges and terminal marginal scute sulci partially preserved. It contacts the suprapygal anteriorly and peripheral 11 laterally. It forms the posterior point of the carapace. In outline it is a nearly regular, anteriorly tapered trapezoid with the anterior edge just over 1/2 the length of the posterior edge and the length of the medial axis about midway between the two. Its anterior margin is concave, and its posterior margin is convex.

Suprapygal.— The suprapygal is heavily reconstructed. It lacks its central portion but preserves nearly all its outline. It contacts the pygal along a posteriorly convex suture. It contacts the entire posterior edge of costal 8 along a line that slants medially from the edge of peripheral 11 and then curves to meet the midline nearly perpendicularly at the anterior point of the suprapygal. Between the posterior corner of costal 8 and the anterior corner of the pygal, it contacts the middle of the medial edge of peripheral 11 along a suture angled ca. 45 degrees to the midline. In outline, the suprapygal is roughly an anterior pointing isosceles triangle with its posterolateral corners truncated and its anterior corner rounded off. It is roughly as long as it is wide.

Neurals.— Portions of the posteriormost three neurals are preserved. Not enough material remains to make a definite observation of the number or shape of the missing anterior neurals, but there appear to have been a total of six neurals. Neural 1 contacts the nuchal anteriorly, costal 1 laterally, and neural 2 posteriorly. Subsequent neurals, in contrast, contact a pair of costal elements on each side. For example, neural 2 contacts costals 1 and 2, neural 3 contacts costals 2 and 3, etc.

From the presence of the edges of surrounding bones, it appears that neural 1 was roughly rectangular in shape with four slightly convex sides. The outlines of

neurals 2 and 3 are not preserved. Neurals 4 and 5 are hexagonal with concave anterior margins, and anterior lobes significantly shorter than the posterior lobes. Neural 6 is pentagonal in outline. All of the neurals appear to have been about the same width, but neural 6 appears to be the shortest along its midline and is about as wide as it is long.

Costals.— All eight left costals are at least partially preserved, and their missing portions can be confidently reconstructed. Costal 1 contacts the nuchal and peripherals 1–4 anteriorly and laterally. It contacts neurals 1 and 2 medially and costal 2 posteriorly. Costal 2 contacts costal 1 anteriorly, costal 3 posteriorly, neurals 2 and 3 medially, and peripherals 4 and 5 laterally. This sets up the pattern for most of the remaining costals, with costal 3 contacting costals 2 and 4, neurals 3 and 4, and peripherals 5 and 6. Costals 6–8 vary from this pattern by contacting their opposite on the midline. Costal 8 further differs by contacting the suprapygal posteriorly.

Costal 1 is much larger than the rest and possesses a broad, dorsally convex surface. Its lateral edge is curved parallel to the anterior corner of the shell. The scute sulci are well preserved on costal 1. They are only partially preserved on the remaining costals, but enough to reconstruct the pleural scute pattern. Costals 2–6 are roughly rectangular, transversely oriented straps that provide most of the dorsal curvature of the shell. Costals 7 and 8 curve toward the posterolateral margin of the shell and are significantly expanded laterally.

Peripherals.— All peripherals except 7 and 8 are at least partially preserved between the two sides of the shell. They preserve distinct scute sulci. Dorsally, each peripheral contacts the previous and subsequent peripheral, with peripherals 1 and 11 contacting the nuchal and pygal medially, respectively. Peripherals 1–3 contact only the first costal, and all posterior to these are offset with respect to the costals such that each peripheral shares near equal contact with two abutting costals. Ventrally, peripherals 3–5 contact the hyoplastron. Peripheral 2 may also contact the hyoplastron, but this relationship is not preserved. Peripherals 5 and 6 contact the mesoplastron and peripherals 7 and 8 likely contact the hyoplastron, but this relationship is not preserved either.

The dorsal surface of each peripheral is essentially rectangular with a slightly convex side opposite its perimetric edge. Peripherals 1 and 2 are also somewhat enlarged compared to those in the middle of the series. Although the perimetric lengths of the peripherals do not vary greatly, the dorsally exposed surface area generally increases posteriorly. The shapes of the ventral surfaces of the peripherals are more variable with those that contribute to the bridge conforming to

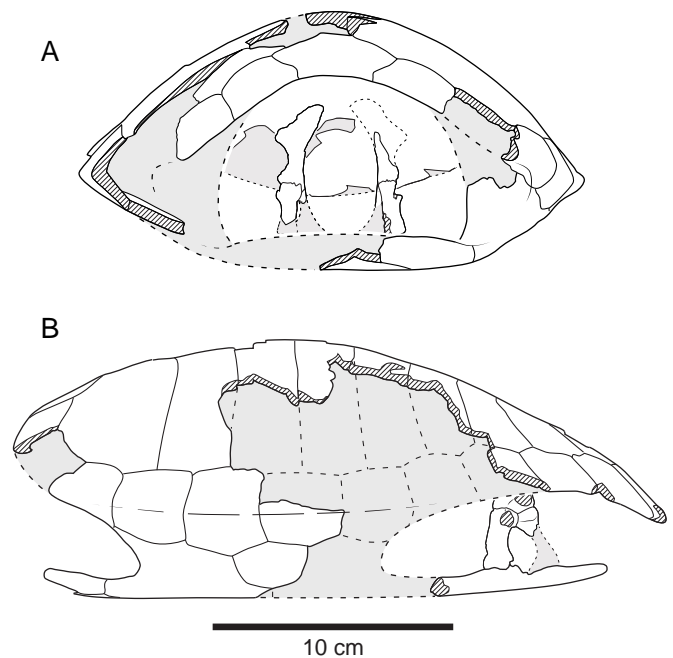


FIGURE 7 — *Cordichelys* aff. *antiqua* (CGM 42191). Line drawing reconstruction of shell in anterior (A) and left lateral (B) views. Dashed lines represent the reconstructed outline and sutures. Note that the dorsal curvature contrasts with the previous descriptions of *Cordichelys* as being either highly domed anteriorly and flattened posteriorly (Andrews, 1906) or remarkably flat (Reinach, 1903; Wood, 1971). See Figure 13 for a reinterpretation of the profile of the YPM 7457 shell.

the shapes of the plastral bones they contact.

Marginal scutes.— Marginal scute sulci are preserved on every peripheral present. On the dorsal surface, the marginals contact each other around the perimeter of the carapace. Marginal 1 contacts the first vertebral scute over the entirety of its anterior edge. Marginals 2–5 contact the first pleural scute. Marginals 5–7 contact the second pleural. Marginals 7–9 contact the third pleural. Marginals 9–11 contact the fourth pleural. Breaking from the pattern, marginals 11–12 contact the fifth vertebral scute. On the ventral surface, marginals 3–5 contact the pectoral scute. The remainder of the ventral relationships is not preserved.

The marginal scutes are generally smaller than the peripheral bones that they overlay, and as a result the preserved sulci are confined to the peripherals except where the ventral edge of marginals 5 and 6 passes briefly through the hyoplastron and mesoplastron, respectively. On the dorsal surface, the medial edge of the anterior marginals is determined by the shape of the contacting pleural, whereas posteriorly, the marginals control the contour of the contact with medial convexity that gives a scalloped lateral edge to pleural 4 and

vertebral 5.

Pleural scutes.— The pleural scute sulci are only partially preserved, but enough are present to observe their general pattern. There are four that contact the marginals peripherally and the vertebral scutes medially. See the description of the marginal scutes for a precise listing of those contacts. The pleurals are offset anteroposteriorly with respect to the vertebrals such that each pleural shares a margin with two vertebrals (pleural 1 with vertebrals 1 and 2, pleural 2 with vertebrals 2 and 3, etc.). The pleurals become progressively smaller posteriorly and are confined to overlapping the costals and marginals. The medial edges of the peripherals do not overlap the nuchal, neurals, suprapygal, or pygal bones.

Vertebral scutes.— The vertebral scute sulci are partially defined and preserve the general pattern and relationships of the vertebral scutes. Anteriorly, vertebral 1 contacts marginal 1. Posteriorly, vertebral 5 contacts marginals 11 and 12. Laterally, the vertebral scutes all contact pleural scutes. For a detailed breakdown of these contacts, see description of the pleurals above.

Vertebral 1 is wider than the nuchal underneath. It also covers most of neural 1 and the anterior corner of costal 1. Vertebrals 2–4 cover the remainder of the neurals and at least part of the medial ends of all eight costals. Vertebral 5 is almost twice as wide as the suprapygal that is centered beneath it. The vertebral scutes form a row on the midline that resembles a lobster tail, gradually tapering posteriorly through vertebrals 1–4 and then flaring out at vertebral 5, which is about as wide as vertebral 1. Each vertebral is nearly equal in length along the midline.

Epiplastron.— The right epiplastron is complete, but none of the bones that contact it are preserved on that side. The left epiplastron is less complete than the right but preserves more of the articulation with the hyoplastron and entoplastron. The epiplastron contacts the hyoplastron posteriorly, the entoplastron posteromedially, and its opposite at the midline.

The epiplastron has a smoothly curved anterior margin and is slightly upturned at its anteromedial tip. The midline suture between the epiplastra is short, about 1/5 of the midline length of the hyoplastron. The suture between the hyoplastra and epiplastra contains a posterior projection that is only visible on the visceral surface of the plastron (on the external surface, this suture is slightly curved, but lacks the projection). The gular-intergular and gular-humeral sulci are clearly visible on the epiplastron. However, if the humeral-pectoral sulcus crosses the epiplastron at any point, it is not well preserved.

Entoplastron.— The entoplastron lacks only the anterior and right edges. It contacts the epiplastron

anterolaterally and the hyoplastron posterolaterally. In ventral outline, the entoplastron is diamond-shaped with slightly convex sides. The humeral-pectoral sulcus meets the midline barely posterior to the center of the entoplastron.

Hyoplastron.— The left hyoplastron has been reconstructed from many small fragments and is nearly completely preserved ventrally and along the bridge, but most of the axillary buttress is missing. It contacts the opposing hyoplastron at the midline, the entire posterolateral edge of the entoplastron anteromedially, and the epiplastron anteriorly. It contacts peripherals 3–5 laterally (and likely peripheral 2, though the contact is not preserved). Posteriorly, it contacts the hypoplastron medially and the mesoplastron laterally, in the bridge. At the bridge, the hyoplastron bends dorsally at ca. 35 degrees to its ventral surface. Due to extensive reconstruction, the flatness of the ventral surface of the hyoplastron cannot be assessed.

Mesoplastron.— The mesoplastron is complete and well preserved on both sides. It contacts the hyoplastron anteromedially, the hypoplastron (not preserved) posteromedially, the fifth peripheral anterolaterally, and the sixth peripheral posterolaterally. The mesoplastron is an irregularly hexagonal “shield” shape roughly symmetrical on its long axis, which is oriented perpendicular to the midline of the shell. It spans the entire plastral portion of the bridge and meets two peripherals along its anterolateral and posterolateral edges. Its anterior and anteromedial edges meet the hyoplastron, and its posterior and posteromedial edges meet with the hypoplastron. It is flat and does not participate in the bent transition between the ventral surface of the plastron and the bridge.

Hypoplastron.— The hypoplastron was not preserved.

Xiphiplastron.— Both sides of the xiphiplastron are complete and nearly perfectly preserved, retaining the entire outline of the xiphiplastron, as well as all four ventral pelvic scars, and well defined anal-abdominal sulci. The xiphiplastron contacts the hypoplastron (not preserved), the opposing xiphiplastron, the pubis, and the ischium. It forms a posteriorly slanting (ca. 10 degrees from perpendicular to the midline axis of the shell) transverse suture with the hypoplastron at its anterior edge and contacts its opposing xiphiplastron along the midline.

The maximum transverse width of the xiphiplastron is about 120% its total anteroposterior length. The lateral outline of the xiphiplastron tapers posteriorly and has two posterior projections with rounded tips and a deeply concave emargination between them. The posterior half of the xiphiplastron gently curves dorsally and the tips of the posterior projections are curved

slightly more dorsally. The anal-abdominal sulcus runs parallel to the anterior margin of the xiphiplastron and meets the midline just anterior to the halfway point along the medial suture.

Pubic and ischial scars are clearly preserved on the dorsal surface of the xiphiplastron. The ischial scars are very close to the margin of the anal notch and nearly meet medially. The long axis of the pubic scars is angled ca. 30 degrees to the midline with the posterior end more laterally positioned. The spacing between the middle of the pubic scars is roughly equal to the spacing between the tips of the xiphiplastral projections. Anteroposteriorly, the pubic scars are centered midway along the midline suture of the xiphiplastron.

Intergular scute.— Sulci for the intergular scute are not completely preserved. It clearly contacts the gular scute laterally, but it may or may not have contacted the humeral scutes. Reconstruction based on preserved sulci shows it as a transversely wide and anteroposteriorly short triangle with convex sides. It covers the medial contact of the epiplastra and the anterior corner of the entoplastron. Its anterior edge meets the margin of the plastron.

Gular scute.— The gular scute sulci are preserved only on the epiplastron. Their posterior and medial contacts cannot be observed. On the epiplastron, it meets the margin of the anterior lobe of the plastron, and contacts the intergular medially and humeral laterally. Because sulci are not preserved on the anterior corner of the entoplastron, it is unclear whether the gulars contacted each other medially or were separated by a posterior extension of the intergular. The intergular-gular and gular-humeral sulci curve anteriorly.

Humeral scute.— The humeral scute is only partially defined by distinct sulci on the entoplastron and epiplastron. If they overlapped the hyoplastron at all, it is not preserved on the specimen. The humeral contacts the gular anteromedially and the pectoral posteriorly. It contacts the opposing humeral at least posteriorly along the midline, but its relationship with the intergular is not preserved in this specimen.

The sulcus crossing near the epiplastral-hyoplastral suture is not well preserved. It may have curved posteriorly terminating at the lateral margin of the hyoplastron. Alternatively, it might have curved anteriorly in the same manner as the intergular-gular and gular-humeral sulci. The posteromedial corner of the humeral is barely posterior to the center of the entoplastron.

Pectoral scute.— Most of the sulci defining the edges of the pectoral scute are preserved on the hyoplastron, entoplastron, and fourth peripheral. The pectoral contacts the humeral scute along an edge described above. It contacts the opposing pectoral along the midline at an

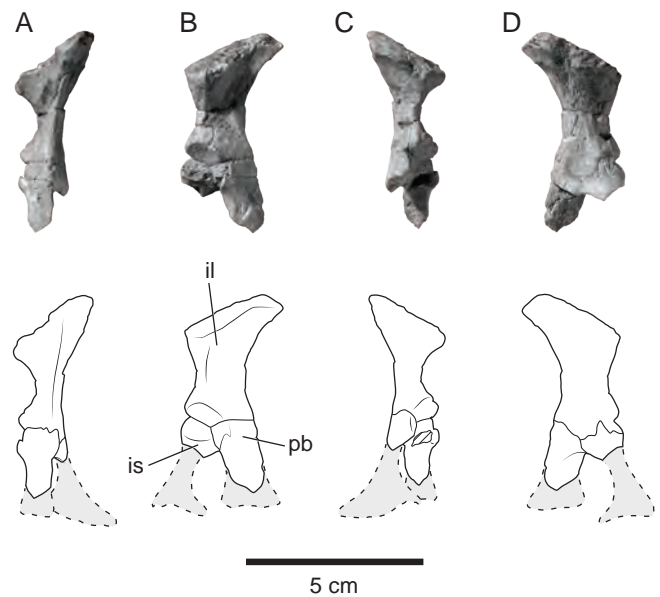


FIGURE 8 — *Cordichelys* aff. *antiqua* (CGM 42191). Photos (top) and line drawings (bottom) of right pelvis in anterior (A), medial (B), posterior (C), and lateral (D) views. Drawings are based on physical reconstructions of both pelvises. The length and shape of the pubis are based on the nearly complete left pubis. The shape of the ischium was based on the size and shape of the ischial scar, whereas the length of the reconstructed ischium is the distance to the ischial scar with the pubis and ilium aligned on the carapace and plastron. The reconstructed pelvises aided in determining the dorsal curvature of the shell. Dashed lines and gray tone indicate reconstructed bone. Abbreviations: *il*, ilium; *is*, ischium; *pb*, pubis.

edge that begins in the middle of the entoplastron and travels posteriorly about two thirds of the way down the midline suture of the hyoplastra. It contacts marginals 4 and 5 laterally (and likely marginal 3 as well, although this is not preserved) along a sulcus that passes over the hyoplastron posteriorly and at least peripheral 4 (possibly peripheral 3 as well) anteriorly. The pectoral meets the abdominal posteriorly along a wavy sulcus that starts at the midline and travels laterally until the bridge, where it curves posteriorly and nearly meets the anterolateral point of the mesoplastron. The pectoral covers the anterior portion of the hyoplastron, and overlaps one quarter of the entoplastron, and the edge of the fourth and possibly more anterior peripherals.

Abdominal Scute.— Only the anterior and lateral edges of the abdominal are preserved by distinct sulci on the hyoplastron, mesoplastron, and peripherals 5 and 6. The abdominal scute contacts the pectoral along its anterior margin, marginals 6 and 7 along its lateral edge, and briefly contacts marginal 5 at its anterolateral corner. All other contacts cannot be observed.

The outline of the abdominal cannot be determined

because the hypoplastra are missing, but it appears to cover the posterior portion of the hyoplastron, nearly the entire mesoplastron, the anterior portion of the hypoplastron and the ventromedial edges of at least peripheral 6 (and possibly subsequent peripherals). The anterior margin of the abdominal scute is the posterior margin of the pectoral and is described above. The lateral margin begins slightly anterior to the anterolateral point of the mesoplastron and barely crosses the lateral point of the mesoplastron and continues across the medial point of peripheral 6. Posterior to peripheral 6, it cannot be observed.

Femoral scute.— The femoral scute is only defined by the presence of the femoral-anal sulcus on the xiphoplastron. Its posterior contact with the anal scute is preserved and clearly defined, but no other relationships can be determined. The posterior edge of the femoral slants posteriorly from its midline origin parallel to the xiphoplastral-hypoplastral suture. At the very least, it covers the anterior 1/3 of the xiphoplastron and some posterior portion of the hypoplastron.

Anal scute.— The outline of the anal scute is completely preserved. The only contact is with the femoral along a sulcus that travels parallel to the xiphoplastral-hypoplastral suture. The anal scute covers the posterior portion of the xiphoplastron including the posterolateral projection. Its shape is defined by its anterior contact with the femoral and the posterior outline of the xiphoplastron.

Pelvis

The pubis and ilium were both present in their entirety, and the basic shape of the ischium could be reconstructed based on its articulation with those bones and the sutural trace on the plastron. The pelvis were found disarticulated from the shell. The pubis articulates neatly with the pubic scar, but the ilium does not fit well due to spalling in the region of the iliac scar on the carapace.

Because the xiphoplastron was disassociated from the rest of the shell, the upright position of the pelvis had to be estimated by matching the angle of the dorsal articular surface on the ilium with the contour of the carapace at the approximate location of attachment. This estimation is supported by the fit of the pubis into the pubic scar and comparison with *E. madagascariensis*. The pubis and ilium are subequal in length, and the acetabulum is oriented slightly posterolaterally.

Pubis.— The left pubis is nearly complete, lacking only its contact with the plastron and a portion of the margin of the acetabulum. The shape of the distal pubis can be reconstructed based on the sutural scar on the xiphoplastron. Based on this, the pubis is approximately

half as wide in the anteromedial-posterolateral dimension as it is tall. The midsection is compressed with the dorsal and ventral ends slightly enlarged.

Ilium.— The right ilium is completely preserved. As in other pleurodires, it is sutured to the carapace and contacts the pubis and ischium to form the acetabulum. The ilium is subrectangular in cross-section, expanded more anteroposteriorly than transversely. Its distal end, which contacts the carapace, is more expanded than its proximal contact with the other pelvic bones. A sharp ridge is present along its anteromedial edge that extends onto the pubis. The lateral surface is approximately flat. The dorsal surface that meets the carapace is roughly crescent-shaped, with the convex edge oriented posteromedially.

Cordichelys sp., MUV 498 (Figs. 9, 10; Table 1)

Locality.— North of Birket Qarun, western Fayum Province, Egypt, WGS-84 GPS coordinates N29.625300, E30.700630 (Fig. 1).

Formation and age.— Qasr el-Sagha Formation, upper Eocene (middle Priabonian).

Material.— A nearly complete cranium lacking only the premaxillae (Figs. 9, 10). The specimen is housed at the Mansoura University Vertebrate Paleontology center, and a cast has been deposited in the collections of the University of Michigan Museum of Paleontology (UMMP 13994). The specimen possesses the partial secondary palate formed by medial expansion of the maxillae and palatines with a midline cleft between them, which is diagnostic of stereogenyine turtles. Although significantly smaller than the other two *Cordichelys* skulls discussed herein (CGM 42191 and YPM 7457), it shares with them a slight interorbital depression, palatine-postorbital contact that separates the jugal from the pterygoid in the septum orbitotemporale, a moderately well developed secondary palate with curved medial edges of the palatal flanges, and a deep and narrow labial ridge. It differs from them in having a slightly convex triturating surface (a trait shared with the New World genus of *Stereogenyina*, *Bairdemys*), orbits that are not exposed dorsally, a narrow skull approximately 80 percent as wide as it is long (from nose to posterior edge of the squamosal that extends more posteriorly than in other specimens), a concave depression in the posterolateral surface of the squamosal that gives it a pinched appearance posteriorly and forms a sharp dorsoventral ridge along its posterior edge, and a maxillary contribution to the palatal flange nearly equal to that of the palatine, a continuous ridge running from the squamosal across the opisthotic and exoccipital to the occipital condyle (this feature cannot

be observed in CGM 42191). It also has a consistently curved skull roof lacking an inflection at the anterior edge of the parietals, a T-shaped basisphenoid as wide as the basioccipital that separates the pterygoids, and a substantial dorsal projection of the palatine that participates in the septum orbitotemporale and in coordination with the relatively slight projection of the postorbital prevents the jugal from contacting the pterygoid. These final three characters are shared with *Stereogenys cromeri*, but with a skull shape more consistent with *Cordichelys* and dramatically different than *St. cromeri*, it seems unlikely that this small specimen represents an early ontogenetic stage of *St. cromeri*. We think it represents a juvenile form or small species of *Cordichelys*, but without shell material to compare with the appropriately sized holotype of *C. antiqua*, we hesitate to assign it a specific designation at this time.

Cranium

The skull is nearly complete, with slight crushing in the skull roof that caused both parietals to fracture. The right maxilla and both premaxillae are missing and the ventral margin of the jugal and quadratojugal is not preserved on either side. The temporal fossae are clear of matrix, though a thin crust of gypsum obscures surface detail on the interior surface of the right fossa. Most of the sutures are clearly visible, but no scute sulci are discernible due to the rough surface preservation of the specimen. Matrix fills the cavum tympani, obscuring the antrum postoticum and incisura columellae auris.

Like other stereogenyine skulls, MUV 498 has a partial secondary palate consisting of flanges formed by extensions of the maxillae and palatines, and like other *Cordichelys* skulls, the secondary palate is smaller than in *Stereogenys*. The triturating surface of the secondary palate is slightly convex. In anterior view, the lingual ridge is curved up substantially toward the midline. In dorsal view, the outline of the skull is broad posteriorly where its lateral sides are nearly parallel to each other. The anterior half tapers along a consistent curve until it reverses curvature near the snout, where it forms a slightly pinched rostrum. The width of the skull is approximately 80% of the midline distance measured from the tip of the rostrum to the posterior edge of the squamosal. The anterolaterally oriented, ovoid orbits are not exposed dorsally. On the dorsal surface between the orbits, the prefrontals display a shallow midline depression. In lateral view, the skull roof is convex and follows a consistent curvature. The temporal fossa is covered by the parietal and quadratojugal. The posterior edge to the temporal roof is moderately emarginated.

Parietal.— The parietal is complete, but matrix and

a superficial crust of gypsum obscure the sutures inside the temporal fossa. On its dorsal surface, the parietal contacts the frontal and postorbital anteriorly, the quadratojugal laterally, and its opposite medially. On the medial surface of the temporal fossa, the parietal contacts the postorbital anteriorly, and the pterygoid and supraoccipital ventrally.

The frontal-parietal suture is a transverse suture spanning about 2/3 of the total width of the parietal at its widest point. The parietal shares a slightly longer contact with the postorbital along a suture that angles posteriorly at ca. 30 degrees to the midline. It contacts the quadratojugal along a suture nearly parallel to the midline that spans from the lateral end of its contact with the postorbital to the posterior margin of the temporal roof. Its contact with the opposing parietal continues to the posterior margin to the exclusion of the supraoccipital, which does not contribute to the dorsal surface of the skull. The parietal is slightly dorsally convex in the transverse axis but is essentially flat in the anteroposterior axis. It forms more than half of the posterior margin of the temporal roof.

Frontal.— The dorsal surface of the right frontal is complete, but its contacts on the interior surface of the orbit are partially hidden under matrix. On the dorsal surface, it contacts the parietal posteriorly, the postorbital laterally, prefrontal anteriorly, and its opposite on the midline. The frontal contacts the parietal along a transverse suture, the postorbital along a suture that runs anteriorly from the lateral end of the frontal-parietal suture at ca. 20 degrees from the midline until reaching the orbital rim, the prefrontal along a transverse suture from its anteromedial corner to the orbital rim, and the opposing frontal along the full length of its medial edge. The medial suture between the frontals is offset slightly right of the midline at its posterior end. Between its contacts with the postorbital and prefrontal, the frontal participates in the orbital rim for approximately the middle third of the orbit. Its dorsal surface is slightly dorsally convex, both in transverse and anteroposterior cross-section.

Prefrontal.— Both prefrontals are nearly complete, lacking only their anterior margin. The prefrontal contacts the maxilla anterolaterally, its opposite on the midline, and the frontal posteriorly along a transverse suture. In dorsal view, the prefrontals taper anteriorly, forming a rounded tip. They are slightly dorsally convex in lateral profile and form a slight midline depression between the orbits. The prefrontal forms the dorsal half of the anterior 1/3 of the orbital margin.

Quadratojugal.— The quadratojugal is nearly complete, missing only a small amount from ventral margin of the temporal roof. It contacts the parietal medially, the postorbital and jugal anteriorly, the

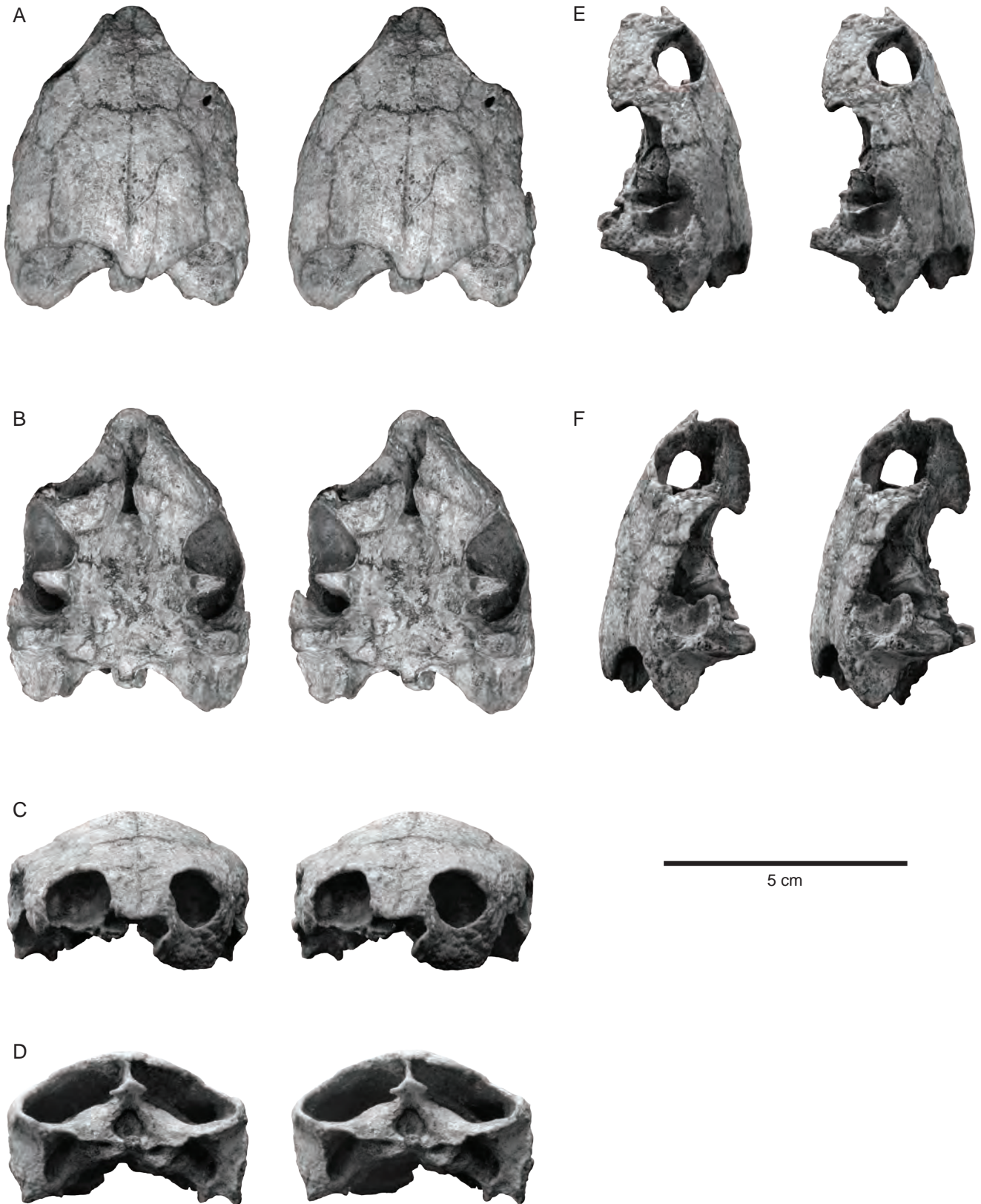


FIGURE 9 — *Cordichelys* sp. (MUV 498). Stereophotographs of skull in dorsal (A), ventral (B), anterior (C), posterior (D), left lateral (E) and right lateral (F) views.

quadrate posterolaterally, and the squamosal at its posterolateral corner. The quadratojugal contacts the parietal along a suture nearly parallel to the midline from the posterior edge of the temporal roof to the postorbital anteriorly. The contact with the postorbital runs ca. 45 degrees to the midline from the parietal to the jugal. The quadratojugal meets the jugal along a dorsoventral suture from the postorbital to the ventral margin of the temporal roof. It contacts the quadrate in a curved suture that starts at the ventral margin of the temporal roof, travels dorsally, and then curves around the cavum tympani traveling posteriorly until it meets the squamosal. The quadratojugal and parietal form nearly the entire temporal roof. The quadratojugal is L-shaped with its anterior and dorsal edges forming a right angle. It separates the quadrate from the parietal dorsally and the postorbital from the jugal anteriorly.

Quadrate.— The quadrate is nearly complete lacking only the anterior portion of the cavum tympani. The cavum tympani is filled with matrix obstructing inspection of the antrum postoticum and incisura columellae auris. On the lateral surface, the quadrate contacts the quadratojugal anteriorly and dorsally, and the squamosal posteriorly. On the ventral surface, it contacts the squamosal and opisthotic posteriorly, the basioccipital and basisphenoid medially, and the pterygoid anteriorly. On the internal surface of the temporal fossa, it contacts the pterygoid anteriorly, the prootic and opisthotic medially, and the squamosal posteriorly.

Its contribution to the lateral portion of the temporal roof is almost exclusively bounded by the quadratojugal, which separates it from the jugal and the parietal. The squamosal contacts it for about half of its total dorsoventral height. The quadrate-squamosal suture travels posteroventrally from the quadratojugal and then curves around the ventral side and travels back dorsally until meeting the opisthotic.

On the ventral surface of the skull, the contact between the quadrate and pterygoid follows a suture that travels anteriorly from the basisphenoid briefly before turning posterolaterally to pass around the posterior margin of the cavum pterygoideus and then dorsally up into the temporal fossa where it meets the prootic. The medial margin of the quadrate on the ventral surface includes a brief contact with the basisphenoid and an even smaller contact with the basioccipital. Its posterior margin ventrally is split almost evenly between its contacts with the opisthotic and squamosal.

On the ventral surface of the temporal fossa, the quadrate meets the opisthotic and the prootic along a suture roughly parallel to the midline. Its contact with the pterygoid travels dorsally and slightly anteriorly until meeting the prootic. The quadrate and squamosal

contact along a suture that travels from the opisthotic ca. 45 degrees to the midline. The surfaces for jaw articulation are strongly concave on the transverse axis and significantly extended ventrally.

Squamosal.— The squamosal is completely preserved. It attaches to the posterior edge of the quadrate, contacting the quadrate, opisthotic, and quadratojugal. The squamosal primarily consists of a thin flange of bone that forms the posterolateral corner of the floor of the temporal fossa. It meets medially with the opisthotic on a surface that is exposed dorsally due to emargination in the posterior edge of the temporal roof. Its posterolateral surface is slightly concave and it forms a dorsoventral ridge along the posterior of the quadrate, lateral to the fenestra postotica.

Jugal.— The jugal lacks only the ventral portion that forms the margin of the temporal roof. On the lateral surface, the jugal contacts the maxilla anteriorly, the postorbital dorsally, and the quadratojugal posteriorly. On the septum orbitotemporale, it contacts the palatine ventrally and posteriorly, and it contacts the postorbital dorsally.

On the dorsal surface of the skull, the jugal-postorbital contact travels along a straight suture roughly parallel to the midline from the quadratojugal to the orbital rim. It contacts the quadratojugal along a straight dorsoventral suture that travels from the postorbital to the ventral margin of the temporal roof. The suture between the jugal and maxilla runs anterodorsally to the posterior rim of the orbit.

The jugal forms a small section of the posterior rim of the orbit. It also participates in the ventrolateral corner of the septum orbitotemporale meeting the maxilla ventrolaterally and the palatine ventromedially. Its participation in the septum orbitotemporale is limited in this species primarily by a dorsal projection of the palatine that encompasses its ventral and medial edges. It has only a brief dorsomedial contact with the postorbital in the septum.

Postorbital.— The postorbital is complete with well-defined borders. On the dorsal surface, the postorbital contacts the parietal posteromedially, the quadratojugal posterolaterally, the jugal anterolaterally, and the frontal anteromedially. In the septum orbitotemporale, it contacts the pterygoid and parietal posteriorly, the palatine ventrally, and the jugal anteroventrally.

The jugal-postorbital suture parallels the midline. The postorbital contacts the frontal along a suture that starts at the rim of the orbit and points directly toward the posteromedial corner of the parietal. Its margin with the parietal travels ca. 45 degrees to the midline from the frontal to the quadratojugal. Its shortest contact dorsally is with the quadratojugal. This contact is slightly shorter than the participation of the postorbital

in the orbital rim of which it forms the posterior 1/3 of the dorsal side.

The postorbital and frontal form most of the roof of the orbit. The postorbital contributes to the septum orbitotemporale, but the bone primarily responsible for separating the jugal from the pterygoid is the palatine. The postorbital only briefly contacts the jugal in the septum orbitotemporale slightly dorsally of palatine-jugal contact.

Maxilla.— The right maxilla is missing, but the left one is completely preserved. On the exterior surface of the skull, the maxilla contacts the jugal posteriorly, and although the premaxilla is missing, the edge of the maxilla where it contacts the premaxilla is complete. On the palate, the maxilla contacts the palatine posteriorly and the premaxilla anteromedially.

The maxilla contacts the jugal along a suture traveling from the posteroventral edge of the orbit to the posterior edge of the maxilla at the corner between the posterior edge of the labial ridge and the ventral surface of the palate. On the ventral surface, it contacts the palatine along a slightly anteriorly convex suture that runs posterolaterally from the medial edge of the palatal flange at ca. 20 degrees from the transverse axis. The maxilla appears to have contacted the premaxilla along the anterior half of its medial flange. A dorsal extension of the maxilla forms the lateral wall of the external nares and then contacts the prefrontal along its dorsal edge.

The lateral surface of the maxilla consists of the labial ridge ventrally and the margin of the orbit dorsally. The labial ridge takes up about half of the total dorsoventral height of the suborbital portion of the maxilla. The maxilla forms almost half of the palatal flange. It also forms a substantial amount of the orbital floor and the enclosed nasal cavity. In ventral view, the lateral edge of the maxilla is convex at its posterior end and concave anteriorly, where it forms the slightly pinched snout.

Palatine.— The palatine is nearly completely preserved. On the ventral surface, the palatine contacts the maxilla anteriorly, the pterygoid posteriorly, the basisphenoid posteromedially, and the opposing palatine anteromedially, although its medially extended flanges do not contact each other. On the medial surface of the temporal fossa, it contacts the jugal anteriorly, the postorbital dorsally, and the pterygoid posteriorly (Fig. 10).

On the ventral surface, the palatine contacts the maxilla along an anteriorly convex suture that runs posterolaterally from the medial edge of the palatal flange. It contacts the pterygoid along an erratic suture that travels laterally along the ventral surface and then anterodorsally up the medial wall of the temporal fossa until it meets the ventral extension of the postorbital.

It contacts the basisphenoid along the posterior two thirds of its medial edge, where an anterior extension of the basisphenoid injects itself between the palatines. Dorsal to the palatal flange and anterior to the palatine-basisphenoid contact, the palatine contacts its opposing palatine along the midline. The anterior end of this contact is not preserved.

The palatine contribution to the medial wall of the temporal fossa is extensive and elaborate. It forms the ventral and posterior boundaries of the jugal and meets the ventral extension of the postorbital approximately half way up the septum orbitotemporale, thus preventing jugal-ptyerygoid contact. Its dorsal extension forms a point that wedges between the jugal and postorbital nearly preventing their contact in the septum orbitotemporale. A medial expansion of the palatine contributes nearly equally with the maxilla to form the palatal flange. The ventral surface of this flange is mildly convex. The medial edge of this flange curves laterally from the anterior corner of the palatine and does not travel parallel to the opposing palatal flange.

Pterygoid.— The pterygoid is nearly completely preserved, missing only the ventral pterygoid flanges. On the basicranium, the pterygoid contacts the palatine anteriorly, the basisphenoid medially, and the quadrate posteriorly. On the medial surface of the temporal fossa, the pterygoid contacts the palatine and postorbital anteriorly, the parietal dorsally, and the quadrate posteriorly. It also likely meets the prootic between its contacts with the quadrate and parietal, but this relationship is hidden by a layer of gypsum on the surface of the bone. It does not contact the jugal.

On the ventral surface, the pterygoid contacts the palatine along an erratic transversely oriented suture. The medial edge of the pterygoid meets with the basisphenoid along a suture that is parallel to the midline except for at its posterior end, where it curves laterally and meets the quadrate. On the ventral surface, the quadrate forms the posterior margin of the pterygoid along a suture that wraps around the posterior margin of the cavum pterygoideus and barely meets the anteromedial corner of the mandibular articulation of the quadrate before heading into the temporal fossa.

On the medial wall and ventral floor of the temporal fossa, the pterygoid has a convex anterior suture that it shares equally with the dorsal extension of the palatine and the ventral extension of the postorbital. It contacts the quadrate along an anterior-leaning dorsomedially oriented suture. Its contacts with the parietal and prootic are partially covered in a superficial layer of gypsum and are not exposed enough to give detailed descriptions.

The trochlear process extends laterally about 2/3 the

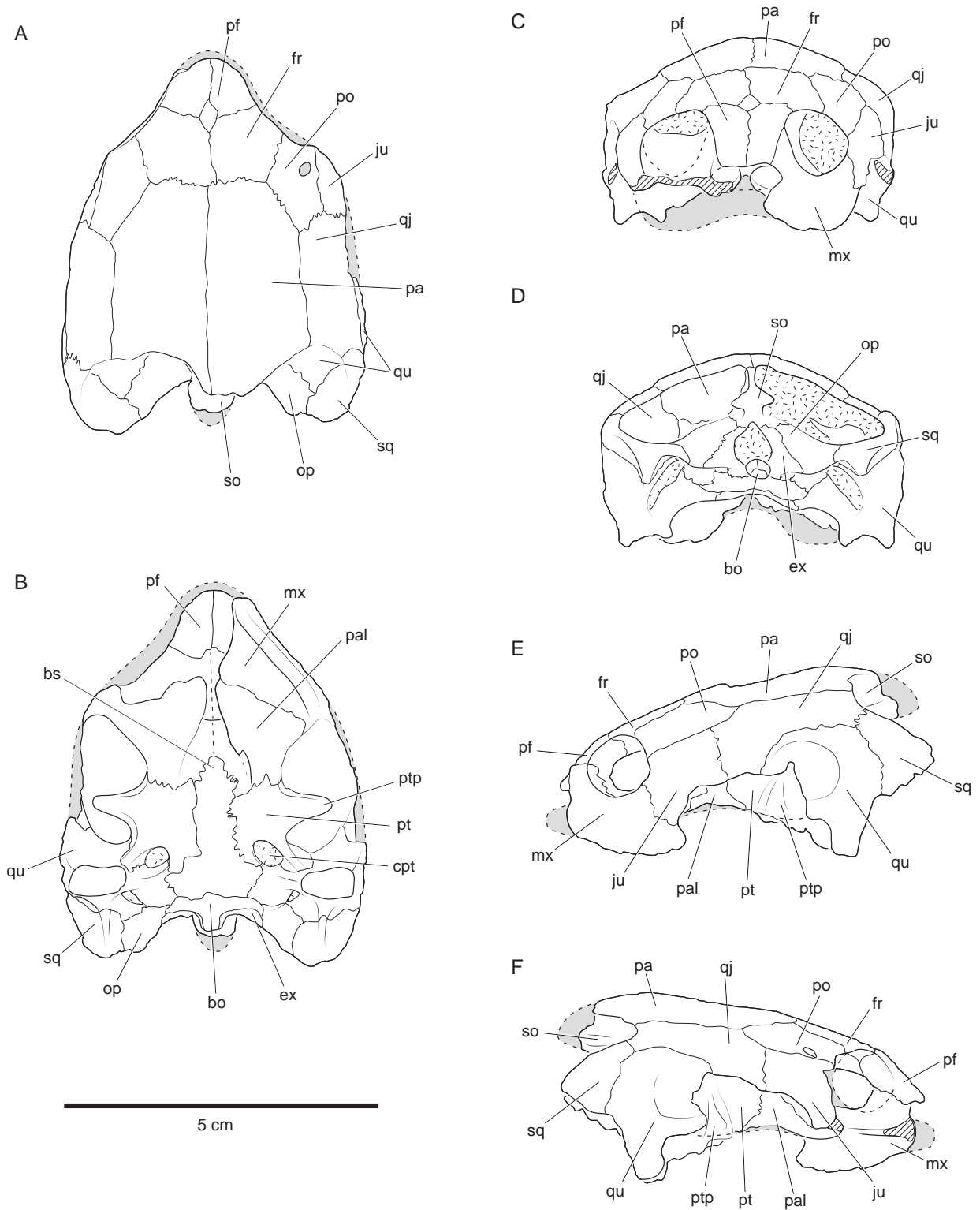


FIGURE 10 — *Cordichelys* sp. (MUV 498). Line drawings of skull in dorsal (A), ventral (B), anterior (C), posterior (D), left lateral (E), and right lateral (F) views. Hatched lines indicate broken surface; dashed lines and gray tone indicate reconstructed bones; stipple indicates matrix. Abbreviations: *bo*, basioccipital; *bs*, basisphenoid; *cpt*, cavum pterygoideus; *ex*, exoccipital; *fr*, frontal; *ju*, jugal; *mx*, maxilla; *op*, opisthotic; *pa*, parietal; *pal*, palatine; *pf*, prefrontal; *po*, postorbital; *pt*, pterygoid; *ptp*, processus trochlearis pterygoidei; *qj*, quadratojugal; *qu*, quadrate; *so*, supraoccipital; *sq*, squamosal.

width of the ventral exposure of the temporal fossa. The pterygoid provides all but the posterior edge of the ventral margin of the cavum pterygoideus. Its lateral contribution to this margin forms a ventrally expanded ridge that doubles as a support strut for the ventrally extended jaw articulation of the quadrate.

Basisphenoid.— The basisphenoid is completely preserved. It contacts the basioccipital posteriorly, the quadrate posterolaterally, the pterygoid laterally, and the palatine anterolaterally. The basisphenoid projects anteriorly, preventing medial contact of the palatines and partially separating the palatines as well. It has a unique T-shape in ventral view with lateral extensions at its posterior edge that contact the quadrate laterally. Its anterior extension has parallel edges that only begin tapering when it reaches the palatines. It lacks the sharply pointed triangular outline present in other *Cordichelys* specimens, and its posterior width is about three times the width of the anterior projection.

Supraoccipital.— The supraoccipital appears to be nearly completely preserved, missing only a small portion of its posterior process. It contacts the exoccipitals ventrally at the dorsal margin of the foramen magnum. It contacts the opisthotic posterolaterally, the parietal dorsally and anteriorly, and the prootic anterolaterally, but the prootic-supraoccipital contact is partially obscured and cannot be described in detail.

Its contact with the exoccipital is limited to the rim of the foramen magnum. The supraoccipital-opisthotic suture begins at the exoccipital near the foramen magnum and travels anterolaterally to the prootic. On the medial wall of the temporal fossa, it meets the parietal dorsally and anteriorly, but the region is obscured by a layer of gypsum coating the bone. The posterior extension of the supraoccipital possesses laterally projecting flanges. This posterior extension does not reach as far as the margin of the squamosal. The supraoccipital does not participate in the dorsal surface of the skull.

Opisthotic.— The opisthotic is preserved and its outline is well defined. On the ventral surface of the temporal fossa, the opisthotic contacts the prootic anteriorly, the supraoccipital medially, the quadrate laterally, and the squamosal briefly at the posterior end of its lateral margin with the quadrate. On the occiput, the opisthotic contacts the exoccipital ventromedially. In ventral view, it contacts the squamosal and quadrate, mirroring the contacts on its dorsal surface. It also briefly contacts the basioccipital ventrally just anterior to the exoccipital contact.

The opisthotic forms the major portion of the posteroventral margin of the temporal fossa. It has a

transversely oriented ridge along its posterior edge that continues medially through the exoccipital to the occipital condyle. The ridge travels laterally through the posterior surface of the squamosal and continues on to become the posterior margin of the quadratojugal and parietal.

Prootic.— The prootic appears to be completely preserved, but its surface and outline is mostly obscured by a layer of gypsum on the internal surface of the temporal fossa (the prootic is located on the internal surface of the temporal fossa and is not visible in the photos or illustrations). Its contacts with the quadrate laterally, opisthotic posteriorly, and supraoccipital medially are exposed and visible through the posterior opening of the temporal fossa. The prootic is small and located immediately anterior to the opisthotic. It prevents the supraoccipital from contacting the quadrate.

Basioccipital.— The basioccipital is completely preserved. It contacts the basisphenoid anteriorly along a short transverse suture and the exoccipitals dorsally along a transverse suture on the occiput. It also briefly contacts the opisthotic and quadrate laterally. On the ventral surface, the basioccipital angles slightly dorsally from the ventral surface posteriorly. Its anterior margin is slightly concave ventrally. On the posterior surface, the basioccipital contributes to the ventral portion of the occipital condyle. It also contributes to the ventral margin and wall of the fossa that contains the foramen nervi hypoglossi.

Exoccipital.— The exoccipital is completely preserved. The exoccipital contacts the supraoccipital dorsally, the opisthotic laterally, and the basioccipital ventrally. The exoccipital forms the major part of the margin of the foramen magnum. It is smaller dorsally where it contacts the supraoccipital and flares ventrally to a transverse ridge that continues through it from the opisthotic ridge to the occipital condyle. It forms the lateral and dorsal portions of the occipital condyle and the dorsal portion of the fossa containing the foramen nervi hypoglossi.

Anomalous bony element.— MUV 498 appears to have a unique additional small bone on the midline at a suture. It is unclear what the significance of this feature is, as it may just be an artifact of crushing. Other fractures on the specimen exhibit the same distinct mineralization that characterize and highlight the sutures. This apparently isolated ‘bone’ may be bounded by some combination of sutures and fractures, giving the illusion of autonomy. However, although it sits at the midline, no suture appears to traverse it.

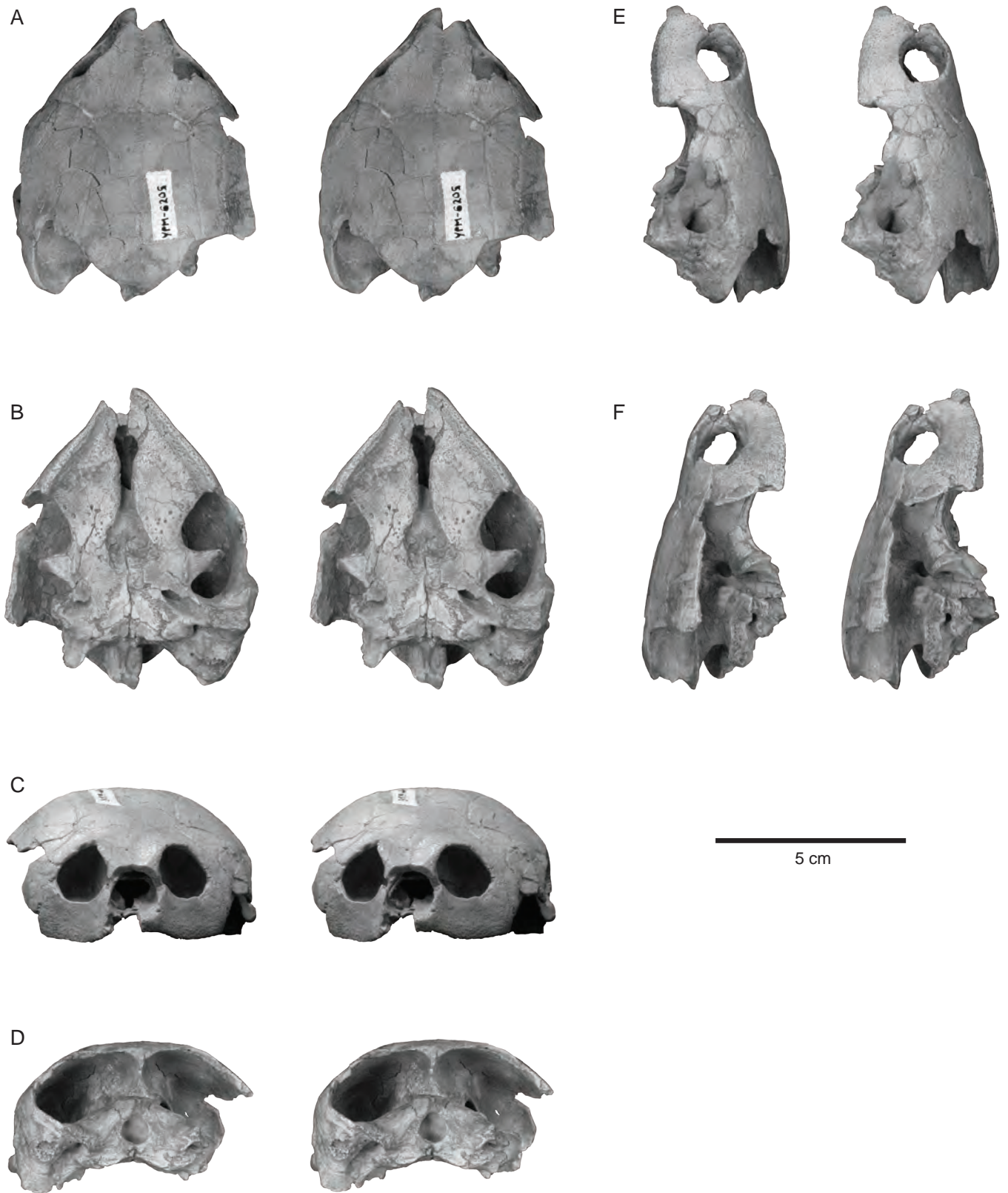


FIGURE 11 — *Cordichelys antiqua* (?) (YPM 7457). Stereophotographs of skull in dorsal (A), ventral (B), anterior (C), posterior (D), left lateral (E), and right lateral (F) views. Specimen also photographed in Wood (1971: pl. 30) and Gaffney et al. (2011: fig. 54). We provide stereophotos for easier comparison with new *Cordichelys* skulls described here.

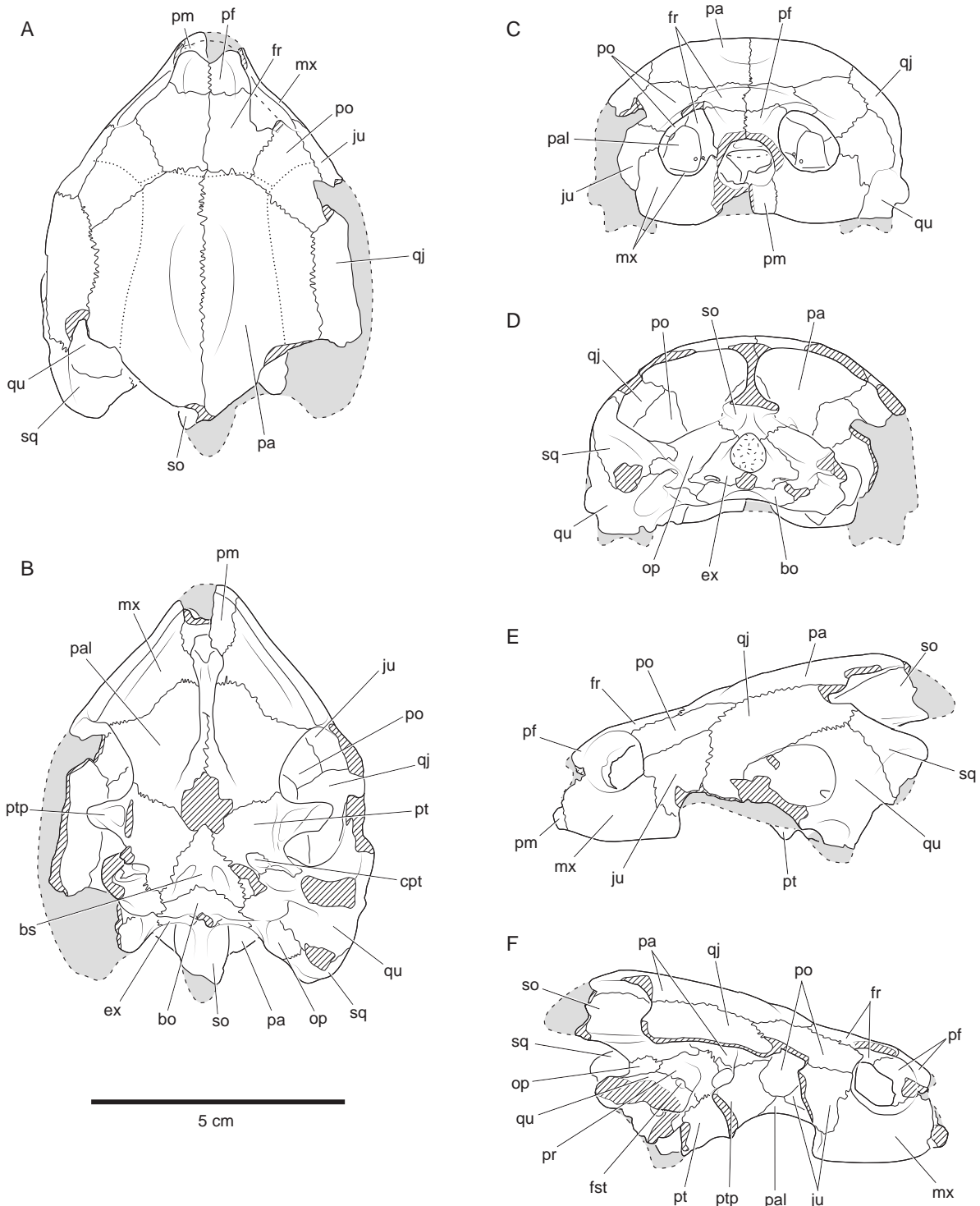


FIGURE 12 — *Cordichelys antiqua* (?) (YPM 7457). Line drawings of skull in dorsal (A), ventral (B), anterior (C), posterior (D), left lateral (E), and right lateral (F) views. Specimen also illustrated in Wood (1971: fig. 26) and Gaffney et al. (2011: fig. 55). We provide new illustrations for easier comparison with new *Cordichelys* skulls described here. Hatched lines indicate broken surface; dashed lines and gray tone indicate reconstructed bones. Abbreviations: *bo*, basioccipital; *bs*, basisphenoid; *cpt*, cavum pterygoideus; *ex*, exoccipital; *fr*, frontal; *fst*, foramen stapedio-temporale; *ju*, jugal; *mx*, maxilla; *op*, opisthotic; *pa*, parietal; *pal*, palatine; *pf*, prefrontal; *pm*, premaxilla; *po*, postorbital; *pr*, prootic; *pt*, pterygoid; *ptp*, processus trochlearis pterygoidei; *qj*, quadratojugal; *qu*, quadrate; *so*, supraoccipital; *sq*, squamosal.

Cordichelys antiqua(?), YPM 7457
(previously YPM 6205)
(Figs. 11–13)

Locality.— Wadi Al Hitan, western Fayum Province, Egypt (Fig. 1). More precise locality information is not available, as discussed below.

Formation and age.— Birket Qarun Formation, upper Eocene (lower Priabonian) according to Gingerich (1992).

Material.— YPM 7457 includes a complete cranium (Figs. 11, 12), carapace, and plastron that currently serve as the basis for the description of the species *Cordichelys antiqua* and the genus *Cordichelys*. However, its assignment to the species *C. antiqua* is placed in doubt by new specimens described above, each of which provides an alternative candidate skull to pair with the holotypic shell of *C. antiqua*. Skull specimen MUVF 498 lacks associated shell material to compare with the shell-only holotype of *C. antiqua* but was collected from the same locality and formation. Meanwhile, skull and shell specimen CGM 42191 is from the same formation as YPM 7457 but more closely matches the description of the holotypic shell of *C. antiqua* (see Cherney, 2011; Cherney et al., 2011).

YPM 7457 differs from other specimens of *Cordichelys* in having an extensive secondary palate with the margins of the median cleft nearly straight and parallel for half the lengths of the palatal flanges, a depression along the dorsal midline between the parietals, raised edges on the dorsal margin of the orbits, a slightly convex bulge on the frontals, a basisphenoid that does not extend beyond to the trochlear process anteriorly and may not completely separate the pterygoids from contacting one another on the midline, a laterally convex squamosal that has a rounded posterior margin (lacking a dorsoventrally oriented ridge), and a minimal contribution of the palatine to the septum orbitotemporale. In contrast to MUVF 498, the ridge along the posterior edge of the opisthotic slopes ventrally and terminates at the lateral edge of the exoccipital (this trait cannot be identified in CGM 42191). Its shell differs from CGM 42191 in having a nuchal about twice as wide in its transverse axis as it is long on its medial axis, a first vertebral scute that contacts the anterior margin of the carapace between the first two marginals, which do not meet medially, a pygal somewhat narrower than the suprapygal such that the anteromedial edge of peripheral 11 is almost completely contained by the suprapygal, an intergular that extends between the gulars to contact the humerals, and a moderately deep V-shaped anal notch bounded by pointed posterior projections of the xiphiplastron. A heart-shaped outline of the carapace is a consequence

of flattening and contrasts with the more ovoid dorsal outline of the reconstructed carapace of CGM 42191. Connecting carapace and plastron in YPM 7457 would impose significant doming (Fig. 13) consistent with the reconstruction of CGM 42191 (Fig. 7). A full description of this specimen is contained in the descriptions of ‘*Shweboemys antiqua*’ (Wood, 1971) and *Cordichelys antiqua* (Gaffney et al., 2011) and is not repeated here. Although photos and illustrations are available from those publications, we have included stereophotos and new illustrations here to facilitate comparisons.

The locality information for YPM 7457 has been contentious. Wood (1971: 154) recorded it as being from the Qasr el-Sagha deposits of Zeuglodon Valley. However, it is very unlikely that both of these details are correct, because the fossil-bearing beds in Wadi Al Hitan (formerly called Zeuglodon Valley) are of the Birket Qarun Formation, not the slightly younger Qasr el-Sagha Formation. Gaffney et al. (2011: p. 49) commented on this apparent inconsistency and questioned the credibility of the locality information, citing photographs that show a turtle specimen in Qasr el-Sagha deposits that might be this specimen. However, based on one of the authors (PDG) having extensive experience in the Fayum, knowledge of the Yale expedition that retrieved the specimen, and familiarity with the typical preservation for fossils from the Qasr el-Sagha and Birket Qarun deposits, we conclude instead that the assignment to Qasr el-Sagha Formation was in error but the locality (Wadi Al Hitan) correct. Here we list the specimen as being from the Birket Qarun Formation of Wadi Al Hitan.

Cordichelys(?) sp., UM 97531 (ZV 161)
(Fig. 14; Table 1)

Locality.— Wadi Al Hitan, western Fayum Province, Egypt, WGS-84 GPS coordinates N29.271206, E30.024233 (Fig. 1).

Formation and Age.— Birket Qarun Formation, upper Eocene (lower Priabonian) according to Gingerich (1992).

Material.— A mostly complete, well-preserved lower jaw missing only its left ramus (UMMP 97531; Fig. 14A–D) was collected on a UMMP expedition. It is similar to *Stereogenys* in having an expanded triturating surface, which is a feature of *Stereogenyina* (Gaffney and Wood, 2002; Gaffney et al., 2011). Within this group, the lower jaws have previously been reported for four species: *Stereogenys cromeri* (Andrews, 1901, 1906), *Bairdemys venezuelensis* (Sánchez-Villagra and Winkler, 2006), *Bairdemys sanchezi* (Gaffney et al., 2008), and *Bairdemys healeyorum* (Weems and Knight, 2013). The lower jaws of these species differ

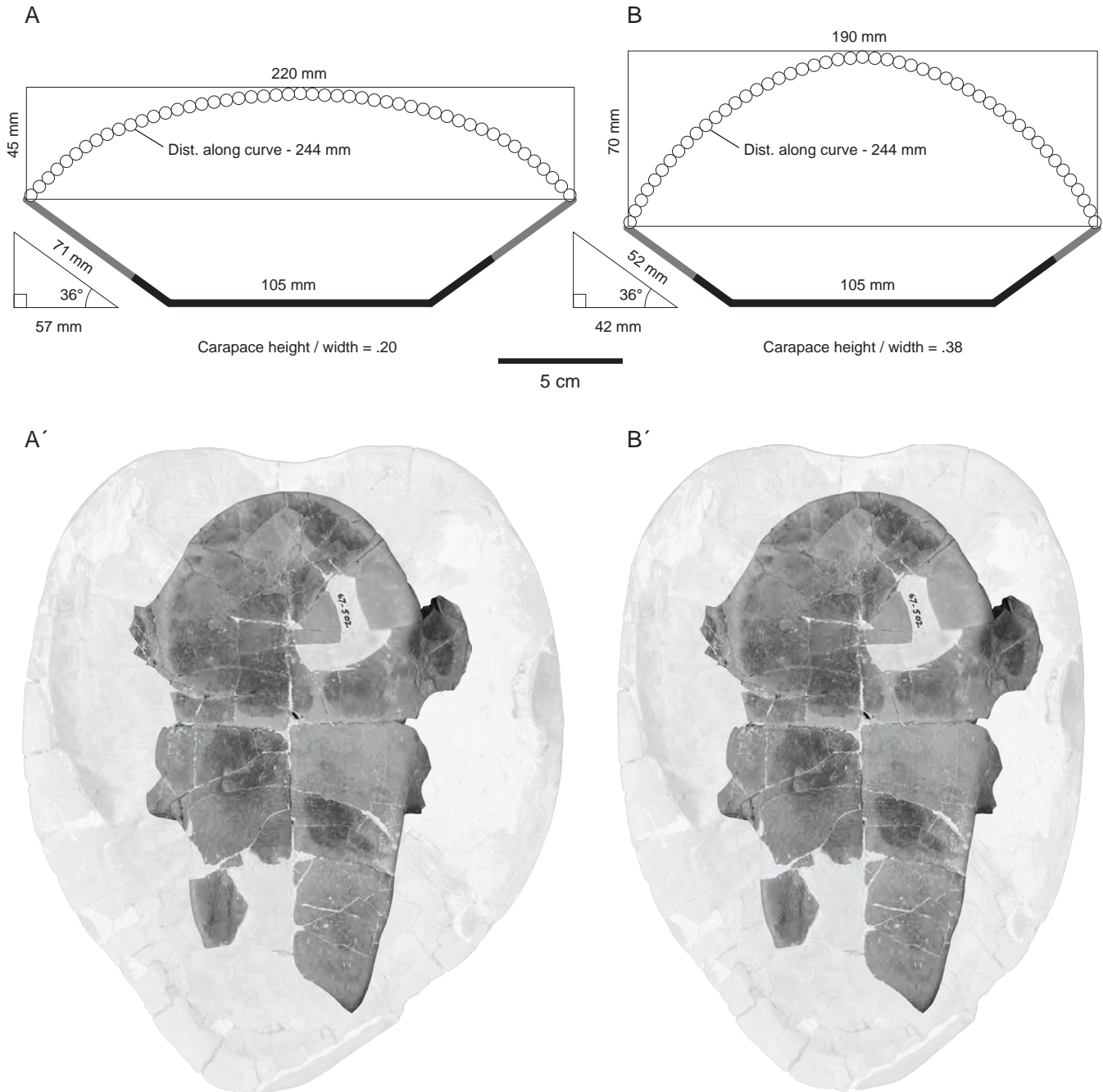


FIGURE 13 — Evidence of distortion in the shell of YPM 7457. **A**, the preserved shell cross-section; **B**, the reconstructed shell cross section. Associated alignments of plastron and carapace depicted in **A'** and **B'**. The preserved cross-section requires an unusually long bridge (71 mm) to connect carapace and plastron. The reconstructed cross-section conserves the bridge angle (36 degrees from the ventral surface of plastron) and imposes a 52 mm bridge length, based on comparison with CGM 42191. The carapace is significantly more domed in the reconstruction, which closely approximates the profile of the reconstructed shell of CGM 42191.

in the length of the symphysis and extent of dentary expansion, among other features (Fig. 14E–I). In those respects, UMMP 97531 is morphologically intermediate between *Stereogenys* and *Bairdemys* species.

UMMP 97531 is most similar to the lower jaw of *B. sanchezi*, which compared to other stereogenyines has a modest coronoid process, a relatively small retroarticular process, depressions on the lingual surface of the expanded dentaries that would have accommodated the secondary palate, mandibular articulations that lack the concavity displayed by *St. cromeri*, and an expanded triturating surface substantially more developed than in *B. venezuelensis*. UMMP 97531 differs from *B. sanchezi* in having a longer symphysis and more expanded triturating surface, a shorter ramus, a smaller retroarticular process, and a more pointed symphyseal tip.

UMMP 97531 was figured and tentatively referred to *Stereogenys cromeri* by Gaffney et al. (2011: fig. 81). As discussed above, we observe differences between it and the jaw of *St. cromeri* (CGM 10027). Further, the expanded portion of lower jaw UMMP 97531 corresponds most closely with the length and shape of the secondary palate in the referred specimen of *Cordichelys* (CGM 42191) described above (Fig. 14D), suggesting it belongs to the same species. However, in the absence of elements that directly overlap *Cordichelys* specimens, we refrain from giving UMMP 97531 a formal taxonomic designation. We expect future discoveries to clarify its relationships.

The jaw has a unique, heart-shaped triturating surface with a long symphysis that extends posteriorly to about halfway between the anterior and posterior margins of the coronoid. It has square dimensions overall, being as long anteroposteriorly as it is wide at its widest point between the lateral edges of the articulars. The triturating surface is heavily pitted along the medial ridge and the anterior margin. In lateral cross-section, the triturating surface is pinched anteriorly and expands significantly posteriorly, where the coronoid forms a dorsally expanded ridge that cups the posterior margin of the triturating surface on each mandible. Its ramus is short, stout, and apparently fused into one element. The rami diverge slightly from the midline.

Dentary.— The dentaries are almost completely fused at the symphysis. In addition to fusion to its opposite, each dentary contacts the coronoid posterolaterally, in dorsal view, along an S-shaped suture that is anteromedially convex laterally and concave medially. In ventral view, the fused dentaries form an anteriorly oriented chevron with posterior points along the axes of the rami that extend almost to the mandibular articulation. The dentaries form the posteromedial margin of the triturating surface between

the coronoids dorsally.

Coronoid.— The coronoid contacts the dentary anteromedially along a sinuous suture that is anteromedially convex for its lateral portion and concave for its medial portion. In posterior view, the coronoid contacts the dentary medially along a suture that from the dorsal margin of the expanded triturating surface travels ventrolaterally and then curves laterally to form the suture between the coronoid and the fused bones of the ramus. In lateral view, the coronoid contacts the dentary along a suture that travels posteroventrally from the edge of the triturating surface. In dorsal view, its posterior suture travels through the fossa meckelii and curves around the lateral edge of the ramus.

The coronoid is large and forms the posterolateral portion of the expanded triturating surface. It does not have a pronounced dorsal process, and its dorsal surface is smoothly rounded laterally. The anteromedial portion of its dorsal surface is deeply concave and the posteromedial edge of its dorsal surface forms a thin dorsally expanded ridge that cups the anterior concavity.

Ramus.— The bones of the ramus are fused, with no trace of sutures between them. The ramus is short and stout, and terminates in a large articular surface that is dorsally convex in the transverse plane. Posterior to the articulating surface is a short, blunt retroarticular process. In lateral view the ramus curves gently dorsally from the flat ventral surface of the dentary to the retroarticular process. The shaft of the ramus is pinched dorsally to form a prominent ridge atop a comparatively large, expanded ventral edge. A pronounced fossa meckelii is present on the dorsal surface of the ramus near its articulation with the coronoid. Depressions are present on the lateral and medial surface of the ramus.

TESTUDINES Linnaeus 1758
 PLEURODIRA Cope 1864
 PODOCNEMIDIDAE Cope 1868
Stereogenys Andrews, 1901

Type species.— *Stereogenys cromeri* Andrews, 1901.

Included species.— *Stereogenys cromeri*. All other species attributed to *Stereogenys* are based on shell-only specimens, and because no shell has been attributed definitively to the type species, these shell-based designations are suspect.

Diagnosis.— (see Gaffney et al., 2011).

Distribution.— *Stereogenys* is known from the late Eocene (middle Priabonian) Qasr el-Sagha Formation of Egypt.

Comments.— Apart from its larger body size, *Stereogenys* primarily differs from *Cordichelys* in possessing a longer secondary palate with a narrower, parallel-sided palatal cleft. In addition, *Stereogenys*

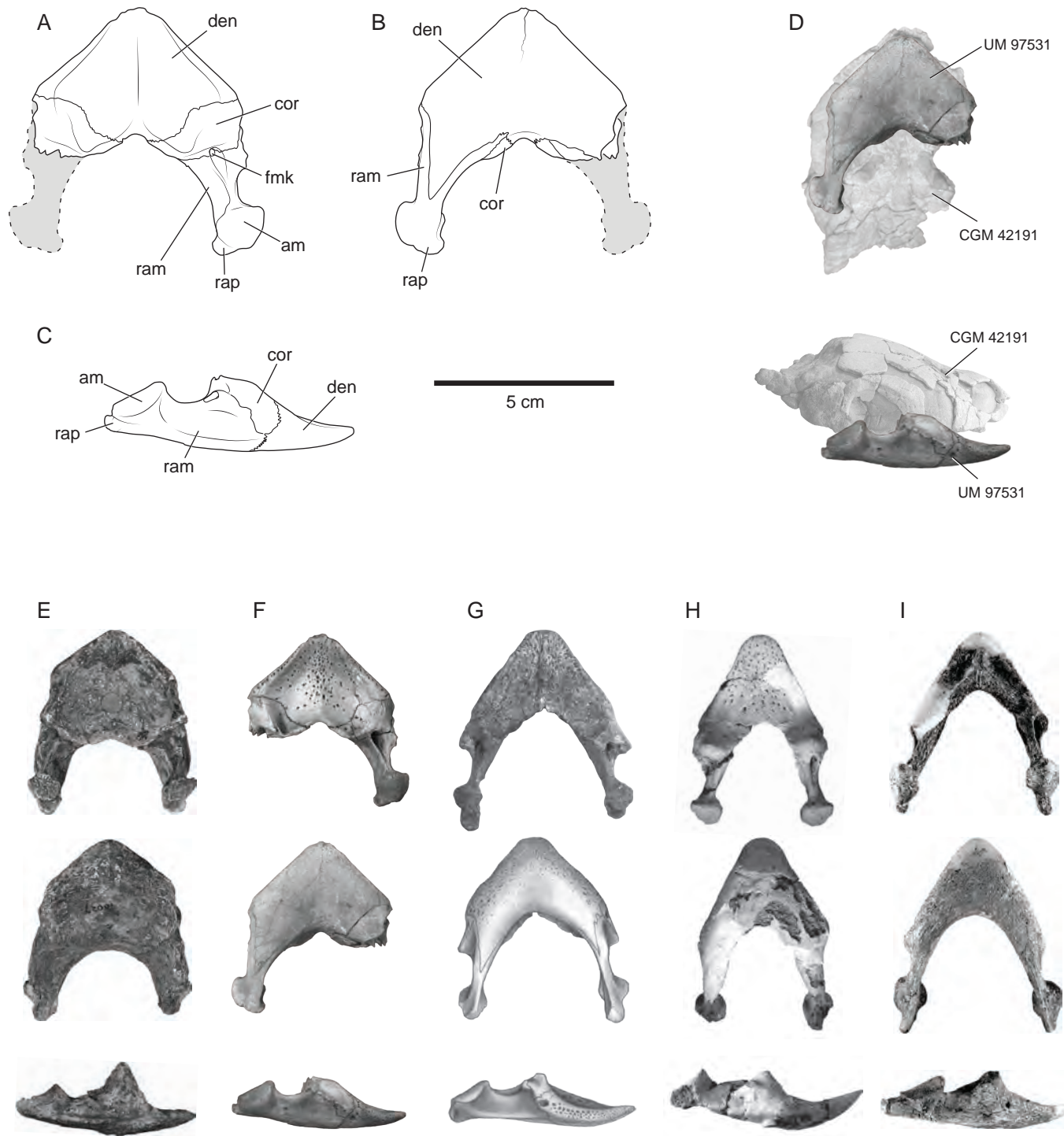


FIGURE 14 — Lower jaws for Stereogenyina. **A–C**, *Cordichelys* (?) (UMMP 97531) in dorsal, ventral, and right lateral views, respectively. **D**, ventral and right lateral views showing UMMP 97531 aligned with CGM 42191. **E**, *Stereogenys cromeri* (CGM 10027); **F**, *Cordichelys* (?) (UMMP 97531); **G**, *Bairdemys sanchezi* (AMU-CURS 186; from Gaffney et al., 2008: figs. 5, 6, reprinted by permission of the publisher); **H**, *Bairdemys healeyorum* (SCSM 90.16; from Weems and Knight, 2013: fig. 18.4; lateral view has been mirror-imaged, reprinted by permission of the publisher); **I**, *Bairdemys venezuelensis* (MCNC-Pal-21-10708; from Sánchez-Villagra and Winkler, 2006: fig. 8, reprinted by permission of the publisher). Images in E–I have been scaled to approximately the same size to facilitate shape comparison. Abbreviations: *am*, area articularis mandibularis; *cor*, coronoid; *den*, dentary; *fmk*, fossa meckelii; *ram*, ramus (fused); *rap*, retroarticular process.

possesses an accessory ridge on the triturating surface, broad separation of the pterygoids on the midline due to anterior projection of the basisphenoid, a large dorsal process of the palatine into the septum orbitotemporale, and a shorter basioccipital. Of these secondary features, however, only the accessory ridge on the triturating surface is clearly distinct from *Cordichelys*, and we did not see the ridge on the holotype skull CGM 10027 or referred skull CGM 10031. Like *Stereogenys*, the *Cordichelys* specimens described above have pterygoids separated by an anterior projection of the basisphenoid and a dorsal extension of the palatine. Though the extent of the basioccipital is not clear in the *St. cromeri* holotype, even the apparently diagnostic “shortest” basioccipital is not markedly different than the basioccipital that is well preserved in *Cordichelys* skulls MUVP 498 and YPM 7457.

The original distinction between *Cordichelys* (then ‘*Podocnemis*’) *antiqua* (Andrews, 1903) and *Stereogenys cromeri* (Andrews, 1901) was based on an erroneous comparison. There was no anatomical overlap between the holotypic specimens of ‘*Podocnemis*’ *antiqua* (a shell) and *Stereogenys cromeri* (a skull) and so proxy comparisons were made. The skull of ‘*Podocnemis*’ *antiqua* was assumed to resemble those of the extant members of *Podocnemis*, which are notably distinct from the skull of *Stereogenys cromeri* (CGM 10027). This apparent taxonomic distinction was reinforced over time with the lack of definitive postcranial remains assigned to *Stereogenys* and paucity of cranial remains referred to *Cordichelys*. The skull and shell specimen YPM 7457 first described by Wood (1971) along with the two additional *Cordichelys* skulls described in this contribution show that the skulls of *Cordichelys* and *Stereogenys* are distinguished by relatively minor features.

Stereogenys(?) sp., CGM 8718
(Fig. 15)

Locality.— North of Birket Qarun (Fig. 1). More precise locality information is not available.

Formation and age.— Qasr el-Sagha Formation, upper Eocene (middle Priabonian) according to Gingerich (1992).

A mostly complete, well-preserved carapace and plastron (Fig. 15) that was collected by Beadnell in 1903. The specimen was observed on display at CGM when one of the authors (MDC) visited in 2010, but only a photo from outside the case was taken due to time constraints. In lateral and dorsal views, the shell closely resembles in shape that of *Cordichelys* but it is much larger. CGM 8718 is approximately 50 cm long, which is about twice the length of the largest

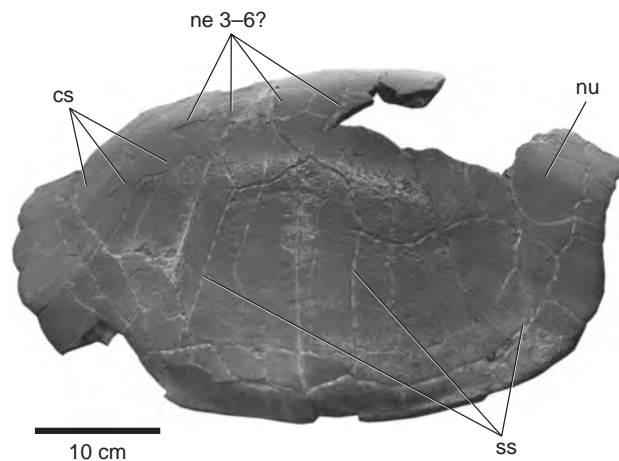


FIGURE 15 — Unidentified turtle shell (CGM 8718) from “north of Birket Qarun” on display at the Cairo Geological Museum (the quoted provenance comes from the specimen label at CGM). The carapace of this specimen closely resembles *Cordichelys* in overall organization, scute pattern, and dorsal curvature in dorsal and lateral views, but it is significantly larger (approximately 50 cm in length). This specimen seems to provide a likely candidate for the shell of *Stereogenys cromeri*, which reflects its close relationship to *Cordichelys*. Abbreviations: *cs*, costal sutures; *ne*, neural; *nu*, nuchal; *ss*, scute sulci.

Cordichelys shells. Its size is appropriate for the largest skulls of *Stereogenys*, which is not yet known from shell material. If the shell does pertain to *Stereogenys*, then it provides additional support for a closer than currently recognized relationship between *Stereogenys* and *Cordichelys*.

DISCUSSION

Notes on the relationship between *Cordichelys* and *Stereogenys*

The taxonomy of the Egyptian Stereogenyina has gone through numerous revisions since the earliest reports at the beginning of the 20th century. The shell-defined genus *Cordichelys* has a long, complicated history that is intertwined with the history of the skull-defined genus *Stereogenys*. Andrews (1901) introduced *Stereogenys cromeri* based on a skull-only holotypic specimen (CGM 10027). Later, Andrews (1903) erected the new species *Podocnemis antiqua* based on shell specimen CGM 10038. Assignment to the genus *Podocnemis* was based on similarities with the shell of ‘*P.*’ *madagascariensis* (now known as *Erymnochelys madagascariensis*). Despite the lack of anatomical overlap needed for comparison of type specimens, and current recognition of a close relationship between

Stereogenys and *Cordichelys*, they are currently considered distinct genera (Gaffney et al., 2011; Ferreira et al., 2015).

Andrews (1903) referred isolated shell material to *Stereogenys cromeri* without association or overlap with the holotypic skull, later explaining (Andrews, 1906: 298):

Although in no case have the carapace and plastron [of *St. cromeri*] been found associated with the skull in such a manner as to leave no doubt that they belong to the same individual, nevertheless the shell ... may be regarded with reasonable certainty as belonging to the present species. In the first place, this form of shell, like the skull, is the commonest occurring in the Qasr-el-Sagha beds, and in the second place it differs widely from the shell of *Podocnemis*, the only other Pleurodiran genus found at this horizon.

The ‘*Podocnemis*’ species Andrews was alluding to in the above excerpt were ‘*P.*’ *fajumensis* (Andrews, 1903), ‘*P. blakenhorni*’ (Reinach, 1903), ‘*P.*’ *antiqua* (Andrews, 1903), and ‘*P. stromeri*’ (Reinach, 1903). At the time, each of these was known only from shell material, and none of them is currently thought to be *Podocnemis*. Two of them, ‘*P.*’ *antiqua* and ‘*P. stromeri*,’ were later reassigned to ‘*Shweboemys*’ *antiqua* (Wood, 1971), and subsequently to *Cordichelys antiqua* (Gaffney et al., 2011), based on the discovery of YPM 7457, a specimen with a shell similar to ‘*P.*’ *antiqua* and a skull displaying the palatal structure that unites “*Shweboemys*-group” taxa (Broin, 1988), now referred to as Subtribe Stereogenyina (Gaffney et al., 2011). With *Cordichelys* having a shell similar to *Podocnemis* and a skull similar to *Stereogenys*, it is now clear that cranial differences between *St. cromeri* and *Podocnemis* do not support combination with the non-‘*Podocnemis*’ shells Andrews described from the Qasr el-Sagha Formation.

Wood (1971) kept ‘*Shweboemys*’ *antiqua* separate from *St. cromeri* based on his own evaluation of the shell material that Andrews (1906) had assigned to *Stereogenys*. He argued that although Andrews’ (1906) justification for the association was erroneous, the absence in the Qasr el-Sagha beds of shell material similar to ‘*Sh.*’ *antiqua*, but large enough to be *St. cromeri* suggested that the properly-sized shells Andrews (1903) referred to *St. cromeri* were probably correctly identified. Despite keeping ‘*Shweboemys*’ *antiqua* separate from *Stereogenys*, Wood (1971) referred some cranial material that had been identified by Andrews (1906) as *Stereogenys* to ‘*Shweboemys*’ *antiqua*.

Gaffney et al. (2011: 49, 56–57) maintained the

distinction between *Stereogenys* and *Cordichelys* based on an analysis of skull characters alone. This interpretation added a level of credibility to the historical separation of *Cordichelys* (along with its previous taxonomic assignments) and *Stereogenys*. However, the increased morphological diversity within *Cordichelys* that results from the addition of the new specimens described above may narrow this generic distinction. Furthermore, some characters that separated the two genera in the Gaffney et al. (2011) analysis, such as the presence in *Stereogenys* of a pinched snout and the large angle of the front of its skull, are of questionable relevance due to ambiguous definitions and distortion in the fossils. Dorsoventral flattening in the *Stereogenys* holotype exaggerates the width of the posterior of the skull and appearance of a pinched snout, and although the snout of *Cordichelys* is not clearly “pinched,” it is more similar to that of *Stereogenys* and *Shweboemys* than to those of other taxa scored as not having a pinched snout. Finally, Gaffney et al. (2011) did not inspect the nearly complete type skull and jaws of *St. cromeri* for their study, and instead based their analysis on several partially complete referred specimens. These factors further challenge the reliability of this conclusion.

Revising the Gaffney et al. (2011) matrix to accommodate the new specimens of *Cordichelys* reduces the scoring conflicts between *Cordichelys* and *Stereogenys cromeri* to only four. One reflects the larger secondary palate in *Stereogenys*—a character only shared with *Shweboemys*. The secondary palate is clearly smaller in *Cordichelys*, but it is also a functional adaptation that may scale allometrically. A second scoring difference reflects a shorter, stouter labial ridge in *Stereogenys*. This trait is hard to assess on the *Stereogenys* holotype and referred specimen in CGM due to poor preservation of the ridge. The third difference is in the dorsal extent of the palatine in the septum orbitotemporale. In *Stereogenys* and *Shweboemys*, the palatine extends dorsally between the jugal, postorbital (anteriorly), and pterygoid (posteriorly) to contact the parietal (Gaffney et al., 2011). In *Cordichelys*, the palatine extends dorsally, contributing to the septum, but does not meet the parietal, instead being bounded by the union of the pterygoid and postorbital dorsally. The final difference is the shape of the antum postoticum, which Gaffney et al. (2011) score as slit-like in *Stereogenys* and *Bairdemys* compared to open and rounded in *Cordichelys*. Despite the limited number of differences, a cladistic analysis of the revised matrix (see Table 2) using TNT v. 1.1 (Goloboff et al., 2008), produces the same tree included in Gaffney et al. (2011), with *Cordichelys* in a monophyletic group with *Bairdemys* and *Latentemys*, and with *Stereogenys* plotting as sister taxon to the Pliocene/Pleistocene *Shweboemys* in a

TABLE 2 — Character scoring modifications to the Gaffney et al. (2011) matrix.

Character	Taxon	Change
1. NA, nasals: 0, present; 1, absent	<i>Cordichelys</i>	? >> 1
10. JU, jugal-parietal contact: 0, absent; 1, present	<i>Stereogenys cromeri</i>	? >> 0
12. SQ, ventral vertical flange: 0, absent; 1, present	<i>Cordichelys</i>	0 >> [0,1]
15. PM, pinched snout: 0, absent; 1, concave outline near premaxilla-maxilla contact, snout not elongated; 2, concave outline posterior to premaxilla-maxilla contact, snout elongated.	<i>Cordichelys</i> <i>Bairdemys hartsteini</i>	0 >> [0,1] 0 >> 1
23. PAL, medial edges of palatal cleft: 0, absent; 1, parallel; 2, curved.	<i>Cordichelys</i>	2 >> [1,2]
25. PAL, dorsal process of palatine contacts parietal in septum orbitotemporale: 0, no; 1, yes	<i>Cordichelys</i>	0 >> [0,1]
44. BO, basioccipital very short: 0, no; 1, yes.	<i>Cordichelys</i> <i>Lemurchelys</i>	0 >> [0,1] 0 >> 1
55. ART, processus retroarticularis: 0, long and posterior; 1, short or absent; 2, long and posteroventral.	<i>Bairdemys sanchezi</i>	? >> 1
61. Carapace, cervical scale: 0, present; 1, absent	<i>Cordichelys</i>	1 >> [0,1]

neighboring clade that also includes *Brontochelys* and *Lemurchelys*. This may be a consequence of missing information—for example, all characters that can be scored for *Shweboemys* match *Stereogenys* in this matrix, but most are missing.

A phylogenetic analysis by Ferreira et al. (2015) focuses on relationships within Stereogenyina. Ingroup taxa include the newest *Bairdemys* species, *B. thalassica* and *B. healeyorum*, the latter of which was considered doubtfully assigned to *Bairdemys*. Character scope and selection were not successful in resolving interrelationships within Stereogenyina. Of the 57 characters used in that study, only 27 include variation within stereogenyines, and three of those are autapomorphies. Relationships within the subtribe are still poorly resolved and fairly fluid, and minor changes to character scoring and taxon inclusion have potentially important impacts on the results. An analysis that focuses on diagnostic features within Stereogenyina could help clarify the phylogeny of this group, but such an undertaking is beyond the scope of the current study.

We concur with Gaffney et al. (2011) and Pérez-García (2019) that shells previously assigned to *Stereogenys* likely represent an entirely different genus. Although no *Stereogenys* shells have been positively identified to date, we think they may have closely resembled large *Cordichelys* shells. One undescribed shell on display in

Cairo (CGM 8718) resembles *Cordichelys*. It was found in the same deposits as *Stereogenys* and is large enough to be appropriate for the skull of *Stereogenys*. If this unpublished specimen does not pertain to *Stereogenys*, then it may represent a large *Cordichelys* individual.

Ecology of *Cordichelys*

All Stereogenyina have expanded flanges of the maxillae and palatines that form a partial secondary palate. This structure provides a broad, hard surface that in each taxon was undoubtedly paired with expanded lower jaws, such as those preserved in *Stereogenys*, *Bairdemys*, and the new specimen we suggest belongs to *Cordichelys*. Previous authors have suggested that this could be an adaptation for a diet of mollusks and crustaceans (e.g., Andrews, 1906; Wood, 1971; Ferreira et al., 2015) and that the modern marine cryptodire *Caretta caretta* (the loggerhead sea turtle) may provide a good analog. *Caretta* has a similarly expanded triturating surface in its jaw and palate that it uses to break up the shells of mollusks and crustaceans in order to extract the flesh inside. In contrast, living fresh water molluscivorous turtles, such as the podocnemidid *Erymnochelys madagascariensis*, do not have this expanded triturating surface and instead use their sharp beaks to puncture the comparably less robust shells

of freshwater mollusks. Thus, the feeding adaptation found in *Stereogenyina* fits with the interpreted marine ecology for the group. Hard-shell crabs, such as *Lobocarcinus* (e.g., Anderson and Feldman, 2016), are common in the late Eocene deposits of the Fayum and may have been one of the target prey items for these turtles.

Our identification of *Cordichelys* in the Birket Qarun Formation corroborates interpretations of a marine habitat for the genus (Wood, 1971; Gaffney et al., 2011; Pérez-García et al., 2017). Previous interpretations were based primarily on features of shell morphology—some of which are called into question by the reconstructed shell of CGM 42191. Association with the near-shore marine Qasr el-Sagha Formation was ecologically ambiguous due to the presence of marine animals as well as terrestrial remains in deltaic deposits. However, the Birket Qarun Formation is interpreted as an offshore barrier bar complex that lacks deltaic deposits and preserves a characteristically marine fauna (Gingerich, 1992). Thus, although we question some of the pretexts in previous literature, we agree with the conclusion that *Cordichelys* were marine turtles.

Reconstructing the original shell curvature of *Cordichelys*

The shape of the *Cordichelys* shell has been debated for over a century. Andrews (1903: 289) described '*Podocnemis antiqua*' as having a carapace "highly arched" anteriorly and flatter posteriorly. Reinach (1903) described '*Podocnemis stromeri*' as having a shallow carapace and listed this as one of the ways it differed from '*P. antiqua*'. Later, '*P. antiqua*' and '*P. stromeri*' were synonymized as '*Shweboemys antiqua*' (Wood, 1971), which was later renamed as the type species for *Cordichelys* (Gaffney et al., 2011). Echoing Reinach's interpretation, Wood described '*S. antiqua*' as having a "rather flat" shell (Wood, 1971: 147). He discounted Andrews' interpretation based on his personal inspection of the poorly preserved holotype carapace of '*P. antiqua*' and saw no evidence of significant arching in the shell of YPM 7457. The Gaffney et al. (2011) description of genus *Cordichelys* accepted Wood's 1971 interpretation.

The evidence that Andrews (1903) saw of significant doming in the holotype of '*P. antiqua*' is unknown and could not be independently evaluated for the present study, because the specimen was missing when one of the authors (MDC) visited the Cairo Geological Museum in November 2010. Reinach's figured shell (1903: pls. 1–3) and YPM 7457 are significantly flatter than our reconstructed shell of CGM 42191. However,

our analysis suggests that the flat appearances are due to taphonomic distortion. Our reconstruction of CGM 42191 is the first 3-D reconstruction of a *Cordichelys* shell. Our evaluation of YPM 7457 shows that it likely had carapacial doming similar to our reconstruction prior to being dorsoventrally crushed.

CONCLUSIONS

Understanding the phylogenetic relationship between *Stereogenys* and *Cordichelys* and their ecologies is necessary for reconstructing the origin, diversification, and geographic expansion of *Stereogenyina*. This study improves the record of variation in *Cordichelys*, and the new specimens support a closer relationship between it and *Stereogenys* than has been previously recognized. Any further ecological interpretations for *Cordichelys* should accommodate the moderately domed shell reconstructed for CGM 42191.

ACKNOWLEDGMENTS

We thank E. Gaffney (AMNH) for providing preview excerpts from "Evolution of the Side-Necked Turtles: the Family Podocnemididae" prior to its publication in 2011, while the lead author (MDC) was completing his M.S. thesis studying the specimens described herein. We also thank J. Gauthier (YPM) for loaning comparative material, M. Abdel Ghany (CGM) for providing access to the CGM collections, and J. Fahlke for providing translations of the German literature. We are also grateful for detailed and thoughtful feedback from two reviewers, S. Evers (University of Fribourg) and A. Pérez-García (UNED Madrid). M. Friedman kindly served as editor for this *Contributions*. We thank M. Talaat Al Hennawy (EEAA) for access to the Wadi Al Hitán Protected Area and for encouragement of this research. Research in Egypt was sponsored by the Egyptian Geological Museum, the Egyptian Environmental Affairs Agency, the Egyptian Mineral Resources Authority, the University of Michigan Museum of Paleontology, the U. S. National Science Foundation (NSF OISE0513544, EAR-0920972), and the National Geographic Society (NGS 7226-04). TNT was used with the Personal Use License made available with the sponsorship of the Willi Hennig Society.

LITERATURE CITED

- ANDERSON, J. L., and R. M. FELDMANN. 1995. *Lobocarcinus lumacopius* (Decapoda: Cancridae), a new species of cancrinid crab from the Eocene of Fayum, Egypt. *Journal of Paleontology*, 69: 922–932.

- ANDREWS, C. W. 1901. Preliminary note on some recently discovered extinct vertebrates from Egypt (Part II). *Geological Magazine, new series*, 8: 436–444.
- . 1903. On some pleurodire chelonians from the Eocene of the Fayum, Egypt. *Annals and Magazine of Natural History, series 7*, 11: 115–122.
- . 1906. A Descriptive Catalog of the Tertiary Vertebrata of the Fayum, Egypt. British Museum of Natural History, London.
- BEADNELL, H. J. L. 1902. A preliminary note on *Arsinoitherium zitteli*, Beadnell from the upper Eocene strata of Egypt. National Printing Department, Cairo, 4 pp.
- BROIN, F. DE. 1988. Les tortues et le Gondwana. Examen des rapports entre le fractionnement du Gondwana au Crétacé. *Studies in Palaeocheloniology*, 2: 103–142.
- , X. MURELAGA, A. PÉREZ-GARCIA, F. FARRÉS, and J. ALTIMIRAS. 2018. The turtles from the upper Eocene, Osona County (Ebro Basin, Catalonia, Spain): new material and its faunistic and environmental context. *Mitteilungen aus dem Museum für Naturkunde in Berlin. Fossil Record*, 21: 237–284.
- CHERNEY, M. D. 2011. Two new species of *Cordichelys* (Pleurodira, Podocnemididae) from the Fayum Depression, Egypt, and comments on the genus *Stereogenys*. Unpublished Master's thesis, University of Michigan, 63 pp.
- , P. GINGERICH, J. WILSON, I. ZALMOUT, and M. ANTAR. 2011. New specimens of *Cordichelys* (Pleurodira, Podocnemididae) from late Eocene marine strata of Fayum, Egypt and a reevaluation of *Cordichelys antiqua*. *Journal of Vertebrate Paleontology*, 31: 87 (abstract).
- COLLINS, R. L., and W. G. LYNN. 1936. Fossil turtles from Maryland. *Proceedings of the American Philosophical Society*, 76: 151–173.
- DACQUÉ, E. 1912. Die Fossilien Schildkröten Aegyptens. *Geologische und Paläontologische Abhandlungen*, 14: 275–337.
- FERREIRA, A. D. RINCÓN, A. SOLÓRZANO, and M. C. LANGER. 2015. The last marine pelomedusoids (Testudines: Pleurodira): a new species of *Bairdemys* and the paleoecology of *Stereogenyina*. *PeerJ*, 3: e1063.
- , S. BANDYOPADHYAY, and W. G. JOYCE. 2018. A taxonomic reassessment of *Piramys auffenbergi*, a neglected turtle from the late Miocene of Piram Island, Gujarat, India. *PeerJ*, 6: e5938.
- GAFFNEY, E. S. 1979. A phylogeny of turtles. *Bulletin of the American Museum of Natural History*, 164: 64–376.
- , and R. C. WOOD. 2002. *Bairdemys*, a new side-necked turtle (Pelomedusoides, Podocnemididae) from the Miocene of the Caribbean. *American Museum Novitates*, 3359: 1–28.
- , H. TONG, and P. A. MEYLAN. 2006. Evolution of the side-necked Turtles: the families Bothremydidae, Euraxemydidae, and Araripemydidae. *Bulletin of the American Museum of Natural History*, 300: 1–700.
- , P. A. MEYLAN, R. C. WOOD, E. SIMONS, and D. DE ALMEIDA CAMPOS. 2011. Evolution of the side-necked turtles: the family Podocnemididae. *Bulletin of the American Museum of Natural History*, 350: 1237.
- , T. M. SCHEYER, K. G. JOHNSON, J. BOCQUENTIN, and O. A. AGUILERA. 2008. Two new species of the side-necked turtle genus, *Bairdemys* (Pleurodira, Podocnemididae), from the Miocene of Venezuela. *Paläontologische Zeitschrift*, 82: 209–229.
- GINGERICH, P. D., 1992. Marine mammals (Cetacea and Sirenia) from the Eocene of Gebel Mokattam and Fayum, Egypt: stratigraphy, age, and paleoenvironments. *University of Michigan Papers on Paleontology*, 30: 1–84.
- , and B. H. SMITH. 1990. Forelimb and hand of *Basilosaurus isis* (Mammalia, Cetacea) from the middle Eocene of Egypt. *Journal of Vertebrate Paleontology*, 10A: 24 (abstract).
- , and M. D. UHEN. 1996. *Ancalocetus simonsi*, a new dorudontine archaeocete (Mammalia, Cetacea) from the early Eocene of Wadi Hiton, Egypt. *Contributions from the Museum of Paleontology, University of Michigan*, 29: 359–401.
- , B. H. SMITH, and E. L. SIMONS. 1990. Hind limbs of Eocene *Basilosaurus*: evidence of feet in whales. *Science*, 249: 154–157.
- GOLOBOFF, P., J. FARRIS, and K. NIXON. 2008. TNT, a free program for phylogenetic analysis. *Cladistics*, 24: 774–768.
- JAIN, S. L. 1977. A new fossil pelomedusid turtle from the Upper Cretaceous Pisdura sediments, Central India. *Journal of the Palaeontological Society of India*, 20: 360–365.
- . 1986. New pelomedusid turtle (Pleurodira: Chelonia) remains from Lameta Formation (Maastrichtian) at Dongargaon central India, and a review of pelomedusids from India. *Journal of the Palaeontological Society of India*, 31: 63–75.

- PÉREZ-GARCÍA, A. 2019. New information and establishment of a new genus for the Egyptian Paleogene turtle '*Stereogenys libyca*' (Podocnemididae, Erymnochelyinae). *Historical Biology*, 31: 383–392.
- PÉREZ-GARCÍA, A., F. DE LAPPARENT DE BROIN, and X. MURELAGA. 2017. The *Erymnochelys* group of turtles (Pleurodira, Podocnemididae) in the Eocene of Europe: new taxa and paleobiological implications. *Palaeontologia Electronica*, 20: 1–28.
- PRASAD, K. N. 1974. The vertebrate fauna from PIRAM Island, Gujarat, India. *Memoirs of the Geological Survey of India*: 41: 1–21.
- REINACH, A. VON. 1903. Schildkrötenreste aus dem ägyptischen Tertiär. *Abhandlungen herausgegeben von der Senckenbergischen Naturforschenden Gesellschaft (Frankfurt)*, 29: 1–64.
- SÁNCHEZ-VILLAGRA, M. R., and J. D. WINKLER. 2006. Cranial variation in *Bairdemys* turtles (Podocnemididae: Miocene of the Caribbean Region) and description of new material from Urumaco, Venezuela. *Journal of Systematic Palaeontology*, 4: 241–253.
- SWINTON, W. E. 1939. A new fossil fresh-water tortoise from Burma. *Records of the Geological Survey of India*, 74: 548–551.
- WEEMS, R. E. 2009. An Oligocene side-necked turtle (*Bairdemys*) (suborder: Pleurodira, family: Podocnemididae) from the Chandler Bridge Formation (Lower Chattian) of South Carolina. In D. Braman (ed.), *Gaffney Turtle Symposium Abstract Volume*, Royal Tyrrell Museum, Drumheller, Alberta. pp. 188–194.
- , and J. L. KNIGHT. 2013. A new species of *Bairdemys* (Pelomedusoides: Podocnemididae) from the Oligocene (Early Chattian) Chandler Bridge Formation of South Carolina, USA, and Its Paleobiogeographic Implications for the Genus. In D. B. Brinkman, P. A. Holroyd, and J. D. Garner (eds.), *Morphology and Evolution of Turtles: Proceedings of the Gaffney Turtle Symposium (2009) in Honor of Eugene S. Gaffney*, *Vertebrate Paleobiology and Paleoanthropology*. ch. 18, Springer, Dordrecht, pp. 289–303.
- WOOD, R. C. 1970. A review of the fossil Pelomedusidae (Testudines, Pleurodira) of Asia. *Breviora*, 357: 1–23.
- . 1971. The Fossil Pelomedusidae (Testudines, Pleurodira) of Africa. Ph.D. dissertation, Harvard University.
- , and M. L. DIÁZ DE GAMERO. 1971. *Podocnemis venezuelensis*, a new fossil pelomedusid (Testudines, Pleurodira) from the Pliocene of Venezuela and a review of the history of *Podocnemis* in South America. *Breviora*, 376: 1–23.
- ZOUHRI, S., B. KHALLOUFI, E. BOURDON, F. D. L. DE BROIN, J.-C. RAGE, L. M'HAÏDRAT, P. D. GINGERICH, and N. ELBOUDALI. 2018. Marine vertebrate fauna from the late Eocene Samlat Formation of Ad-Dakhla, southwestern Morocco. *Geological Magazine*, 155: 1596–1620.