Oligocene Pancheloniid Sea Turtles from the Vicinity of Charleston, South Carolina, U.S.A.

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INTRODUCTION

A great many papers have been published concerning the abundant fossil vertebrate remains recovered over the centuries from the South Carolina Lowcountry, a region that includes Charleston, South Carolina (Fig. 1A, B). A detailed synopsis of this older literature can be found in Sanders and Anderson (1999). Among these papers, only three have direct bearing on the fossil vertebrate remains of the Ashley and the Chandler Bridge formations (Fig. 1C). The first was by Hay (1923a), in which he described, without illustrations, a new genus and species of pancheloniid sea turtle that he named *Ashleychelys wilsoni*, from the Eocene marls of Charleston, South Carolina. Later that same year, after better preparation of the type skull, Hay (1923b) published an emended diagnosis of this genus and species along with sharp photographs of the type specimen. In this paper, he also described and illustrated a humerus that he thought might pertain to the same species. Additionally, he noted that the preponderance of geologic thinking had moved toward the conclusion that the marls near Charleston were Oligocene rather than Eocene in age. Weems (1974) suppressed the name *Carolinochelys* and referred *C. wilsoni* to the genus *Procolopchelys*. As discussed below under taxonomic descriptions, that designation was correct for the referred humerus but incorrect for the type skull, and *Carolinochelys* is reinstated here.

Although abundant new pancheloniid turtle material has been found in recent decades, nothing has been published on it until now. In addition to the far more complete material of *Carolinochelys* described here, and the recognition of a new genus here named *Ashleychelys*, rare remains of yet a third kind of large Oligocene pancheloniid sea turtle have been found in recent years that are referable to a new species of the genus *Procolopchelys* Hay, 1908. Thus, we now can document and characterize three taxa of pancheloniid sea turtles that inhabited the coastal waters of South Carolina in the mid-Oligocene. These three taxa, along with three taxa of dermochelyid sea turtles yet to be described, indicate that a taxonomically diverse and numerically abundant population of sea turtles thrived in the coastal waters of the southeastern United States during the middle part of Oligocene time (Fig. 1C).

GEOLOGIC AND GEOGRAPHIC SETTING

Although Oligocene strata are well represented in the Gulf Coastal Plain (Fig. 1A), they crop out in the Atlantic Coastal Plain only in a few limited areas (Weems et al., 2004). One of these areas is near Charleston, South Carolina, where the Ashley and the Chandler Bridge formations are frequently exposed (Fig. 1C). The “Ashley marl” was first recognized and described by Tournay (1848) and more fully described and discussed by Sloan (1908). The name was abandoned by Wilmarth (1938), reinstated and formalized as the Ashley Member of the Cooper Formation by Ward et al. (1979), and then raised in rank to the Ashley Formation of the Cooper Group by Weems and Lemon (1984). The Chandler Bridge Formation was recognized and named as a distinct and separate stratigraphic unit by Sanders et al. (1982). Both units fall within the Trent Supergroup (Weems et al., 2004). Their detailed distribution in the Charleston region is summarized in Weems and Lewis (2002). Most of the South Carolina Lowcountry that surrounds Charleston is blanketed by a veneer of Quaternary sediments.
Below it, occasionally in outcrops but more often in shallow excavations, there are limited outcrops of older strata. Despite their very limited exposures, however, both the Ashley and Chandler Bridge formations contain such an abundance of vertebrate remains that a considerable assemblage has been collected and preserved from the few exposures of both units that are available. This material has been collected from as far west of Charleston as the Edisto River valley, from where that river swings south at the Great Bight of the Edisto southward almost to Jacksonboro. Eastward, material has been collected through the headwaters of the Ashley River and then southeastward down its valley throughout the old Ashley River phosphate mining district. In the vicinity of Summerville, the productive outcrop belt starts to turn eastward again through Ladson and then turns sharply northward through Goose Creek toward Monks Corner, South Carolina (Fig. 1B).

The Ashley Formation is late Rupelian (Weems et al., 2006) and the Chandler Bridge Formation is early Chattian (Sanders
et al., 1982), but even so they are close in age. Both units fall within nanoplankton zone NP24 and so accumulated over a span of no more than 2.4 million years, or about one-quarter of Oligocene time (Fig. 1C). Because the Oligocene is formally split into only two stages (Rupelian succeeded by Chattian), it is not acceptable to designate this time interval formally as middle Oligocene, but the informal term mid-Oligocene is acceptable and used here to refer collectively to the age of these two formations. The late Rupelian Ashley Formation represents a somewhat offshore continental shelf depositional environment east of any barrier islands, whereas the Chandler Bridge represents a much shallower, lagoonal, and barrier-island-to-shoreline-offshore depositional setting (Sanders et al., 1982; Weems and Sanders, 1986). The scarcity of land or freshwater animal remains in the nearshore Chandler Bridge Formation suggests that there was a large lagoonal region to the west of the surviving areas of outcrop that effectively separated this coastal barrier environment from the mainland, perhaps in a setting similar to that of the modern Cape Hatters and Outer Banks areas in coastal North Carolina (location immediately west of ‘H’ in Fig. 1A).

**TAXONOMIC NOTES**

Some significant differences exist between the cetacean assemblages found in the Chandler Bridge and Ashley formations (Weems et al., 2006). In contrast, the turtle assemblages of both units show no apparent differences or changes throughout this time interval. It should be noted, however, that none of the recovered turtle material is known to represent the lower part of the Ashley Formation; the turtle remains described here are probably exclusively from the upper Ashley and Chandler Bridge formations. Because no differences are apparent between panchanneloid turtles from these two units, the specimens from both are described together.

Hay (1923a) designated without illustration a nearly complete skull (MCZ 1005-A) as the type of the genus Carolinochelys and the species **C. wilsoni**. This is fortunate, because later in the same year he described, illustrated, and referred a nearly complete humerus to this species (Hay, 1923b). For reasons discussed below in the section on *Procolpochelys*, the humerus pertains to *Procolpochelys* and not Carolinochelys. Weems (1974) recognized that this humerus pertained to *Procolpochelys* and so assigned *Carolinochelys wilsoni* to *Procolpochelys* as *P. wilsoni*, not realizing that the skull and humerus were incorrectly associated. Because the humerus is not the type, Weems’s suppression of the name Carolinochelys was in error and is corrected here. The holotype specimen of Carolinochelys wilsoni is, therefore, formally restricted to the skull (MCZ 1005-A), and the referred humerus (MCZ 1005-B) is assigned to *Procolpochelys charlestonensis*, sp. nov., described below. Similar incorrect associations of skulls, humeri, and shells have occurred all too often in the history of fossil chelonian research (e.g., *Osteopygis* as corrected in Parham, 2005).

**SYSTEMATIC PALEONTOLOGY**

**Order** TESTUDINES Linnaeus, 1758  
**Suborder** EUCRYPTODIRA Gaffney, 1975  
**Family** CHELONIIDAE Gray, 1825  
**CAROLINOCHELYS** Hay, 1923a  
**CAROLINOCHELYS WILSONI** Hay, 1923a  
*(Figs. 2–8)*

*Carolinochelys wilsoni* Hay, 1923a.  
*Procolpochelys wilsoni* (Hay, 1923a) (nov. comb.) (see Weems, 1974).

**Holotype**—MCZ 1005-A, a nearly complete skull.

**Type Locality**—The two specimens described and figured by Hay (1923a, 1923b) were obtained from what then was known as the ‘Eocene marl’ in the vicinity of Charleston, South Carolina. According to the original label with the type specimen and incorrectly referred humerus, both specimens came from the commercial marl pits at Ingleside in Berkeley County, South Carolina, located 22.5 km (14 miles) northwest of Charleston (Weems, 1974). The marl exposed in this region northwest and west of Charleston now is known as the Ashley Formation of early Oligocene (late Rupelian) age, rather than Eocene age (Weems et al., 2006). Based on Hay’s (1923a, 1923b) description and discussion, these specimens very likely came from the upper part of the Ashley Formation. Much of the other material discussed here came from the Chandler Bridge Formation.

**Referred Material**—Ashley Formation: ChM PV8309, Chandler Bridge Formation: ChM GPV524, ChM PV2143, PV2144, PV2145, PV2148, PV2151, PV2167, PV2168, PV2171, PV2172, PV2178, PV2179, PV2184, PV2189, PV2190, PV2209, PV2227, PV2297, PV4267, PV4792, PV4367, PV4368, PV4820, PV5927, PV5928, PV6081, and PV7003.

**Diagnosis**—Large sea turtle with a deep skull and round orbit; prefrontals form the anterior border of the orbit, whereas frontals form only a small portion of the dorsal rim of the orbit; quadrate turns back only slightly beneath squamosal; cavum tympani not compressed and broadly rounded at its posterior end; secondary palate moderately developed, with the vomer contributing only about a third of its length to the secondary palate; maxillary palate furnished on both sides with two sharp ridges; pterygoid flanges only slightly developed; planar joint between sixth and seventh cervical vertebrae; carapace strongly convex with a length up to 70 cm, distinctly more elongate than wide, with the neural-costal portion of the carapace widest across the fourth costals; vertebral scutes as long as wide and hexagonal in younger individuals but becoming longer than wide and almost rectangular in older individuals; costoparietal fontanelles are long and narrow but persistently present even in adults; uniquely among well known panchelonids, deep notches are present along the outer border of the second peripherals; carapace surface covered by a rugose verruform pattern; angle between scapular rods about 130°; shaft of humerus strongly curved downward, unlike in *Ashleychelys palmeri* and *Procolpochelys charlestonensis*.

**Description**—In its skull morphology, *C. wilsoni* is a very generalized stem-panchanneloid turtle. Its external surface is rough and covered by a ubiquitous network of shallow pits and vermiform troughs. The holotype skull (Fig. 2C, D) accurately can be restored accurately (Fig. 3). It is relatively high-arched in its vertical dimension (ChM PV5927) gives a good idea of its appearance in anterior and lateral views (Fig. 2A, B). The skull can be restored accurately (Fig. 3). It is relatively high-arched for a panchelonid turtle, with orbits that face obliquely outward and forward. In dorsal view, the parietals are very nearly pentagonal in shape, being exceptionally wide and sharply angled where they meet the suture between the postorbital and the squamosal. The dorsal rim of the orbit may be smoothly curved or it may project outward slightly above the eye socket. In ventral view, although the vomer provides a relatively small contribution to the secondary palate, the vomerine pillar beneath it extends far posteriorly. The pterygoids are relatively narrow between wide foramina orbito-nasale vacuities and have only a hint of pterygoid flanges on their external lateral borders. The basiphenoid extends far posterior laterally in front of the basioccipital, so that it fully separates the pterygoids from the basioccipital. The supraoccipital is relatively short and stout.

A number of partially articulated specimens of *C. wilsoni* have been recovered in recent decades that consistently associate
**FIGURE 2.** The skull of *Carolinochelys wilsoni*. A, anterior view of ChM PV5927; B, right lateral view of ChM PV5927; C, ventral view of holotype specimen, MCZ 1005-A; D, dorsal view of holotype specimen, MCZ 1005-A.

*C. wilsoni* skulls with the shells and limb elements described hereafter. The common and consistent association of skulls with these other skeletal elements allows us to assign this material confidently to *C. wilsoni*. Among the carapace material that has been recovered, one specimen (PV4792) is especially complete and has been restored by Bruce Erickson and the Science Museum of Minnesota to as close to its original appearance as can be done given the small but pervasive compaction-induced distortions in the carapace elements (Figs. 4, 5). In adults, the carapace has elongate but narrow costoperipheral fontanelles in its posterior part. A decidedly smaller specimen (PV2143) possesses an even longer costoperipheral fontanelle that is notably wider for its size, though still relatively narrow for a pancheloniid (Fig. 6B). In anterior view, the carapace of *C. wilsoni* is more strongly arched than in most pancheloniid sea turtles (Fig. 5B), being reminiscent of the modern species *Caretta caretta*.

The carapace of *C. wilsoni* is rather generalized with one notable exception. Within each second costal, on both sides of the carapace, there is a broad and wide indentation along its external border (Fig. 5B). These indentations are pronounced, quite symmetrical, and fall in a position that would logically serve as holdfasts for the enlarged, elongate, and curved claws found on the front flippers of pancheloniid males, which they are known to use in modern species to grasp females during mating. The notches seem to be natural features in the shell, but the notch on the second right peripheral element of PV4792 also possesses a scoured groove that appears to have been abraded into the swale of the notch (Fig. 5C). This supports the idea that the notches served as holdfasts during mating. On other parts of this carapace, there also are elongate (Fig. 5D) to round (Fig. 5E) pits of a very different nature that appear to have been caused by parasites or epizoans such as turtle barnacles.

Much of the plastron of *C. wilsoni* is known. Typical examples of the hyoplastron, the hypoplastron, and the epiplastron, are shown in Figure 7A–C. These, like the carapace, are covered by low but ubiquitously developed pits and vermiform troughs on their external (ventral) surfaces. At least one example of all plastral elements is known except for the entoplastron and xiphiplastron (Fig. 7D).

Girdle elements are poorly known, but a large part of a scapula and most of an ischium are complete enough to be illustrated (Fig. 8D, E). The angle between the scapular rods is about 130°. None of the preserved humeri are perfect, but they consistently show an exceptionally down-curved shaft, unlike that of modern cheloniid turtles (Fig. 8F). Modern cheloniids have lost the primitive sigmoidal curvature in their humeral shafts that non-marine turtles normally retain (e.g., *Echmatemys*, sp. indet. [Hay, 1908:fig. 369] and *Geochelone orthopygia* [Hay, 1908:fig. 594]), and this modification has helped pancheloniids use their forelimbs as efficient paddles for flying locomotion in their marine environment (Hirayama, 1994). The presence of an intermediate shaft curvature in *C. wilsoni* suggests that it had a humerus distinctly less well adapted to an open-marine environment than the humeri of *Ashleychelys palmeri* (Fig. S2D in Supplementary Data), *Procolpochelys charlestonensis* (Fig. S4E in Supplementary Data), and modern cheloniids. Similarly, a nearly complete femur of *C. wilsoni*, PV6081 (Fig. 8A–C), has trochanters that are not connected by a bony ridge to the femoral caput as in modern cheloniids, indicating that the rear limbs were not strongly adapted to be rudders as they are in modern cheloniids.
A sixth cervical vertebra is preserved with PV4267, which shows that *C. wilsoni* possessed a planar joint between the centra of the sixth and seventh cervicals (Fig. 8I, J).

ASHLEYCHELYS, gen. nov.
ASHLEYCHELYS PALMERI, sp. nov.
(Figs. 9–15, S1–S3)

Holotype—ChM PV7002, a largely complete skeleton including the skull, lower jaw, much of the carapace and the plastron, girdle elements, humerus, and femur.

Type Locality—East bank of Limehouse Branch, 0.12 km (0.08 miles) east of intersection of Ohio Way and Houston Drive (33°01’30.2″N, 80°05’50.7″W); Berkeley County, South Carolina.

Formation and Age—Upper part of Ashley Formation, upper Rupelian, early Oligocene, within lower nannoplankton zone NP24.

Etymology—Genus named for the formation in which the type and paratype specimens were found; species named for Billy T. Palmer who found the specimen and donated it to The Charleston Museum.

Paratypes—SCSM 90.19.1, skull, from ditch in Crowfield subdivision (Ashley Formation), Berkeley County, South Carolina; ChM PV6860, skull and greater portion of carapace, from Mill Creek near Summerville (Ashley Formation), Berkeley County, South Carolina.

Referred Material—Ashley Formation: ChM GPV523, ChM PV6861, and PV7202. Chandler Bridge Formation: ChM PV2000, PV2140, PV2141, PV2142, PV2153, PV2174, PV2176, PV2181, PV2215, PV2220, PV2247, PV2259, PV2265, and PV7740.

Diagnosis—Moderately large sea turtle with a flattened and elongated skull and an anteroposteriorly elongated orbit; prefrontals form the anterodorsal border of the orbit, whereas frontals form only a small portion of the dorsal rim of the orbit; prominent brow ridges formed by the postorbitals lie above most of the dorsal rim of the orbit; quadrate turns strongly backward beneath squamosal; cavum tympani elongate, narrow, and tightly rounded at its posterior end; secondary palate moderately developed, with the vomer contributing about half of its length to the secondary palate; maxillary palate slightly rugose without pronounced troughs or ridges; pterygoid flanges robustly developed; planar joint between the sixth and seventh cervical vertebrae; carapace moderately convex with a maximum length estimated to be about 55 cm, almost as wide as long, and with the third costals most elongate; vertebral scutes hexagonal and about twice as wide as long; elongated costoperipheral fontanelles are persistently wide into adulthood; neurals exhibit a medial narrow low ridge unlike *Carolinochelys wilsoni* or *Procolphocelys charlestonensis*; carapace surface covered by an anastomosing pattern of grooves; hyoplastron and hypoplastron are angled sharply rather than gently upward away from the midline;

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FIGURE 4. Carapace of Carolinochelys wilsoni, ChM PV4792, in dorsal view.

xiphiplastra much narrower and longer than in *P. charlestonensis*; angle between scapular rods about 130°; shaft of humerus very straight.

**Description**—The holotype skull (Fig. 9) and paratype skull (Fig. 10) are from relatively young individuals that clearly show most of the suture lines and sulcal grooves. Between them, they permit a fairly detailed reconstruction of the skull in dorsal, lateral, and posterior views (Fig. 11). Like *C. wilsoni*, *A. palmeri* has a rather generalized stem-pancheloniid skull, with an external surface covered by a ubiquitous pattern of shallow pits and vermiform troughs. A distinctive feature is the pronounced brow ridges (Fig. 11A, D), formed by the postorbitals, which overhang the orbits more strongly than in *C. wilsoni* or *P. charlestonensis*. These two skulls do not offer a good view of the palate, but this portion of the skull can be seen on the paratype adult skull SCSM 90.19.1 (Figs. 12, 13). In ventral view, the secondary palate is moderately well developed, rather rough-surfaced, but without any prominent maxillary ridges or troughs. The basisphenoid does not separate the basioccipital from the pterygoids as it does in *C. wilsoni*. This adult skull is nearly identical in morphology to the ones in Figures 9 and 10, but about twice as large as the holotype. This indicates that the type was only about half grown at death.

The lower jaw is moderately expanded in its symphyseal region and has elongate jaw rami (Fig. 9C).

Portions of the fourth (ChM PV2142), sixth (PV6860), and seventh (PV2142) cervical vertebrae can be recognized (Fig. S1A–E in Supplementary Data). The fourth cervical is biconvex, the sixth has a concave anterior face and a planar posterior face, and the seventh has a planar anterior face and a slightly convex posterior face. These vertebrae are typical of moderately advanced pancheloniid turtles.

An imperfect scapula is present in specimen ChM PV2141 (Fig. S1L), and is complete enough to indicate that it had an angle of about 130° between the scapular rods. The humerus is very similar to that of modern cheloniids (Fig. S2), but differs strikingly from the humerus of *C. wilsoni* and *P. charlestonensis* in that its shaft is very nearly straight. In this regard, *A. palmeri* was more specialized for cheloniid-style aquatic-flying locomotion than either of the other two species. The femur associated with the holotype (Fig. S1F–J) has a bony ridge connecting the trochanter major with the femoral head, which represents a partial development of the bony ridges found between the femur head and the trochanters in modern crown cheloniids to improve their rear limbs as steering organs.

The carapace of the holotype of *A. palmeri* is missing its central region (Fig. 14A), but that part of the carapace is preserved in paratype ChM PV6860 (Fig. 14B). The features of these two specimens can be combined into a composite representation of the entire carapace (Fig. 15A). It is moderately convex, attains an
estimated length up to 55 cm (based on the size of the adult skull relative to the holotype skull and its associated carapace), and is slightly more elongate than wide with the neural-costal portion of the carapace widest across the third costals. The most notable features of this carapace are the wide and elongate costoperipheral fontanelles and the very wide vertebral scutes, which are about twice as wide as long.

All but the anterior portion of the plastron is preserved in the holotype (Fig. S3A). These elements can be supplemented by several other specimens (including paratype ChM PV6860 and PV9404; Fig. S3B–F), and the epiplastra are preserved with PV2141 (Fig. S1K). The proportions of the entoplastron can be reasonably estimated from the other elements, and a reconstruction of the entire plastron is shown in Figure 15B. The most notable features of this plastron are the remarkably elongate and thin xiphiplastra and the presence of a distinctly angular, anteroposteriorly trending bend in both the hyoplastra and hypoplastra, giving the plastron an angular rather than smooth shape in transverse cross-section.

**PROCOLPOCHELYS** Hay, 1908

**Diagnosis**—Large turtle with a deep skull, dorsal and lateral skull surfaces faintly ornamented by ridges, grooves, or pits in its anterior region; orbit round with prefrontals forming the anterior border; frontals form only a small portion of the dorsal orbit border; medially they project strongly forward along the midline between the prefrontals; supraoccipital process elongate; ventral surface of skull apparently has a moderately well developed secondary palate with longitudinal ridges on the palatal surface of the maxillae; planar joint between the sixth and seventh cervicals; carapace moderately convex, up to 95 cm in length, markedly longer than wide with the neural-costal portion of the carapace widest across the second costals; costoperipheral fontanelles wide and persistent throughout life; dorsal surface smooth and unsculptured or only very faintly sculptured; vertebral scutes hexagonal and about as wide as long; neurals in the central carapace region usually split transversely into anterior and posterior pieces of unequal size, the smaller piece bearing an internal scar for attachment to the tip of an underlying neural spine; xiphiplastra shorter and much wider than in *Ashleychelys palmeri*; angle between the scapular rods is about 120°; humerus large and stout with a rather short but robust lateral tubercle; femur has a bony ridge connecting the caput with the trochanter major.

**PROCOLPOCHELYS CHARLESTONENSIS**, sp. nov. (Figs. 16, 17, S4–S6)

**Holotype**—ChM PV6056, a largely complete carapace associated with a few fragmentary vertebrae, pectoral girdle elements, humerus, and femur.

**Type Locality and Horizon**—Ditch bank in Turnberry Place subdivision, 8.04 km (5 miles) north of S.C. Route 7 (Sam Rittenberg Boulevard) via S.C. Route 61 (32°51′21.76″N, 80°04′21.76″W), Charleston County, South Carolina. Chandler Bridge Formation, lower Chattian, late Oligocene, upper nannoplankton zone NP24.

**Referred Material**—The type specimen is supplemented by a skull fragment (Fig. S5A, B), consisting of much of the parietal, the frontal, and the prefrontal (ChM PV6055), found in the Chandler Bridge Formation near the Mark Clark Expressway in Charleston County, South Carolina. Although not associated with other skeletal elements, the large size of this specimen and its similarities with the skull of *Procolpochelys grandaeva*
(described below) make its allocation to *P. charlestonensis* reasonably certain. The humerus (Fig. S4C), ascribed by Hay (1923b) to *Carolinochelys wilsoni* (MCZ 1005-B) probably came from the Ashley Formation; it is nearly identical in appearance to the type specimen humerus of *P. charlestonensis* (Fig. S4D–F) and even slightly larger. Therefore, based both on its morphology and its great size, MCZ 1005-B is assigned here to *Procolpochelys charlestonensis*.

**Diagnosis**—So far as known, most elements are similar to *P. grandaeva*. Characteristics that distinguish *P. charlestonensis* from *P. grandaeva* are the relatively narrower costals and relatively wider vertebral scutes in the new species. Both species of *Procolpochelys* have supernumerary neurals and exceptionally thick costals and neurals that are unsculptured or only faintly sculptured on their dorsal surface. In these traits, both species differ from *Carolinochelys wilsoni* and *Ashleychelys palmeri*.

**Description**—The skull fragment referred to this species (Fig. S5A, B) consists of much of the left parietal, frontal, and prefrontal. The parietal is essentially complete along its medial edge and the medial portion of its posterior edge. The frontal is essentially complete and the posterior portion of the prefrontal is preserved. On its ventral side, the anterior portion of the parietal preserves the dorsal surface morphology of the brain cavity. This obviously was a very large turtle, with at least the posterior portion of its dorsal skull surface nearly smooth and with only a faint development of the vermiform grooves and pits that are so prominent on the skulls of both *Ashleychelys palmeri* and *Carolinochelys wilsoni*. A nearly smooth external surface similarly is found in the parietal region of the Miocene species *P. grandaeva* (see below), and this supports association of this skull fragment with the genus *Procolpochelys*.

Several vertebrae are preserved with the type. One is the seventh cervical (Fig. S5L, M), which has a ventral keel, a posteriorly convex centrum, and a planar anterior centrum. Another is a first sacral (Fig. S5G–I), and the third is an anterior caudal, probably the first (Fig. 16).

Most of one side or the other of the type carapace is preserved (Fig. 16). The costals and neurals are unusually thick, and this is also true of *P. grandaeva*. There is no sign of sculpturing on the external surface of the carapace bones as is seen in *C. wilsoni* and *A. palmeri*. The sulcal grooves are clearly visible, so the bone surfaces are not deeply worn or eroded. The carapace elements in *P. grandaeva* also are nearly smooth (Zangerl and Turnbull, 1955; Weems, 1974), so unsculptured costals and neurals are a real and diagnostically useful characteristic of this turtle. As is also typical for *P. grandaeva*, many of the neural elements are split transversely into anterior and posterior parts, the smaller of which bears an internal scar where the tip of a vertebral spine attached beneath it. The other element lay in the space between vertebral spines. Many of the costals, on their medial ends, have a scalloped indentation into which fit the neural elements that attached to the vertebral spines. Although not present on all of the costals, where this scalloped pattern occurs it is a very characteristic feature of both *P. grandaeva* and *P. charlestonensis*. In *P. charlestonensis*, the costals are stout, being less elongate laterally and longer anteroposteriorly than the equivalent elements.
in *P. grandaeva* (Fig. 17). Another important distinction between these two species is that the vertebral scutes in *P. charlestonensis* are relatively wider than they are in *P. grandaeva* (Fig. 17).

The hyoplastra and hypoplastra are not preserved with the type specimen, but a left epiplastron and right xiphiplastron are present (Fig. S6). The most notable feature in these elements is the exceptional width of the xiphiplastron.

The pectoral girdle elements (scapula and coracoid) are both preserved in the type (Fig. S4A, B). The angle between the scapular rods is about 120°. A single ilium (Fig. S5F) was the only element of the pelvic girdle recovered. The humerus is large and stout, with a rather short but robust lateral tubercle (Fig. S4D–F); in lateral view, its shaft has a slight but distinct downward curvature that is less pronounced than in *Carolinochelys wilsoni* but more pronounced than in *Ashleychelys palmeri.* The femur (Fig. S5C–E) is somewhat damaged but shows typical advanced pancheloniid proportions and has a ridge connecting the caput with the damaged trochanter major, suggesting that the rear limbs were partially adapted to being organs.

**PROCOLPOCHELYS GRANDAEVA** (Leidy, 1851)  
(Figs. 18, 19)

**Comments**—The carapace and the plastron of the Miocene sea turtle *P. grandaeva* were first adequately described by Zangerl and Turnbull (1955). Additional material referable to this taxon, including humerus, femur, and part of a basicranium, later was described by Weems (1974). Since that time, a much more complete skull of *P. grandaeva* (USNM 358862) (Fig. 18) was found by R.E.W. in the lower Miocene (mid-Burdigalian) Popes Creek Member of the Calvert Formation in Charles County, southern Maryland, in the bluffs along the Potomac River south of Popes Creek. At this long-collected locality, the only two kinds of pancheloniid carapace elements that have been found are those of *Trachyaspis lardyi* (= *Syllomus crispatus* Cope) and *P. grandaeva.* The skull of *T. lardyi* is known (Weems, 1980), and it is smaller and quite different from the more generalized pancheloniid skull described here. The additional information for *P. grandaeva* provided by this skull (USNM 358862) offers important supplemental information for defining and differentiating the genus *Procolpochelys.*

**Description**—Much of the morphology of the skull of *P. grandaeva* can be reconstructed from this specimen (Fig. 19). Its parietal, frontal, and prefrontal are quite comparable to the portions of those elements preserved in the only known skull fragment of *P. charlestonensis.* In dorsal view, the snout of *P. grandaeva* is short and rather pointed. In ventral view, the foramina orbito-nasale are relatively large and the pterygoids are comparatively quite narrow. The skull of *P. grandaeva* is here reconstructed with moderate pterygoid flanges (Fig. 19B), but this is only inferential because that region of the skull was not preserved on either side of the midline. Similarly, although the squamosal was not recovered, its bordering suture on the parietal indicates that its contribution to the roof of the skull was relatively small.

**EVOLUTIONARY GRADE OF THE SOUTH CAROLINA Oligocene Pancheloniid Turtles**

The morphological characteristics of Oligocene pancheloniid turtles from South Carolina are compared and contrasted in Table 1. Only a few of these character traits are known to be useful for determining the evolutionary grade of these turtles (Hirayama, 1994; Parham and Pyenson, 2010), and these were used to create the tree in Figure 20. Based on the presence or absence of these particular character states, *Carolinochelys wilsoni* is the most primitive of the three pancheloniid turtles found in the Ashley and Chandler Bridge formations. All three species possess a planar joint between the sixth and seventh cervicals and all have a scapular rod angle greater than 110°. Both of these characteristics are derived features not found among primitive pancheloniid turtles (Hirayama, 1994). Two other
derived character traits, typical of more advanced pancheloniid turtles, are found in *Ashleychelys palmeri* and *Procolpochelys charlestonensis*, but not in *C. wilsoni*. These are the presence of an attachment between the eighth costal rib and the eleventh peripheral and the presence of a ridge connecting the trochanter major to the femoral caput. None of these turtles, however, possesses the full complement of character traits that define the crown Cheloniidae (Hirayama, 1994), which include *Trachyapsis lardydi* plus the six living species *Natator depressus*, *Lepidochelys kempii*, *L. olivacea*, *Eretmochelys imbricata*, *Caretta caretta*, and *Chelonia mydas* and any fossil species nested within this group (e.g., *Caretta patriciae* Zug, 2001). By these definitions, *C. wilsoni* belongs among moderately advanced members of the stem group of Pancheloniidae, but the primitively arched shaft of the humerus and the absence of the other two advanced character-istics found in *P. charlestonensis* and *A. palmeri* place it near the bottom of this grade. Although the notches in the second peripheral elements of *C. wilsoni* are an autapomorphy that precludes it from being an ancestor to any later or living chelonid sea turtles, its general appearance nevertheless suggests a convergence in lifestyle with the living loggerhead turtle *Caretta caretta*.

*Procolpochelys charlestonensis* is a more advanced panche-loniid than *Carolinochelys wilsoni* but less advanced than *Ash-leychelys palmeri* (Fig. 20). Zangerl and Turnbull (1955) con-sidered *P. grandaeva* to be a primitive carettenine turtle, but that species and *P. charlestonensis* both have remarkably thick neurals and costals and attained exceptionally large size. Neither characteristic would be expected in an ancestor of modern carettenine turtles. Moreover, only a few of the characteristics found in crown cheloniids are present in this genus, even though some of these same character states are present in the contemporary *A. palmeri*. Therefore, the carettenine-like features seen in *Procolpochelys* seem to have evolved independently of the modern carettenine lineage.

*Ashleychelys palmeri* is the most advanced of the three pancheloniid turtles found in the Ashley and Chandler Bridge forma-tions. This is demonstrated by its very straight humeral shaft and the presence of a ridge connecting the femoral trochanters, both characteristics reflecting better adaptation to marine locomotion than was present in *Carolinochelys wilsoni* and *Procolpochelys charlestonensis*. An important advanced character-istic not found in *A. palmeri* is a ‘V’-shaped lateral tubercle on

---

**FIGURE 8.** Girdle and limb elements of Carolinochelys wilsoni. A–C, femur of ChM PV6081 in A, proximal, B, posterior, and C, anterior views; D, partial scapula of ChM PV8309; E, ilium of ChM PV8309; F, G, right humerus in F, anterior and G, ventral views (lateral tubercle broken away); H–J, sixth cervical vertebra in H, anterior, I, ventral, and J, posterior views.
the humerus. The absence of this characteristic indicates that *A. palmeri* was approaching the level of locomotor sophistication found among crown cheloniids but was not quite there. A number of autapomorphies debar *A. palmeri* from being ancestral to the crown cheloniids, including its flattened skull profile, flattened orbit, rearward tilted cavum tympani, and very wide vertebral scutes.

### A SYNOPSIS OF OLILOGENE PANCHELONIID SEA TURTLES

Only two early Oligocene (early Rupelian) sea turtles are known (Fig. 21). These are *Glarichelys knorri* from Germany (Karl, 2007) and possibly Poland (Mlynarski, 1959; but this material may be late Eocene) and *Allopleuron lipsiensis* (Karl, 2007) from Germany. *'Chelonia' caucasica*, originally reported as...
coming from the early Oligocene of Russia (Riabinin, 1929; Lapparent de Broin, 2001), instead comes from the early Miocene (Chkhikvadze, 1983, 1989) and currently is considered to be a nomen dubium (Averianov, 2002).

The record of mid-Oligocene (late Rupelian–early Chattian) sea turtles is more diverse and widespread. It includes the three species described here from South Carolina plus six nominal species from Europe and one species from western Asia. A number of other species have been named, but most or all are indeterminate, invalid, or junior synonyms of other species (Lapparent de Broin, 2001).

In Belgium, four nominal species have been described from the mid-Oligocene: *Chelone* (*Bryochelys*) *waterkeynii*, *Chelone vanbenedenii*, *Chelyopsis littoreus*, and *Oligochelone rupeliensis*. *Ch. vanbenedenii*, *Ch. waterkeynii*, and *Cl. littoreus* were described by Smets (1886, 1887a, and 1887b, respectively), who soon after published another paper concluding that *Cl. littoreus* was a chimera with vertebral and girdle elements coming from *Psphophorus rupeliensis* and other elements coming from *Chelone vanbenedenii* (Smets, 1888:194). As the type species of *Chelyopsis* is *Cl. littoreus*, *Chelyopsis* became a nomen nudum. Similarly, Dollo (1909) announced a new genus and species, *Oligochelone rupeliensis*, about which he was planning to publish in the then near future. This apparently never happened, however, and Lapparent de Broin (2001:183) has concluded that this taxon also is a nomen nudum. Thus, only two valid species of Oligocene sea turtles are presently recognized from Belgium. Neither of these species can be validly assigned to *Chelonia* or to the defunct genus *Chelone vanbenedenii*. Although both species are based on very fragmentary material, they appear to be valid. Characterization of these two species has been complicated because Smets (1888:208) concluded that the snout that he originally referred to *Ch. vanbenedenii* actually belonged to *B. waterkeynii*. He distinguished between the carapaces of these two species by noting *Bryochelys waterkeynii* has “expansions foliac´ees,” whereas *Chelone vanbenedenii* lacks them (Smets, 1888:123–124). This seemingly means that *B. waterkeynii* has a sculptured or reticulate pattern on its carapace, whereas ‘*Ch.’ vanbenedenii’ does not.

Five nominal species have been described from the mid-Oligocene of Germany and Switzerland: *Glarichelys knorri* (Gray, 1831) (see Zangerl, 1958), *Chelyopsis holsaticus* Dames, 1894, *Chelonia gwinneri* Wegner, 1917, *Chelyopsis halleri* Karl, 1989, and *Rupelchelys breitkreutzi* Karl and Tichy, 1999. Recently, Karl (2007:29, 38) synonymized *Cl. holsaticus*, *Ch. gwinneri*, and *C. halleri* with *G. knorri*, leaving only *G. knorri* and *R. breitkreutzi* as recognized species from this region. A nearly complete panchelonid skull and other material from the...
mid-Oligocene of Azerbaijan was referred to *G. gwinneri* (now *G. knorri*) by Aslanova et al. (1979), who also reported remains of *Glarichelys* from Romania and probably Kazakhstan. This species therefore was widespread in central Europe and western Asia.

Two other species have been named from the mid-Oligocene. One of these, *Chelone* *acuticostata* from Italy (Bergounioux, 1954), is very poorly known and cannot be meaningfully diagnosed or compared with the other species (Lapparent de Broin, 2001). The other species, *Chelonia* *aralis* from the Aral Sea area of Kazakhstan (Khosatzky, 1945), likewise is very poorly known and presently is considered to be Cheloniidae indet. (Averianov, 2002).

Identifiable pancheloniid sea turtles are all but unknown from the later Oligocene (middle to upper Chattian) except for *Glarichelys* *knorri* from the later Oligocene (middle to upper Chattian) except for *Glarichelys* *knorri* from the later Oligocene (middle to upper Chattian) except for *Glarichelys* *knorri*.

Neither of the Belgian Oligocene pancheloniid sea turtles appears to be particularly close to any of the South Carolina Oligocene species. The plastron of *Bryocheles* *waterkeynii* (Smets, 1888) differs from that of *Ashleychelys* *palmeri* in that *A. palmeri* has a much more anteroposteriorly elongate hyoplastron (Fig. 15B). The deep pit in the premaxillae of *B. waterkeynii* for reception of an upturned tip of the dentaries (Smets, 1886) also is quite different from *A. palmeri*. *Bryocheles* *waterkeynii* has a plastron that obviously differs from the plastron of *Carolinaochelys* *wilsonii*, for *C. wilsonii* has a much wider sutural border between the hyoplastron and hypoplastron (Fig. 7D). The fourth left costal of *B. waterkeynii*, though not extremely elongate, still is about twice as long as it is wide (Smets, 1888). In this characteristic, it differs obviously from the fourth costal of *Procolpochelys* *charlestonensis*, which is only slightly wider than it is long (Fig. 17B).

*Chelone* *vanbenedenii* (Smets, 1886) has wide vertebral scutes on its carapace that are similar to the scutes on *Ashleychelys* *palmeri* (Fig. 14B) but quite unlike the much narrower vertebral scutes found on *Carolinaochelys* *wilsonii* (Fig. 6) and *Procolpochelys* *charlestonensis* (Fig. 17B). In other regards, *Ch.* *vanbenedenii* is quite different from *A. palmeri*. Its nuchal has an elongate neck that projects posteriorly about halfway back between the first costals (Smets, 1886), and this characteristic is quite unlike the nuchal of *A. palmeri* (Fig. 15A) that does not project at all rearward between the first costals. Similarly, the sixth costal of *Ch.* *vanbenedenii* (Smets, 1886) is relatively less elongated than the sixth costal of *A. palmeri* (Fig. 15A). The proximal end of the third costal (Smets, 1886) shows no hint of a scalloped emargination to accommodate a supernumerary split neural such as is characteristic of *P. charlestonensis* and *P. grandaeova* (Fig. 17B, C).

None of the German/Swiss Oligocene pancheloniid turtles shows any obvious close relationship to either the South Carolina or Belgian turtles. *Rupelchelys breitkreutzi* is based on a partial carapace that has unusually narrow neural elements (Karl and Tichy, 1999); it is quite unlike any of the South Carolina turtles described here. The prefrontals of *Glarichelys* *knorri* are quite elongate and its humerus has a very poorly developed lateral
FIGURE 13. Ashleychelys palmeri, gen. et sp. nov. A–C, restoration of adult skull, based on SCSM 90.19.1, in A, dorsal, B, ventral, and C, right lateral views. Abbreviations: bo, basisphenoid; bs, basisphenoid; eo, exoccipital; fr, frontal; ju, jugal; mx, maxilla; op, opisthotic; pa, parietal; pal, palatine; pf, prefrontal; pm, premaxilla; po, postorbital; pt, pterygoid; qj, quadratojugal; qu, quadrate; soc, supraoccipital; sq, squamosal; v, vomer.

FIGURE 15. *Ashleychelys palmeri*, gen. et sp. nov. A, composite restoration of the carapace based on Figure 14A–B; B, composite restoration of the plastron of *Ashleychelys palmeri* based on the holotype ChM PV7002, paratypes ChM PV6860 and ChM PV9404, and epiplastra from ChM PV2141. Entoplastron is unknown.

FIGURE 16. *Procolpochelys charlestonensis*, sp. nov. Carapace of holotype, ChM PV6056.
tubercle (Zangerl, 1958). Both of these traits debar _G. knorri_ from either the ancestry of or synonymy with any of the South Carolina species, all of which have a robust and elongate lateral tubercle and prefrontals with normal pancheloniid proportions. Additionally, the short and wide snout of _G. knorri_ (Zangerl, 1958) with its very short secondary palate (if the specimen illustrated by Aslanova et al. [1979] is correctly assigned to _G. knorri_) is quite different from the snouts of all of the South Carolina species. The carapace has very large fontanelles, even in adults, and its surface is nearly smooth. In this trait it is somewhat reminiscent of the carapace of _P. charlestonensis_, but the carapace of _G. knorri_ is even more reduced and shows no indication of the split neurals that are so characteristic of the genus _Procolpochelys_. Similarly, _Allopleuron lipsiensis_ (Karl, 2007) also has very large fontanelles as in _Procolpochelys grandaeva_ and _P. charlestonensis_, but again there is no hint of split neurals.

**DISCUSSION AND CONCLUSIONS**

The turtle material found in the Ashley and Chandler Bridge formations shows that three species of pancheloniid sea turtles inhabited coastal North American waters in what is now South Carolina during mid-Oligocene time. In terms of the numbers of specimens found, the most common of these was _Carolinochelys wilsoni_. Less common but still abundant was _Ashleychelys palmeri_, whereas _Procolpochelys charlestonensis_ was relatively rare in this area. The carapace of _A. palmeri_ is estimated to have reached a length of about 55 cm, the carapace of _C. wilsoni_ is known to have reached a length of about 70 cm, and the carapace of _P. charlestonensis_ was about 95 cm long.

Most of the specimens of _C. wilsoni_ and _A. palmeri_ represent juvenile individuals that are less than half grown; adult specimens are uncommon. In contrast, only three specimens, all adult, are known of _P. charlestonensis_. This disjunct distribution of growth stages among the discovered remains strongly suggests that _C. wilsoni_ and _A. palmeri_ nested in or near the coastal South Carolina region. The hatchlings stayed in the coastal region until about half grown before heading out to open waters, returning thereafter only to lay eggs. In contrast, _P. charlestonensis_ apparently was only a seasonal adult visitor that nested and grew up elsewhere. The occurrence of half-grown specimens of _P. grandaeva_ in the Miocene Calvert Formation (Weems, 1974), suggests that _P. charlestonensis_ may have nested in Oligocene time well north of the South Carolina region.

Notable in the Oligocene of South Carolina is the absence of any turtle remains referable to durophagous stem cheloniids. Turtles of this sort were present in eastern North America (what is now the eastern U.S.A.) throughout the Paleocene (Weems, 1988), but after that their remains are unknown from the Atlantic Coastal Plain. In contrast, a durophagous stem-pancheloniid turtle ( _Pacifichelys_ ) has been documented from deposits as young as the middle Miocene in California (Lynch and Parham, 2003) and western South America (Parham and Pyenson, 2010), indicating the persistence of this lineage at least through the middle Miocene along the Pacific coasts of North and South America. The complete absence of durophagous stem pancheloniids in the Oligocene and Miocene deposits of the Atlantic Coastal Plain (and conversely the complete absence of _Procolpochelys_ along the Pacific Coast of North America) provides compelling negative evidence that, by the mid-Oligocene, the pancheloniid sea turtles of the southeastern United States had become an endemic assemblage that was isolated from other Oligocene sea turtle assemblages found elsewhere in the world. This sense of geographic isolation seemingly is reinforced by the cetacean assemblage that
TABLE 1. Comparison of the morphological characteristics of *Ashleychelys*, *Carolinochelys*, and *Procolpochelys*, with crown Cheloniidae (*Trachyaspis*, *Natator*, *Lepidochelys*, *Caretta*, *Chelonia*, *Eretmochelys*).

<table>
<thead>
<tr>
<th>No.</th>
<th>Character</th>
<th>Carolinochelys</th>
<th>Procolpochelys</th>
<th>Ashleychelys</th>
<th>Crown Cheloniidae</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Skull profile (height/length)</td>
<td>Normal (0.5)</td>
<td>Normal (0.5)</td>
<td>Flattened (0.4)</td>
<td>Flattened or normal (0.4–0.5)</td>
</tr>
<tr>
<td>2</td>
<td>Orbit shape (height/width)</td>
<td>Subround (0.7)</td>
<td>Subround (0.8)</td>
<td>Flattened ellipse (0.5)</td>
<td>Subround to nearly equant (0.7–0.9)</td>
</tr>
<tr>
<td>3</td>
<td>Skull surface texture</td>
<td>Sculptured</td>
<td>Smooth</td>
<td>Sculptured</td>
<td>Sculptured to smooth</td>
</tr>
<tr>
<td>4</td>
<td>Cavum tympani tilt</td>
<td>Near vertical</td>
<td>Near vertical</td>
<td>Rearward</td>
<td>Near vertical to rearward</td>
</tr>
<tr>
<td>5</td>
<td>Supraorbital ridge</td>
<td>Slight</td>
<td>Slight</td>
<td>Prominent</td>
<td>Slight to prominent</td>
</tr>
<tr>
<td>6</td>
<td>Prefrontal location on orbital rim</td>
<td>Anterodorsal</td>
<td>Anterodorsal</td>
<td>Dorsal</td>
<td>Dorsal</td>
</tr>
<tr>
<td>7</td>
<td>Frontal: max. external length/max. midline</td>
<td>1.6</td>
<td>2.2</td>
<td>1.6</td>
<td>1.2–3.0</td>
</tr>
<tr>
<td>8</td>
<td>Narial height/width</td>
<td>0.7</td>
<td>0.8</td>
<td>1.0</td>
<td>1.0</td>
</tr>
<tr>
<td>9</td>
<td>Snout shape</td>
<td>Slight</td>
<td>Slight</td>
<td>Prominent</td>
<td>Slight to prominent</td>
</tr>
<tr>
<td>10</td>
<td>Premaxilla on palate</td>
<td>Long</td>
<td>Short</td>
<td>Long</td>
<td>Short to long</td>
</tr>
<tr>
<td>11</td>
<td>Pterygoids</td>
<td>Very narrow</td>
<td>Very narrow</td>
<td>Narrow</td>
<td>Narrow</td>
</tr>
<tr>
<td>12</td>
<td>Maxillary palatal trough</td>
<td>Deep</td>
<td>Deep</td>
<td>Shallow</td>
<td>Shallow to deep</td>
</tr>
<tr>
<td>13</td>
<td>Palatoceous articulation between 6th and 7th</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
</tr>
<tr>
<td>14</td>
<td>Carapace surface texture</td>
<td>Sculptured</td>
<td>Faintly sculptured</td>
<td>Sculptured</td>
<td>Faint to strong sculpture</td>
</tr>
<tr>
<td>15</td>
<td>Carapace thickness</td>
<td>Moderate</td>
<td>Thick</td>
<td>Moderate</td>
<td>Moderate</td>
</tr>
<tr>
<td>16</td>
<td>Carapace width/Carapace length</td>
<td>0.7</td>
<td>0.7</td>
<td>0.9</td>
<td>0.7–1.1</td>
</tr>
<tr>
<td>17</td>
<td>Location of greatest width across neurals and</td>
<td>Across fourth costals</td>
<td>Across second costals</td>
<td>Across third costal</td>
<td>Across third or fourth costal</td>
</tr>
<tr>
<td>18</td>
<td>2nd peripherals notched</td>
<td>No</td>
<td>No</td>
<td>No</td>
<td>No</td>
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<td>19</td>
<td>Neurals</td>
<td>Single</td>
<td>Split</td>
<td>Single</td>
<td>Single or split</td>
</tr>
<tr>
<td>20</td>
<td>Medial neural ridge</td>
<td>No</td>
<td>No</td>
<td>Yes</td>
<td>Yes or no</td>
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<tr>
<td>21</td>
<td>Costoperipheral fontanelles</td>
<td>Narrow</td>
<td>Wide</td>
<td>Wide</td>
<td>Narrow or wide</td>
</tr>
<tr>
<td>22</td>
<td>Vertebral scutes</td>
<td>No</td>
<td>No</td>
<td>Yes</td>
<td>Yes</td>
</tr>
<tr>
<td>23</td>
<td>8th costal rib attaches to 11th peripheral</td>
<td>No</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
</tr>
<tr>
<td>24</td>
<td>Humeral shaft</td>
<td>Strongly curved</td>
<td>Slightly curved</td>
<td>Straight</td>
<td>Straight</td>
</tr>
<tr>
<td>25</td>
<td>Humerus with 'V'-shaped lateral tubercle</td>
<td>No</td>
<td>No</td>
<td>No</td>
<td>No</td>
</tr>
<tr>
<td>26</td>
<td>Scapular rod angle &gt;110°</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
</tr>
<tr>
<td>27</td>
<td>Trochanter major connected to femoral caput by</td>
<td>No</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
</tr>
<tr>
<td>28</td>
<td>Femoral trochanters connected by ridge</td>
<td>No</td>
<td>No</td>
<td>Yes</td>
<td>Yes</td>
</tr>
</tbody>
</table>

Abbreviation: max., maximum.
FIGURE 19. Restoration of the skull of *Procolpochelys grandaeva* based on USNM 358862. **A**, dorsal; **B**, ventral; **C**, posterior; and **D**, left lateral views. The central palatal region of *P. grandaeva* is unknown and thus shown by dashed lines. Abbreviations: bo, basioccipital; bs, basisphenoid; eo, exoccipital; fr, frontal; ju, jugal; mx, maxilla; oc, occipital condyle; op, opisthotic; pa, parietal; pal, palatine; pf, prefrontal; pm, premaxilla; po, postorbital; pt, pterygoid; qu, quadrate; soc, supraoccipital; sq, squamosal; v, vomer.

FIGURE 20. Cladogram constructed by Hennig argumentation, showing the relative relationships of *Carolinochelys*, *Ashleychelys*, and *Procolpochelys* to each other and to earlier and later pancheloniids. The numeric designations for the character states used in this cladogram are shown in Table 1. Character states 13 and 26, common to all three taxa, are not present in primitive pancheloniids and thus serve to place all of them above that evolutionary grade. Character state 25 is present in all crown cheloniids (living genera plus *Trachyaspis*) and thus serves to place all three below that evolutionary grade.
co-occurs with these turtles, because two of the most primitive odontocete families (Xenorophiidae and Agorophiidae) are presently known only from the Carolina region, and xenorophids are abundant on a scale similar to that of Carolinochelys wilsoni (Whitmore and Sanders, 1977).

Except for the advanced Miocene chelonid Trachyaspis lardy (senior synonym of Syllomus aegyptiacus; Lapparent de Broin, 2001), the pre-Pliocene fossil record of pancheloniid turtles suggests that regionally localized distributions of coastal-dwelling genera and species, incompletely adapted to high-seas life, were the norm among these turtles. Truly cosmopolitan high-seas chelonids are rare before the Pliocene and completely unknown before the Miocene. This change in habitat from predominantly coastal forms to high-seas forms closely corresponds to (and is probably directly related to) the Neogene decline of dermochelyid turtles, which were represented in Oligocene time by at least three species in South Carolina and today are represented by only one worldwide. It is not at all clear, however, whether chelonids have moved into an increasingly vacated dermochelyid ecological niche or whether chelonids have in some way contributed directly to the decline of the dermochelyids.

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LITERATURE CITED


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