

# More-complete remains of *Procolpochelys charlestonensis* (Oligocene, South Carolina), an occurrence of *Euclastes* (upper Eocene, South Carolina), and their bearing on Cenozoic pancheloniid sea turtle distribution and phylogeny

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**Abstract.**—New and more-complete material of *Procolpochelys charlestonensis* Weems and Sanders, 2014 provides the first detailed information on the skull, jaw, and plastron of this species, which occurs in the Oligocene Ashley and Chandler Bridge formations near Charleston, South Carolina. This material allows a much more detailed comparison of this turtle with the co-occurring pancheloniid species *Ashleychelys palmeri* Weems and Sanders, 2014 and *Carolinochelys wilsoni* Hay, 1923a, as well as with its Miocene successor *Procolpochelys grandaeva* (Leidy, 1851). Fused dentaries, found in the Cooper River north of Charleston, belong to the pancheloniid genus *Euclastes*, previously known only from the Upper Cretaceous and Paleocene. This specimen, apparently from the upper Eocene Parkers Ferry Formation, expands the temporal range of this genus and indicates that *Euclastes* survived in the North Atlantic basin far longer than was previously known. These new finds, combined with previous records of fossil pancheloniid sea turtles, provide an improved picture of the temporal distribution, evolutionary trends, and likely phylogeny of pancheloniids from the Late Cretaceous to the present.

## Introduction

A pancheloniid sea turtle, *Carolinochelys wilsoni*, was first described from the Oligocene of the Charleston, South Carolina (S.C.) region by Hay (1923a, 1923b) based on a well-preserved skull and a humerus that he presumed represented the same species. Based on a great many specimens found in the Charleston region over the past forty years, Weems and Sanders (2014) recently provided a much more complete description of *C. wilsoni* and named two more Oligocene pancheloniid species (*Ashleychelys palmeri* and *Procolpochelys charlestonensis*). Both *Carolinochelys* and *Ashleychelys* were represented by enough material to establish most of their skeletal anatomy, but the third species (*Procolpochelys charlestonensis*) was largely based on a single specimen that included good carapace material, but only a scattering of other elements. Fortunately this associated material included the humerus, which shows that the humerus Hay (1923b) ascribed to *Carolinochelys* actually pertains to *P. charlestonensis* Weems and Sanders, 2014. Recently, much more complete material of *P. charlestonensis* has been discovered in the Charleston, S.C. region (Fig. 1) and placed in the Mace Brown Museum of Natural History at the College of Charleston. This material is described here to largely complete documentation of the axial skeleton of this turtle, which now can be compared in much greater detail to the skeletons of the other two South Carolina Oligocene pancheloniid species. A pair of fused dentaries, referable to the pancheloniid genus *Euclastes*, also recently came to light, which

appears to document the persistence of this turtle throughout most or all of the Eocene.

## Materials and methods

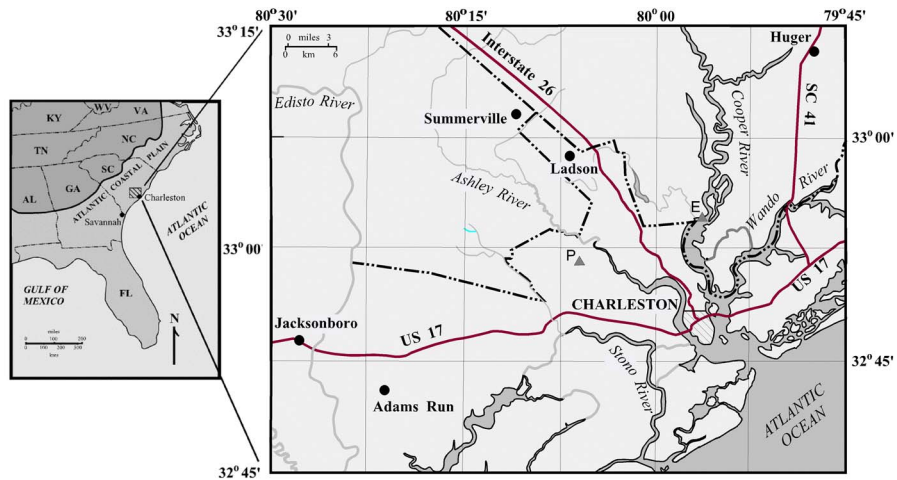
*Repositories and institutional abbreviations.*—The material examined for this study is housed in the College of Charleston Natural History Museum (CCNHM) and in the vertebrate paleontology collections of the Charleston Museum (ChM PV). Anatomical nomenclature used in the descriptions provided herein follows Gaffney (1979), especially his fig. 9.

## Systematic paleontology

Class Reptilia Laurenti, 1768  
Order Testudines Linnaeus, 1758  
Suborder Eucryptodira Gaffney, 1975  
Family Pancheloniidae Joyce, Parham, and Gauthier, 2004  
Genus *Procolpochelys* Hay, 1908  
*Procolpochelys grandaeva* (Leidy, 1851)  
Figures 2, 3, 6

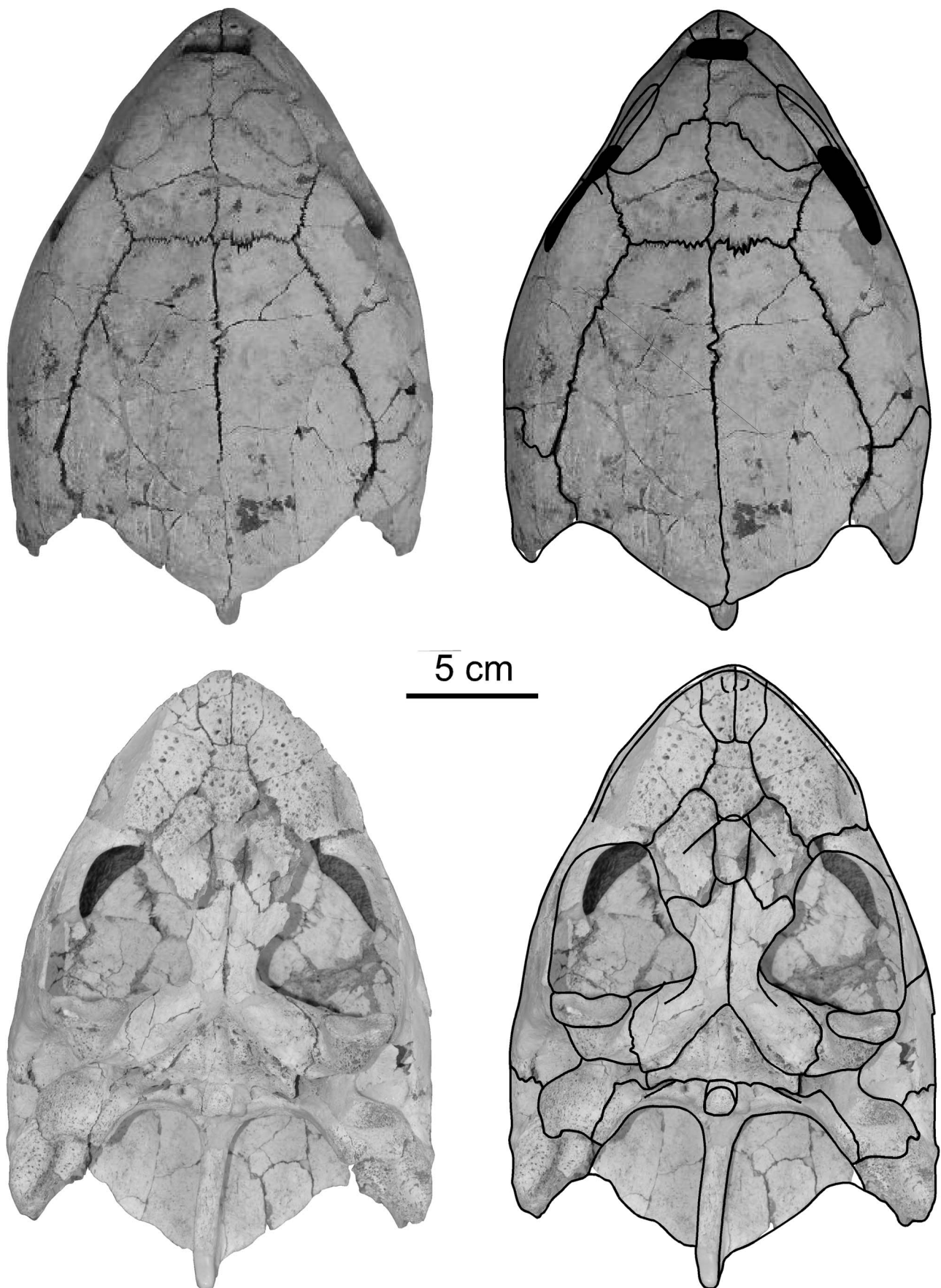
*Materials.*—CCNHM 893, associated skull and lower jaws; CCNHM 300.1, associated carapace and plastron.

*Occurrence.*—These specimens were collected from the Chandler Bridge Formation (upper Oligocene, mid-Chattian) in Charleston County, South Carolina. More specific locality data

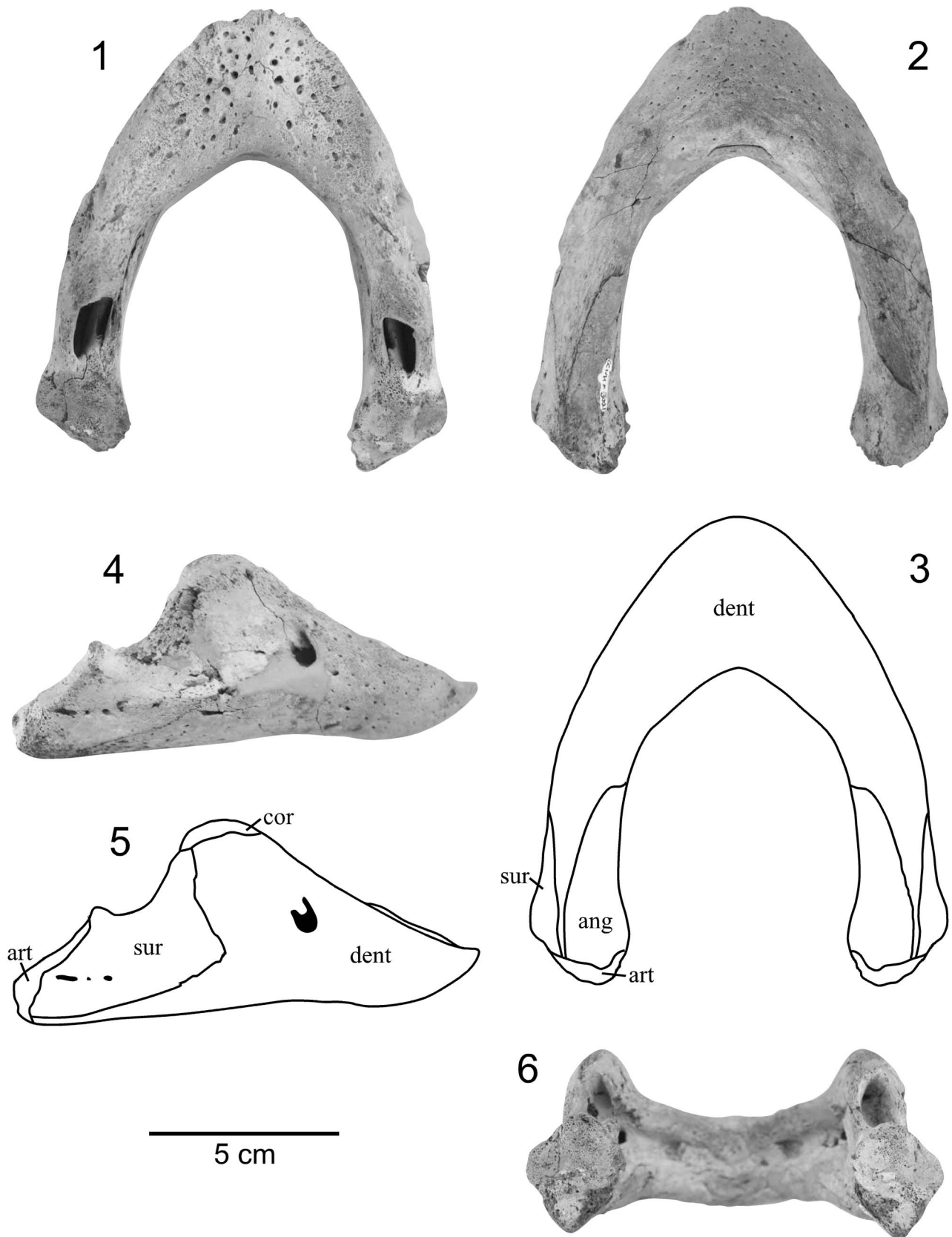


NP/NN ZONE	SERIES (Stage)	STRATIGRAPHIC UNIT	
NN 1-4	UPPER OLIGOCENE (Chattian)	Edisto Formation	
NP 25		Chandler Bridge Formation	
NP 24			
NP 23	LOWER OLIGOCENE (Rupelian)	Cooper Group	Ashley Fm.
NP 22			Givhans Ferry Mem.
NP 21			Runnymede Marl Mem.
NP 19/20	UPPER EOCENE (Priabonian)		Gettysville Mem.
NP 18			Harleyville Formation
			Parkers Ferry Formation
			Tupelo Bay Formation, Pregonnall Member

**Figure 1.** (Top) Regional map showing the Charleston, South Carolina region and the approximate areas where the specimens discussed here were found. Exact locality data is available from College of Charleston Natural History Museum. P=*Procolpochelys* localities, E=*Euclastes* locality. (Bottom) Upper Eocene and Oligocene stratigraphic units known from the Charleston region.



**Figure 2.** Skull of *Procolpochelys charlestonensis* (CCNHM 893). (Left) unretouched photos, (right) photos with skull element boundaries marked for clarity.



**Figure 3.** Lower jaws of *Procolpochelys charlestonensis* (CCNMH 893) in (1) dorsal, (2, 3) ventral, (4, 5) right lateral, and (6) posterior views. Ang = angular, art = articular, cor = coronoid, dent = dentary, sur = surangular.

is available at the Mace Brown Museum of Natural History at the College of Charleston.

*Expanded description.*—One of the two new specimens (CCNHM 893) consists of an associated skull and lower jaws (Figs. 2, 3). Skull fragments associated with the type specimen of *P. charlestonensis* are quite similar to comparable parts of the skull described here, which also is similar to the skull of the Miocene species *P. grandaeva* (Weems and Sanders, 2014). In dorsal view, *P. charlestonensis* has a broad snout but otherwise a fairly standard cheloniid arrangement of skull elements, with orbits facing laterally, parietals much longer than wide, premaxillae not fused together, and weak temporal emargination. Sulci marking the borders of the dermal scutes of the skull are not preserved in this specimen. In ventral view, *P. charlestonensis* has a well-developed secondary palate that completely covers the vomerine pillar but does not extend quite as far back as the anterior borders of the fossae temporalis inferior openings. The antero-lateral borders of the vomer are concave, which causes the anterior end of the vomer to have somewhat restricted contact with the premaxillae. Vomer and premaxillae are nearly equal in length on the secondary palate. The pterygoids have a mid-ventral ridge and their processus pterygoideus externus are reduced and have a strongly rounded border. The skull of *P. charlestonensis* is distinctly different from the skulls of *Carolinochelys wilsoni* and *Ashleychelys palmeri* in a number of features (Fig. 4). The snout of *P. charlestonensis* (width/length ratio = 0.60) is relatively shorter than the snouts of *A. palmeri* (0.64) and *C. wilsoni* (0.72). The palate of *P. charlestonensis* (palate length/snout length ratio = 0.86) is relatively longer than the palates of *C. wilsoni* (0.63) and *A. palmeri* (0.79). *Procolpochelys charlestonensis* is like *A. palmeri*, and unlike *C. wilsoni*, in that the vomerine ridge is not visible in ventral view, the supraoccipital ridge is thin, the processus pterygoideus externus are well developed, the palatine is a major contributor to the antero-lateral rim of the fossa temporalis inferior, the vomer is as long or longer than the premaxilla on the surface of the secondary palate, and the parietals are longer than they are wide. *Procolpochelys charlestonensis* is like *C. wilsoni*, and unlike *A. palmeri*, in that the prefrontal is located on the antero-dorsal rim of the orbit rather than on the dorsal margin, the tip of the snout is angular rather than rounded, and the pterygoids are very narrow at their most constricted mid-length point. These similarities and differences demonstrate that these are three distinctly different genera of turtles.

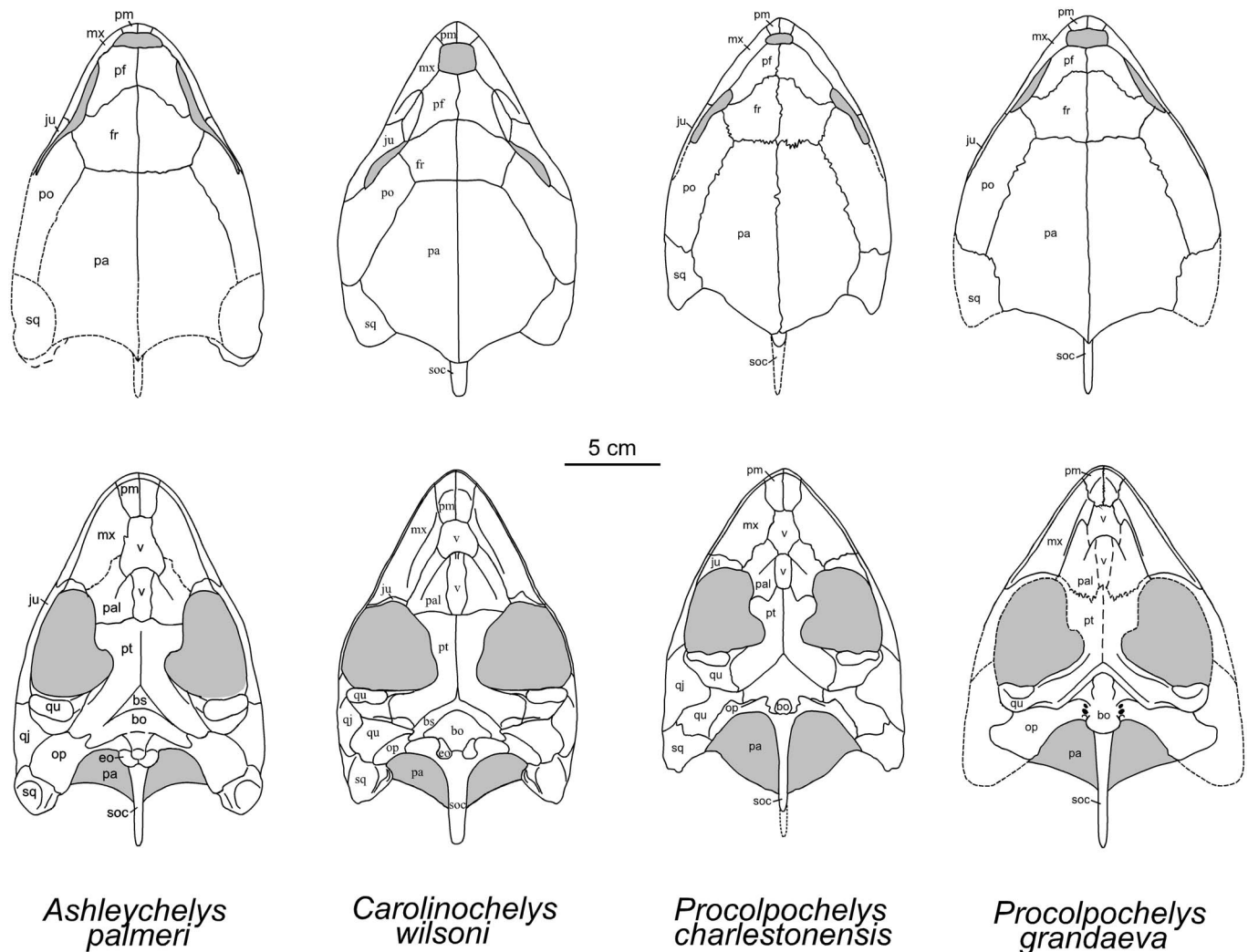
The well-preserved lower jaws (Fig. 3) allow useful comparisons with the lower jaws of the other two pancheloniid species in this fauna (Fig. 5). In *P. charlestonensis*, the high coronoid ridge on the dentary, the expansion of the symphyseal region of the lower jaws into a broad triturating surface, and the absence of a strongly upturned tip to the beak all indicate that this animal had a powerful, dominantly crushing bite. The Meckelian grooves on each jaw ramus also are notably short and rounded in dorsal appearance. This extends the crushing lateral edges of the lower jaws far rearward relative to most cheloniid turtles, which resulted in a greatly shortened posterior jaw region. This appears to be an adaptation for increasing the crushing force that could be generated by the jaw musculature. In sharp contrast (Fig. 5), the lower jaws of *A. palmeri* are

relatively much narrower, the distal tip of the beak is much sharper, and the jaw rami are much straighter and far less robust. These characteristics suggest that *A. palmeri* was adapted to shearing food rather than crushing it (Parham and Pyenson, 2010). The lower jaw of *C. wilsoni* is intermediate in its conformation, though somewhat closer to *Procolpochelys* in terms of its robustness.

The second new specimen of *Procolpochelys charlestonensis* (CCNHM 300.1) includes a nearly complete carapace and plastron (Fig. 6), of which the carapace is quite comparable in its size and overall morphology to the holotype carapace of *P. charlestonensis* (Fig. 7) except for the much narrower costoperipheral fontanelles in the new specimen. The narrowness of these fontanelles indicates that this animal was much older and more mature than the holotype at the time of its death. Even so, the costoperipheral fontanelles remained open throughout life (Fig. 6, lower right) and did not tend to close up with age, as in *C. wilsoni* (Fig. 7). The new specimen unfortunately does not preserve the shallow grooves that mark the borders of the dermal scutes that overlay the bones of the carapace, but these are present in the holotype. The rib-free peripheral element in the posterior shell lies between the seventh and eighth costal ribs and not between the sixth and seventh costal ribs.

Comparative illustrations of the plastra of the three Oligocene cheloniid species from South Carolina plus the Miocene species *P. grandaeva* are shown in Figure 8. The most notable difference among these is that the central fontanelle of the plastron of *C. wilsoni* is much narrower than that of either *A. palmeri* or *P. charlestonensis*. Although the central fontanelle is about equally wide in both *A. palmeri* and *P. charlestonensis*, the length of the central fontanelle in *P. charlestonensis* is relatively about twice as long as the central fontanelle in *A. palmeri*. The mid-lateral fontanelles are much wider in *A. palmeri* than they are in the other two genera, so *A. palmeri* had a more reduced plastron than either *C. wilsoni* or *P. charlestonensis*.

*Expanded diagnosis.*—Large turtle with a deep skull and wide but angular beak; dorsal and lateral skull surface faintly ornamented by ridges, grooves, or pits in its anterior region; orbits round with prefrontals forming their antero-dorsal borders; frontals form only a small portion of the dorsal orbit border but medially project strongly forward along the midline between the prefrontals; parietals longer than wide; supraoccipital process elongate; ventral surface of skull has an elongate secondary palate with the vomerine ridge covered and thus hidden from view, premaxillae and vomer of nearly equal length on the secondary palate surface; longitudinal ridges present on the palate surface of the maxillae; palatines form the antero-medial border of the fossa temporalis inferior; pterygoids very narrow in their mid-length region, with a prominently developed processus pterygoideus externus along the antero-lateral margin of each; planar joint between the sixth and seventh cervicals; carapace moderately convex, up to 110 cm in length, markedly longer than wide with the central (neural-costal) portion of the carapace widest across the second costal region; tenth peripheral has no attachment socket to receive the rib of either the seventh or eighth costal; costoperipheral fontanelles wide and persistent throughout life; dorsal surface smooth or only very faintly sculptured; vertebral scutes hexagonal and about as wide as long; juvenile carapace with normal pancheloniid thickness, but



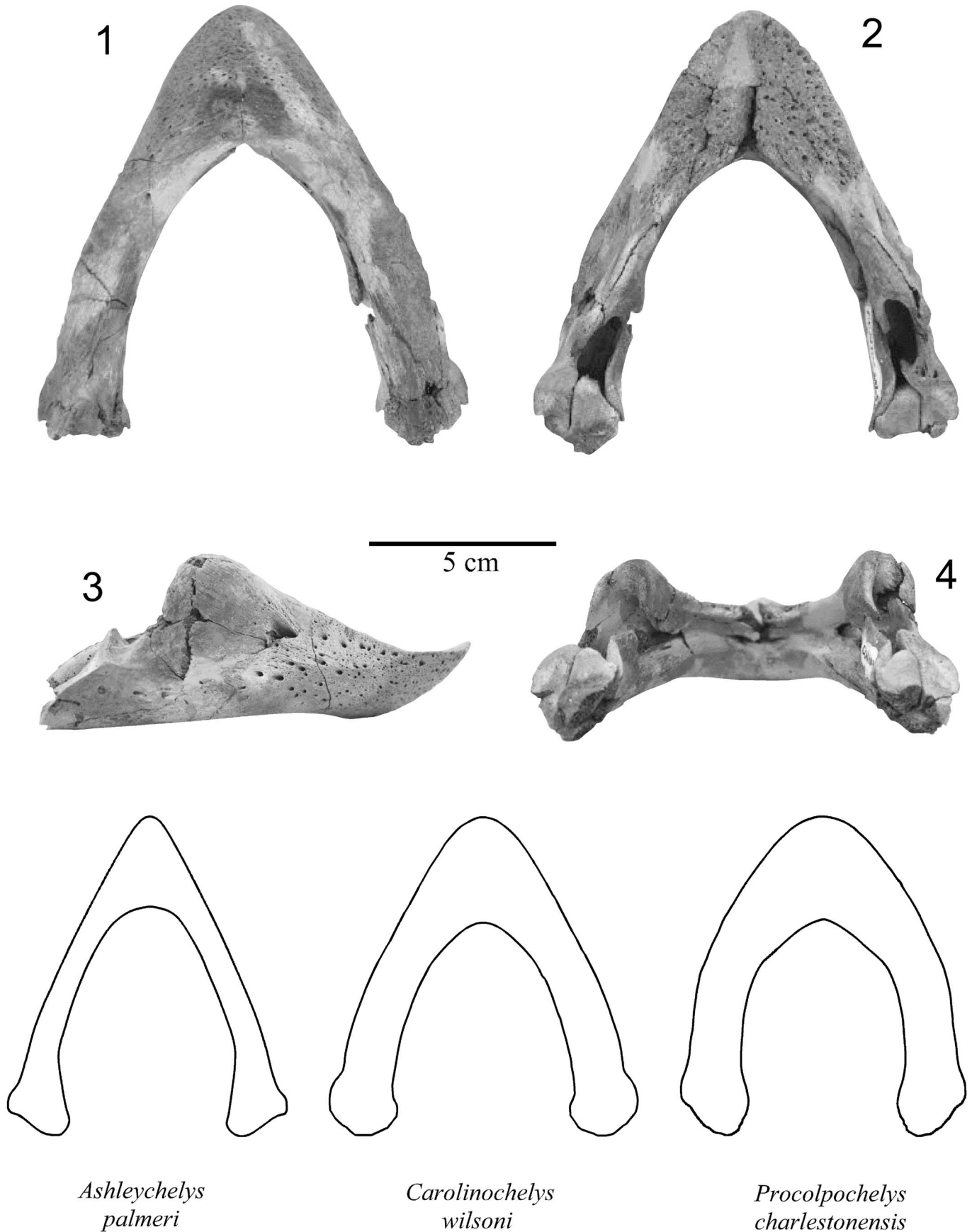
**Figure 4.** Comparison of the skulls of *Ashleychelys*, *Carolinochelys*, and *Procolpochelys*. Bo = basioccipital, bs = basisphenoid, eo = exoccipital, fr = frontal, ju = jugal, mx = maxilla, op = opisthotic, pa = parietal, pal = palatine, pf = prefrontal, pm = premaxilla, po = postorbital, pt = pterygoid, qj = quadratojugal, qu = quadrate, soc = supraoccipital, sq = squamosal, v = vomer

carapace thickens rapidly with age so that adults have extremely thick costal and neural elements; 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; plastron reduced with typical pancheloniid conformation, central fontanelle wide and elongate anteroposteriorly, lateral fontanelles small; angle between the scapular rods is about  $\sim 120^\circ$ ; humerus large and stout, shaft slightly curved, with a rather short but robust lateral tubercle that is not “V”-shaped; femur has a bony ridge fully connecting the caput with the trochanter major, but the trochanter major and trochanter minor are not fully connected by a bony ridge. Differs from *P. grandaeva* in that *P. charlestonensis* has relatively narrower parietals, relatively less-elongate squamosals, relatively narrower costals, and relatively wider vertebral scutes.

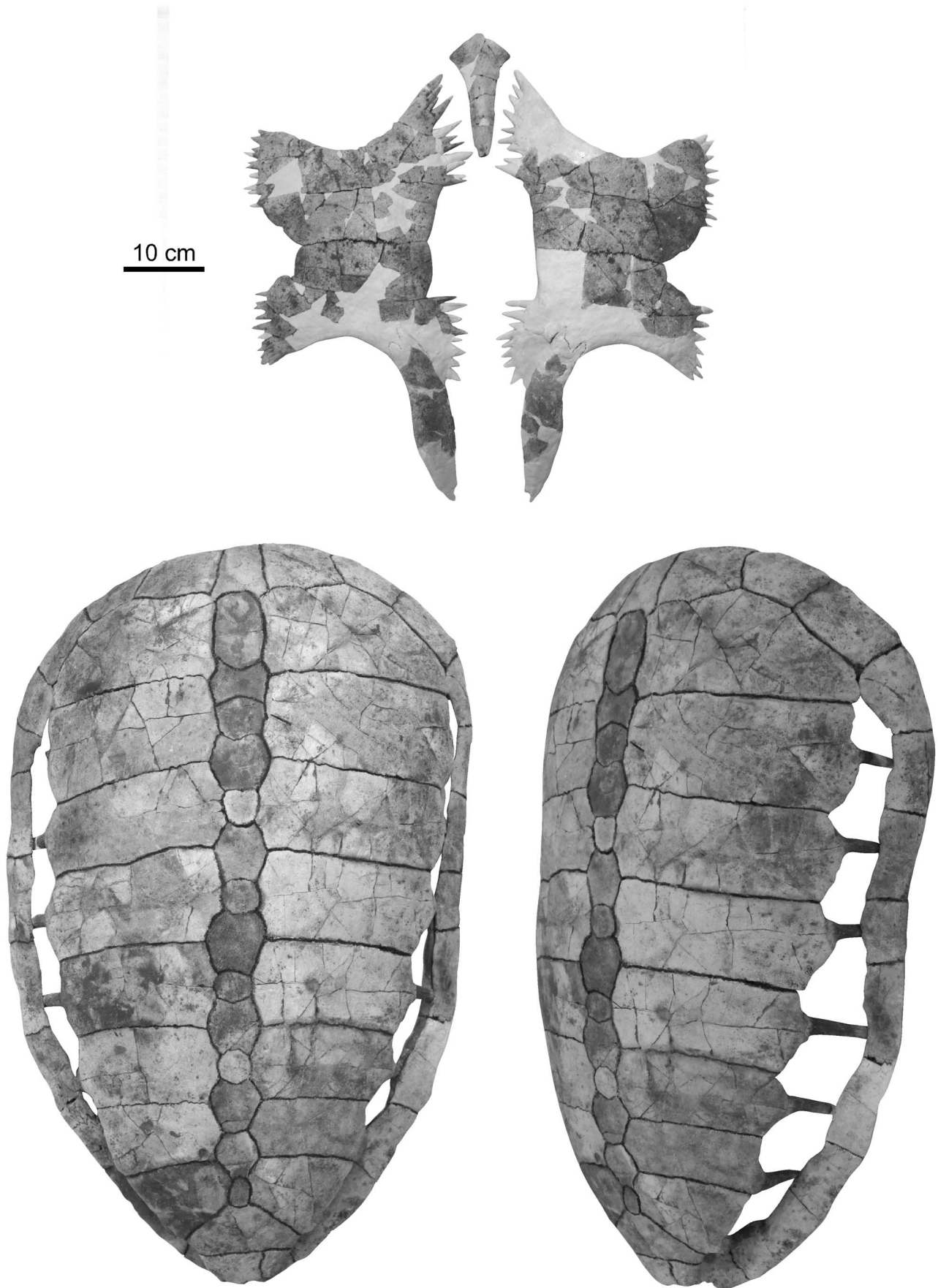
### Recognition of *Euclastes* from the Eocene of South Carolina

Until now, the only sea turtle specimens recovered from the Eocene deposits of South Carolina were two partial carapaces of

the dermochelyid turtle *Psephophorus*. One (ChM PV9102) is from the upper middle Eocene Cross Member of the Tupelo Bay Formation and the other (ChM PV7808) is from the overlying lower upper Eocene Harleyville Formation (Fig. 1; Weems et al., 2016). The specimen documented here (CCNHM 552) is the first pancheloniid recovered from the Eocene of South Carolina. It consists of a pair of fused dentaries (Fig. 9) that form an extensive crushing surface that complemented the expanded secondary palate present between the upper jaws of this genus. Such an extensive crushing battery has been documented in only three genera of Cenozoic pancheloniid turtles (Fig. 10): *Euclastes* from the Upper Cretaceous and Paleocene of the southeastern United States (Zangerl, 1953; Weems, 1988, 2014; Parham, 2005); *Erquelinnesia* from the lower Eocene of Belgium (Zangerl, 1971); and *Pacificchelys* from the middle Miocene of the eastern Pacific coastal region of North and South America (Lynch and Parham, 2003; Parham and Pyenson, 2010). The morphology of the specimen described here matches that of *Euclastes*, especially in its broadly rounded anterior border, so it can be assigned to that genus without hesitation. Because it is significantly younger than either of the two

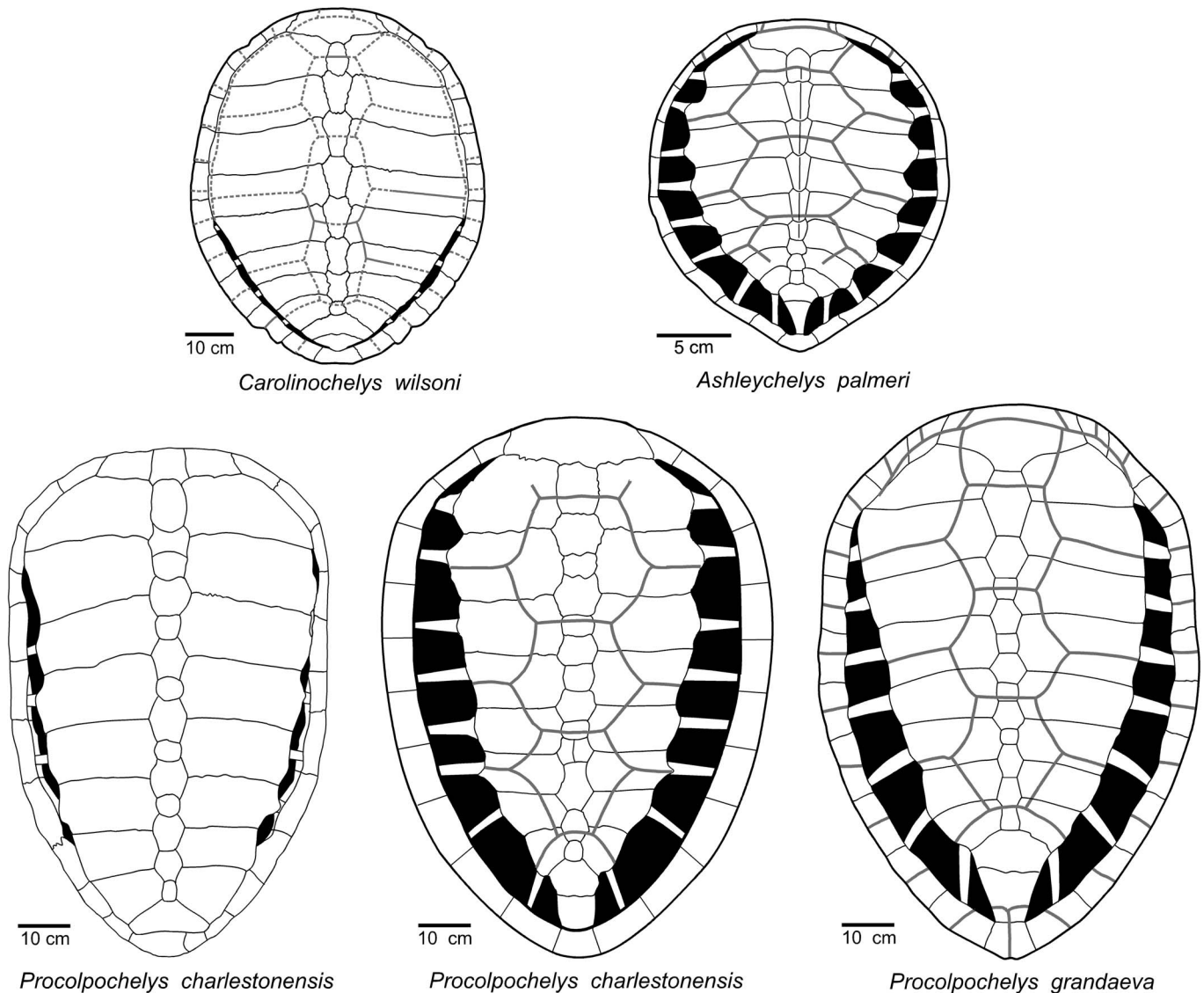


**Figure 5.** Top and middle: lower jaws of *Carolinochelys wilsoni* (CCNHM 302.5) in (1) ventral, (2) dorsal, (3) right lateral, and (4) posterior views. Bottom: outlines of lower jaws of *Ashleychelys*, *Carolinochelys*, and *Procolpochelys* in ventral view.



**Figure 6.** Associated plastron (top) and carapace (bottom) of *Procolpochelys charlestonensis* (CCNHM 300.1).





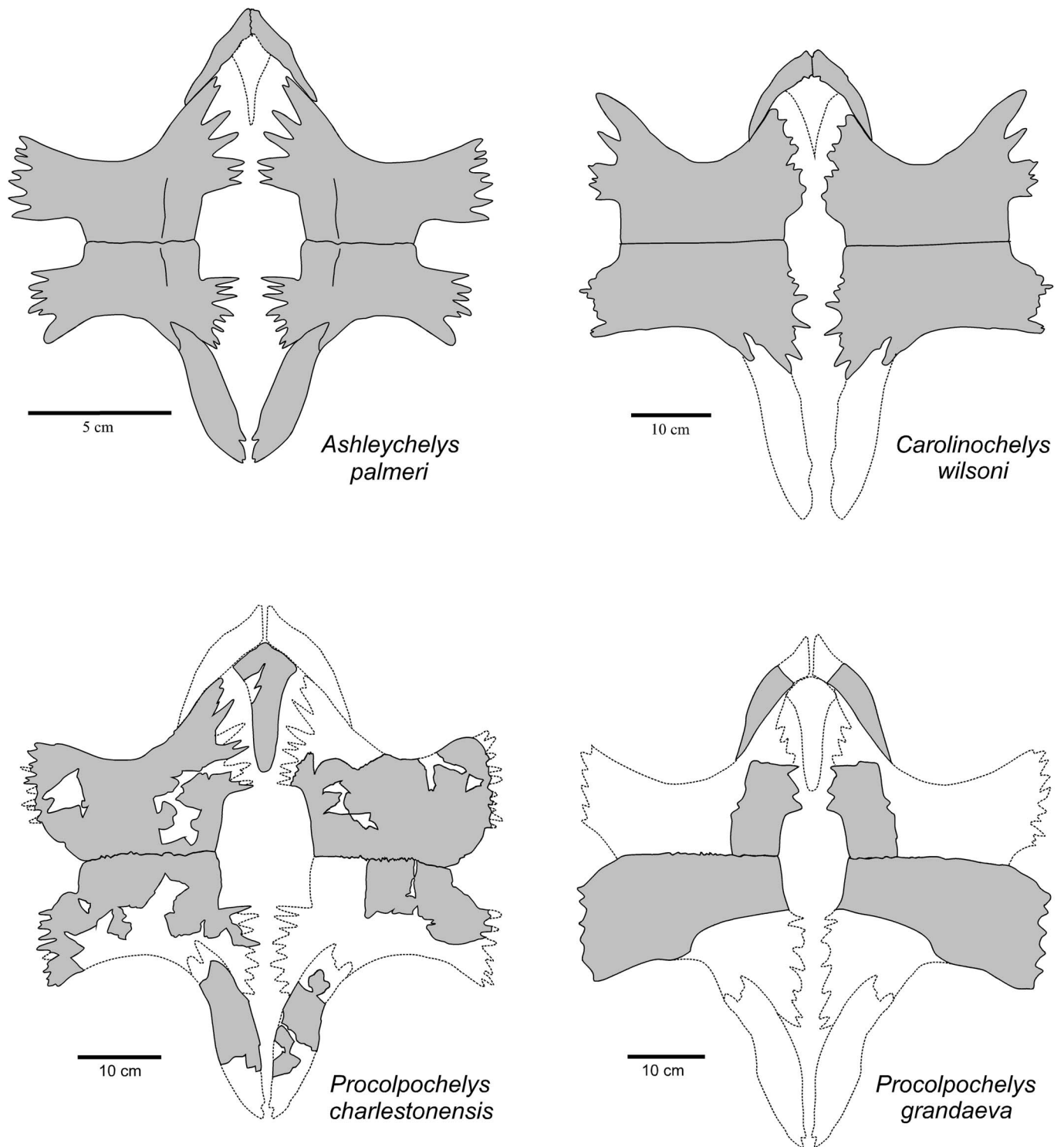
**Figure 7.** Comparison of the carapaces of *Ashleychelys*, *Carolinochelys*, and *Procolpochelys*. Solid gray lines represent sulcal grooves; dashed gray lines represent areas where the positions of the sulcal grooves are poorly constrained; black areas represent costoperipheral fontanelle gaps in the carapaces.

described species of *Euclastes*, it likely represents a new species. This single specimen, however, is insufficient to properly characterize a new species, so it is reported here only as *Euclastes* sp.

This specimen of *Euclastes* was found by divers searching for fossils in the Cooper River north of Charleston (Fig. 1). Associated with this specimen were bones referable to the basilosaurid whale *Dorudon serratus* Gibbes, 1845. The Pregnall Member of the Tupelo Bay Formation is the oldest stratigraphic unit that has produced any whales referable to the family Basilosauridae; the slightly older Cross Member of the Tupelo Bay Formation has produced abundant whale remains, but those are referable only to the more basal family Protocetidae (Geisler et al., 2005). Therefore, the holotype of *Dorudon* almost certainly did not come from any unit older than the Pregnall Member (Fig. 1). The highest Eocene unit in South Carolina that produces basilosaurids, the Harleyville Formation, is exposed in quarries to the northwest of the Wando River region near Harleyville, South Carolina, near Interstate 26 (northwest of the

inset area shown in Fig. 1). The Harleyville Formation has been extensively collected in these quarries, but no remains referable either to *Dorudon* or *Euclastes* have been found. Therefore, the Harleyville Formation also is an unlikely source for the Cooper River specimens discussed here. Between these two units (Fig. 1) lies the Parkers Ferry Formation, which is very poorly exposed in the Charleston region and so far has yielded no identifiable vertebrate remains. This is, however, the only upper Eocene unit that has been identified from anywhere near the upper Cooper River area (Weems and Lemon, 1985, 1989, 1993; Weems et al., 1985), and thus it is the most plausible source unit for the Eocene specimens discussed here.

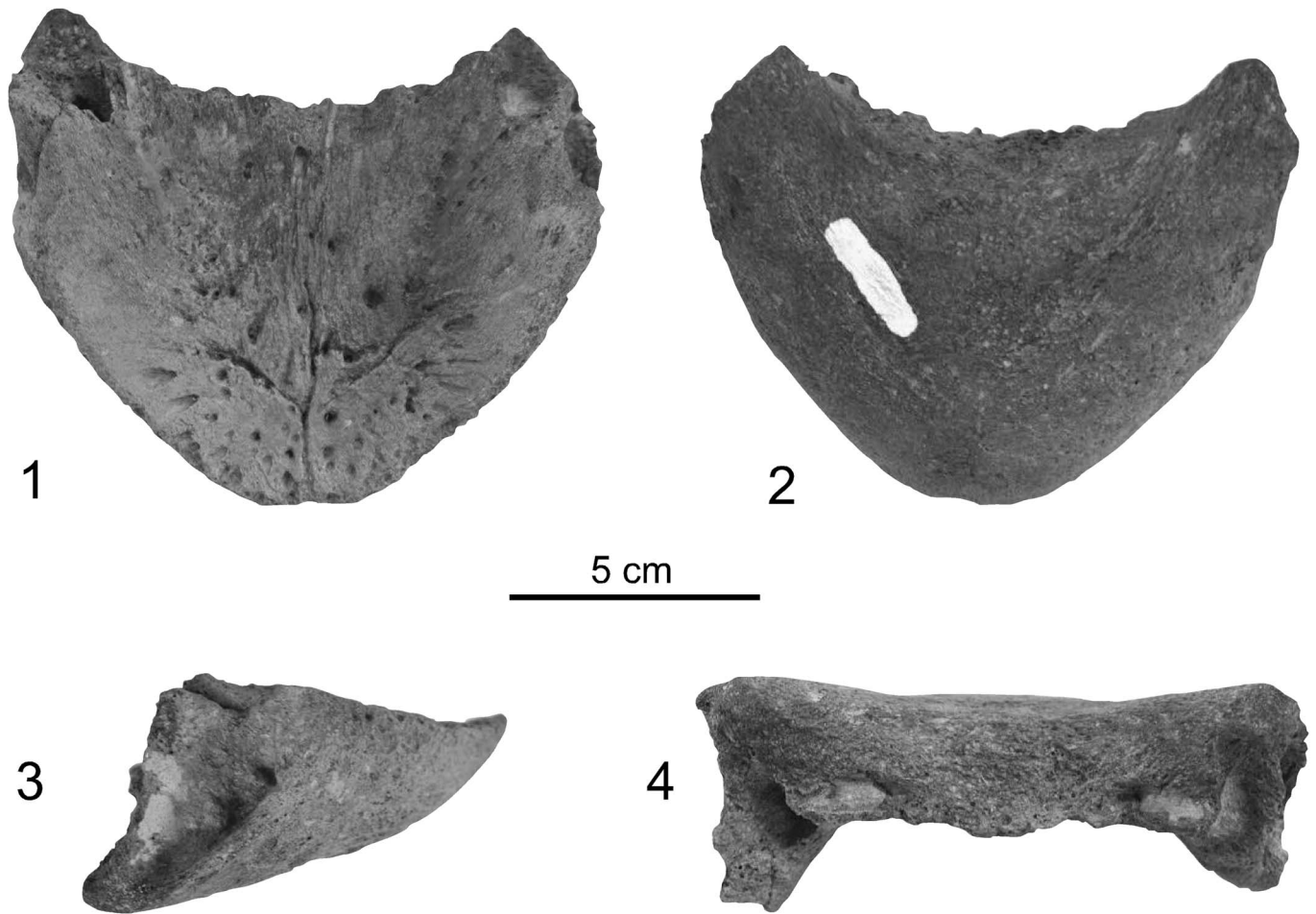
The *Euclastes* dentaries were picked for any possible matrix preserved in their nutrient foramina, but only a few grains were recovered and no identifiable nannofossils were found within them (J.M. Self-Trail, personal communication, 2016). This also indirectly suggests that the specimen came from the soft and easily eroded Parkers Ferry Formation and not from the much more compact and semi-lithified Pregnall Member.



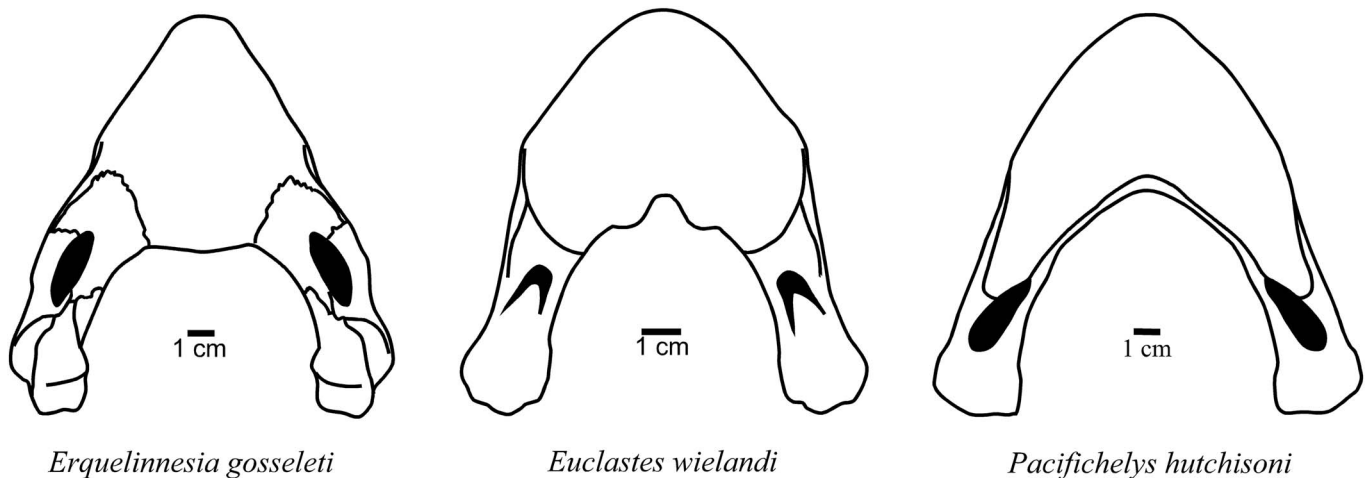
**Figure 8.** Comparison of the plastra of *Ashleychelys*, *Carolinochelys*, and *Procolpochelys*. *Ashleychelys* and *Carolinochelys* after Weems and Sanders (2014), *P. grandaeva* after Zangerl and Turnbull (1955). Gray-shaded areas are known elements; elements and portions of elements shown in white are unknown but inferred.

Until now, *Euclastes* has been reported only from Upper Cretaceous (Campanian/Maastrichtian) and Paleocene strata (Zangerl, 1953; Weems, 1988, 2014; Hirayama and Tong, 2003; Parham, 2005; Parham et al., 2014; Schwimmer et al., 2015). In Upper Cretaceous strata, *Euclastes* has been found in North America, South America, and Africa, but in the Paleocene it is

only known from North America and Africa (Parham et al., 2014). The presently reported occurrence extends the range of this genus upward through most of the Eocene, but only in the southeastern United States. This temporal and geographic distribution indicates that, after a strong initial expansion of its range in the Late Cretaceous, the range of *Euclastes* steadily



**Figure 9.** The fused dentaries of *Euclastes* sp. from the upper Eocene of South Carolina (CCNHM 552) in (1) dorsal, (2) ventral, (3) lateral, and (4) posterior views.



**Figure 10.** Comparison of the lower jaws of *Erquelinnesia*, *Euclastes*, and *Pacifichelys*. *Erquelinnesia* after Zangerl, 1971; *Euclastes* after Hirayama and Tong, 2003; *Pacifichelys* after Lynch and Parham, 2003.

dwindled until its extinction at or near the end of the Eocene. Its extinction likely was related to the dramatic earliest Oligocene cooling event that caused widespread extinctions and transformed marine vertebrate communities worldwide (e.g., Prothero et al., 2003).

**The phylogeny of Upper Cretaceous and Cenozoic pancheloniid sea turtles**

Pancheloniid sea turtle skulls and associated carapaces and plastra are well represented at a few stratigraphic levels within a few



A phylogenetic analysis was performed using TNT (Goloboff et al., 2008) consisting of 1,000 Wagner tree replicates, followed by a TBR cycle of all trees retained in the buffer. In contrast to Parham and Pyenson (2010), all multistate characters that form morphoclines were ordered, in particular characters 6 and 29. The search resulted in eight equally parsimonious trees with 76 steps. A search using TNT's pruned tree function, combined with observation of all eight trees, reveals that all taxa are retrieved in the same arrangement in all trees with the exception of *Euclastes*, which holds a different position in each tree (all indicated by asterisks on the time-calibrated phylogeny shown in Fig. 11). Bremer and bootstrap support values are provided to the left and right of each clade, respectively, when applicable. Implementation of a backbone constraint that enforces a sister group relationship between *Chelonia mydas* (Linnaeus, 1758) and *Natator depressus* (Garman, 1880), which has been suggested by recent molecular data (Naro-Maciel et al., 2008), does not change the results of the analysis.

*Euclastes* is problematic for two reasons: first because there is no consistent position where it is retrieved within the phylogeny, and second because none of the places where *Euclastes* is retrieved is consistent with stratigraphic information. *Euclastes* ranges back to the middle of the Campanian stage of the Upper Cretaceous (Schwimmer et al., 2015), which, if incorporated within the proposed phylogeny, would pull many of the lineages of Paleogene species far back into the Upper Cretaceous through ghost lineages not known from the fossil record. The most parsimonious conclusion is that proposed by Parham and Pyenson (2010); *Euclastes* represents a basal pancheloniid lineage that had a skull shape convergent with, but not ancestral to, the skull shapes found in later pancheloniid forms.

Except for *Euclastes*, the remainder of the phylogeny is stable. The lineages for the living cheloniid turtles *Caretta*, *Chelonia*, *Eretmochelys*, and *Lepidochelys* are all extended back to the base of the Pliocene at the generic level, because they all have been documented from the lower Pliocene Bone Valley Formation of Florida (Dodd and Morgan, 1992). The Plio-Pleistocene lineages leading to the modern species are not given any additional line weight in Figure 11 to indicate their fossil ranges, however, because the available Pliocene material can be confidently assigned to those genera, but not to any of the living species.

Based on several character states present in the carapace of *Procolpochelys grandaeva*, Zangerl and Turnbull (1955) concluded that it was a caretine sea turtle that belonged among the crown cheloniids. This conclusion has not been disputed by most subsequent authors who have discussed this genus (e.g., Weems, 1974; Parham and Fastovsky, 1997; Brinkman, 2009). However, in the phylogeny presented here, based in part on much more complete material of *Procolpochelys* than previously available, *Procolpochelys* lies well below and away from the living crown cheloniids plus *Trachyaspis* (Fig. 11). Therefore, the caretine-like features seen in the carapace of *Procolpochelys* appear to be yet another example of evolutionary convergence among lineages of pancheloniid sea turtles that are not very closely related.

**Summary and conclusions**

Notable within the retrieved phylogeny (Fig. 11) is the presence of three significant Cenozoic pancheloniid radiations during the

**Table 1.** Taxonomically important character states of the better-known genera of Late Cretaceous and Cenozoic pancheloniid sea turtles. Data are from Parham and Pyenson (2010), with the addition of data for *Tasbacka* based on *Tasbacka altdabergeni* Nessov, 1987 and *Tasbacka ruhoffi* (Weems, 1988) (Weems, 2014); for *Euclastes* based on *Euclastes wietlandi* (Parham, 2005) and *Euclastes roundsi* (Weems, 1988) (Weems, 2014); and for *Ashleychelys palmeri*, *Procolpochelys charlestonensis*, *Procolpochelys grandaeva*, and *Carolinochelys wilsoni* based on personal observations of the specimens described in Weems and Sanders (2014) and herein.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	
Outgroup	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>T. latremis</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>M. coahuilaensis</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Lophochelyinae	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>A. cuneiceps</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>E. brabanitica</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>E. gosseleti</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>P. camperi</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Tasbacka</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Euclastes</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>C. wilsoni</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>P. charlestonensis</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>P. grandaeva</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>A. palmeri</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Pacificchelys</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>C. mydas</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>N. depressus</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>T. lardyi</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>E. imbricata</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>C. caretta</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Lepidochelys</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

**Table 2.** Sources used to establish the age ranges of the cheloniid taxa shown in Figure 11.

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*Argillochelys cuneiceps* (Owen, 1849)—Lowest and highest occurrences are in the lower Eocene (Ypresian) London Clay, England (Moody, 1997).

*Ashleychelys palmeri* Weems and Sanders, 2014—Lowest occurrences are in the lower Oligocene (upper Rupelian) Ashley Formation, South Carolina (Weems and Sanders, 2014) and Old Church Formation, Virginia (Weems, 2014); highest occurrences are in the upper Oligocene (mid-Chattian) Chandler Bridge Formation (Weems and Sanders, 2014; Weems et al., 2016).

*Caretta caretta* (Linnaeus, 1758)—No fossil record has been reported for this modern species, but other material assigned to this genus has been reported from the lower Pliocene Bone Valley Formation, Florida (Dodd and Morgan, 1992) and the lower Pliocene part of the Yorktown Formation, North Carolina (Zug, 2001).

*Carolinochelys wilsoni* Hay, 1923b—Lowest occurrences are in the lower Oligocene (upper Rupelian) Ashley Formation, South Carolina (Weems and Sanders, 2014) and the lower Oligocene (upper Rupelian) Old Church Formation, Virginia (Weems, 2014); highest occurrences are in the upper Oligocene (mid-Chattian) Chandler Bridge Formation, South Carolina (Weems and Sanders, 2014; Weems et al., 2016).

*Chelonia mydas* (Linnaeus, 1758)—No fossil record has been reported for this species, but specimens assigned to this genus without a species designation are reported from the lower Pliocene Bone Valley Formation, Florida (Dodd and Morgan, 1992).

*Euclastoneura brabantica* Dollo, 1903—Lowest and highest occurrences are in middle Eocene (Lutetian) strata at Saint Remy-Geest, Belgium (Casier, 1968).

*Eretmochelys imbricata* (Linnaeus, 1766)—No fossil record has been reported for this modern species, but specimens assigned to this genus without a species designation are reported from the lower Pliocene Bone Valley Formation, Florida (Dodd and Morgan, 1992).

*Erquelinnesia gosseleti* (Dollo, 1886)—Lowest and highest occurrences are in lower Eocene (lower Ypresian) strata at Erquelinnes, Belgium (Zangerl, 1971).

*Euclastes* spp. (*Eu. wielandi* [Hay, 1908] + *Eu. roundsi* [Weems, 1988])—Lowest occurrence of *Euclastes wielandi* is in the Upper Cretaceous (middle Campanian) Coachman Formation, South Carolina (Schwimmer et al., 2015), highest occurrence is in the lower Paleocene (Danian) Brightseat Formation, Maryland (Weems, 2014); lowest and highest occurrences of *Euclastes roundsi* are in the upper Paleocene (Thanetian) Aquia Formation, Maryland and Virginia (Weems, 2014); genus ranges upward into upper Eocene (Priabonian) Parkers Ferry Formation, South Carolina (this paper).

*Lepidochelys* spp. (*L. olivacea* [Eschscholtz, 1829] + *L. kempii* [Garman, 1880])—No fossil record has been reported for these modern species, but specimens assigned to this genus without a species designation are reported from the lower Pliocene Bone Valley Formation, Florida (Dodd and Morgan, 1992) and the lower Pliocene part of the Yorktown Formation, North Carolina (Zug, 2001).

Lophochelyiinae – Lowest occurrence of this subfamily is in the Upper Cretaceous (Santonian) lower Mooreville Chalk, Alabama ([http://fossilworks.org/bridge.pl?a=taxonInfo&taxon\\_no=127991](http://fossilworks.org/bridge.pl?a=taxonInfo&taxon_no=127991)); highest occurrences are in the lower Paleocene (Danian) Brightseat Formation, Maryland (Weems, 2014) and in Paleocene strata (stage unspecified), West Africa (Wood, 1973).

*Mexichelys coahuilaensis* (Brinkman et al., 2009)—Lowest and highest occurrences are in the Upper Cretaceous (upper Campanian) Cerro del Pueblo Formation, Mexico (Brinkman et al., 2009).

*Nاتور depressus* (Garman, 1880)—No fossil record has been reported for this modern species (Zangerl et al., 1988).

*Pacificchelys* spp. (*P. urbinae* Parham and Pyenson, 2010 + *P. hutchisoni* [Lynch and Parham, 2003])—Lowest and highest occurrences of these two species respectively are in the middle Miocene (stage not specified) Pisco Formation, Peru and the middle Miocene (Langhian) Round Mountain Silt Formation, California (Parham and Pyenson, 2010).

*Procolpochelys charlestonensis* Weems and Sanders, 2014—Lowest occurrences are in the lower Oligocene (upper Rupelian) Ashley Formation, South Carolina (Weems and Sanders, 2014) and Old Church Formation, Virginia (Weems, 2014); highest occurrences are in the upper Oligocene (Chattian) Chandler Bridge Formation, South Carolina (Weems and Sanders, 2014; Weems et al., 2016).

*Procolpochelys grandaeva* (Leidy, 1851)—Lowest occurrences are in the lower Miocene (Burdigalian) Kirkwood Formation, New Jersey (Zangerl and Turnbull, 1955) and lower Calvert Formation, Maryland (Weems and Sanders, 2014); highest occurrences are in the upper Miocene (Tortonian) St. Marys Formation, Maryland (multiple unpublished specimens in the collection of the Calvert Marine Museum, including CMM-V-5913, CMM-V-3115, and CMM-V-2978).

*Puppigerus camperi* (Gray, 1831)—Lowest occurrences are in the lower Eocene (Ypresian) London Clay, England (Moody, 1974); highest occurrence is in the middle Eocene (Lutetian) Bracklesham Beds, England (Moody, 1997).

*Tasbacka* spp. (*T. aldabergeni* Nessov, 1987 + *T. ruhoffi* [Weems, 1988])—Lowest and highest occurrences for *T. aldabergeni* are in the upper Paleocene (Thanetian) Ouled Abdoun phosphate basin, Morocco; lowest and highest occurrences for *T. ruhoffi* are in the upper Paleocene (Thanetian) Aquia Formation, Maryland.

*Toxochelys latiremis* Cope, 1873—Lowest occurrences are in the Upper Cretaceous (upper Santonian-lower Campanian) Niobrara Formation, Kansas (Nicholls, 1988); the highest occurrences are in the Upper Cretaceous (lower Maastrichtian) Ripley Formation, Tennessee (Nicholls, 1988).

*Trachyasps lardyi* Meyer, 1843—Lowest well documented occurrences are in the lower Miocene (Burdigalian) lower Calvert Formation, Maryland (multiple unpublished specimens in the collection of the Calvert Marine Museum, including CMM-V-243); the highest occurrence is in an unnamed upper Pliocene (lower Piacenzian) unit at La Farfanara, Salsomaggiore Terme (PR) Italy (Villa and Raineri, 2015).

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Paleocene, early Oligocene, and late Miocene. Each of these radiations followed times of exceptional extinction within this group. The first radiation occurred in the Paleocene, and it is readily explained as the result of sea turtle survivors of the Cretaceous-Paleogene extinction event undergoing rapid evolutionary radiation to fill niches vacated by victims of that event. Similarly, the early Oligocene radiation of pancheloniid turtles likely resulted from the filling of niches vacated due to extinctions caused by the end-Eocene cooling event that accompanied the beginning of widespread Antarctic glaciation at the beginning of the Oligocene (e.g., Prothero et al., 2003). This extinction event affected pancheloniid turtles (e.g., *Puppigerus* and *Euclastes*) and caused extinction among many other groups of marine animals, including the paleophid sea snakes and most archaeocete whales. The cause of the late Miocene radiation of modern cheloniid sea turtles is less obvious, but it does coincide with the late Miocene global climatic deterioration that heralded the beginning of significant

northern hemisphere glaciation leading up to the Pleistocene ice ages (Maslin et al., 1996).

An interesting result of this phylogeny is the close relationship indicated for *Ashleychelys* and *Procolpochelys*. This likely reflects the strong regional endemism that developed among pancheloniid turtles during the Oligocene (Weems and Sanders, 2014) and further supports their suggestion that the southeastern United States was an ecosystem somewhat isolated from other parts of the Oligocene coastal marine world. Although *Carolinochelys* is an Oligocene South Carolina taxon that shows close relationship to the living branch of cheloniid turtles, this taxon is a rather specialized form that has strongly bent humeral shafts and thus is an unlikely ancestor for any of the later or living cheloniid turtles.

This conclusion is reinforced by the fact that no close relatives of the living cheloniid lineages show up in the western Northern Atlantic region until the early Miocene with the abrupt appearance of *Trachyasps lardyi* Meyer, 1843, a specialized

pseudodont sea turtle not directly ancestral to any of the living forms. Probably the evolutionary center of living cheloniid turtles was in the Indo-Pacific region, where the oldest turtle convincingly referable to the crown cheloniids has been reported from lower Miocene strata along the eastern margin of the Pacific basin (Brinkman, 2009). This conclusion also is supported by the fact that the most basal of the living cheloniid sea turtles, *N. depressus*, occurs only in the vicinity of Australia, and there is no evidence that it ever was present in any other part of the world ocean (Zangerl et al., 1988).

By early in the Pliocene, four of the five living cheloniid genera (*Caretta*, *Chelonia*, *Eretmochelys*, and *Lepidochelys*) had migrated into the North Atlantic basin (Dodd and Morgan, 1992). Even so, *Trachyaspis lardyi* continued to persist there well into the Pliocene despite the arrival of these new competitors (Zug, 2001). It is possible that it persisted in this region entirely through the Pliocene, because *T. lardyi* is known to have persisted into the late Pliocene in Italy (Villa and Raineri, 2015). By the Pleistocene, however, *T. lardyi* apparently was extinct, and the sea turtle fauna of the North Atlantic basin took on its present complexion.

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