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Paleogene chelonians from Maryland and Virginia

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Fossil remains of 22 kinds of Paleogene turtles have been recovered in Maryland and Virginia from the early Paleocene Brightseat Formation (four taxa), late Paleocene Aquia Formation (nine taxa), early Eocene Nanjemoy Formation (five taxa), middle Eocene Piney Point Formation (one taxon), and mid-Oligocene Old Church Formation (three taxa). Twelve taxa are clearly marine forms, of which ten are pancheloniids (*Ashleychelys palmeri*, *Carolinochelys wilsoni*, *Catapleura coatesi*, *Catapleura* sp., *Euclastes roundsi, E. wielandi,* ?*Lophochelys* sp., *Procolpochelys charlestonensis*, *Puppigerus camperi*, and *Tasbacka ruhoffi*), and two are dermochelyids (*Eosphargis insularis* and cf. *Eosphargis gigas*). Eight taxa represent fluvial or terrestrial forms (*Adocus* sp., *Judithemys kranzi* n. sp., *Planetochelys savoiei*, cf. "*Trionyx*" *halophilus*, "*Trionyx*" *pennatus*, "Kinosternoid B," Bothremydinae gen. et sp. indet., and Bothremydidae gen. et sp. indet.), and two taxa (*Aspideretoides virginianus* and *Allaeochelys* sp.) are trionychian turtles that probably frequented estuarine and nearshore marine environments. In Maryland and Virginia, turtle diversity superficially appears to decline throughout the Paleogene, but this probably is due to an upward bias in the local stratigraphic column toward more open marine environments that have preserved very few remains of riverine or terrestrial turtles.

Keywords: Bothremydidae, "Macrobaenidae," Kinosternoidea, Trionychia, Dermochelyidae, Pancheloniidae

INTRODUCTION

Before the late twentieth century, only a few Paleogene turtle remains had been reported from the widespread marine deposits of this age in Maryland and Virginia (Clark 1895, 1896, Clark and Martin 1901, Lynn 1929). It was not until 1988 that a diverse assemblage was reported by Weems (1988) from a number of Paleocene sites in this region (Fig. 1). Subsequently, Weems (1999) described a smaller assemblage of turtles and other reptiles from an early Eocene site. Since then, a number of taxonomic revisions have been made on the Paleogene turtles of Maryland and Virginia. Parham (2005) convincingly demonstrated that the skulls previously associated with *Osteopygis emarginatus* Cope 1868 cannot belong to the type carapace material, and so referred the skull material to *Euclastes wielandi* (Hay 1908) and left only the shell material in *Osteopygis* Cope 1869a. The skull material described by Weems (1988), synonymized with *E. wielandi* by Parham & Pyenson (2010) now should be called *E. roundsi* (Weems 1988). Hutchison and Weems (1998) reassigned to *Adocus* Cope 1868 the specimen assigned by Weems (1988) to *Agomphus* Cope 1868, and Hutchison (2012) has reinterpreted the suprapygal region of *Planetochelys savoiei* Weems1988 and erected the new family (Planetochelyidae Hutchison 2012) to include it. Hirayama (2006) synonymized *Catapleura ruhoffi* Weems 1988 with *Tasbacka aldabergeni* Nessov 1987 and *Dollochelys coatesi* Weems 1988 with *Catapleura repanda* Cope 1868. The generic reassignments are correct, but the two species are still valid and are reclassified here as *Tasbacka ruhoffi* (Weems 1988) n. comb. and *Catapleura coatesi* (Weems 1988) n. comb. In addition to these changes, new specimens representing 10 previously unrecognized taxa have been collected since Weems (1988) and that material is described here along with a taxonomic update of the previously described Paleogene turtles from Maryland and Virginia.

STRATIGRAPHIC SETTING

Five formations of Paleogene age are recognized from surface exposures in Maryland and Virginia (Fig. 2). The early Paleocene Brightseat Formation is the oldest of these and crops out only in Maryland; its equivalent outcrop belt reappears northward as the Hornerstown Formation in New Jersey and Delaware. The late Paleocene Aquia Formation and the early Eocene Nanjemoy Formation crop out in the western coastal plain of both states, and significant collections have been made from the outcrops of these units. The middle Eocene Piney Point Formation and the early Oligocene Old Church Formation crop out only in central Virginia. The Piney Point is time-equivalent to the Castle Hayne Limestone in North Carolina and the Santee Limestone in South Carolina, while the Old Church is time-equivalent to the River Bend Formation

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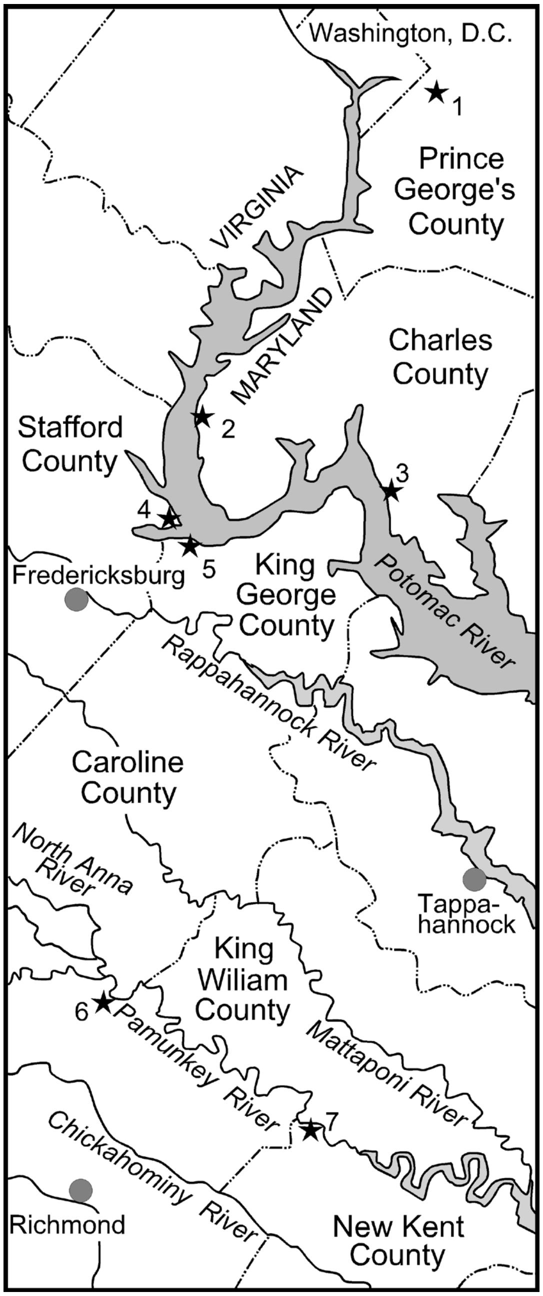

Figure 1. Map showing major localities from which Paleogene turtle remains have been collected in Maryland and Virginia. Locality 1—Hampton Mall near Central Avenue and Interstate 95, Prince George's County, Maryland; Locality 2—Blue Banks south of Liverpool Point, Charles County, Maryland; Locality 3—Bluffs north and south of Popes Creek, Charles County, Maryland, with Loyola Retreat toward the north end; Locality 4—Bluffs along Potomac River northwest of mouth of Potomac Creek, Stafford County, Virginia; Locality 5—Bluffs along Potomac River southeast of Potomac Creek, King George County, Virginia; Locality 6—Bluff along upper Pamunkey River, Hanover County, Virginia; Locality 7—Bluffs along Pamunkey River, forming in this area the boundary between King William County (north) and New Kent County (south), Virginia.

in North Carolina and the Ashley Formation in South Carolina. Not surprisingly, the vertebrate fauna in each of these units is quite similar to the faunas found in their laterally equivalent strata in nearby states.

These units are all of marine origin, but occasional finds of fruits and seeds of land plants (Tiffney 1999) and bones and teeth of land animals (Rose 1999, 2000, 2010) attest to the occasional introduction of remains of terrestrial flora and fauna into these marine depositional environments. Turtle remains pertaining to marine species are most abundant, as would be expected in such a setting, but occasionally remains of fluvial and even terrestrial turtles are found.

SYSTEMATIC PALEONTOLOGY

Institutional abbreviations—**CMM-V**, Calvert Marine Museum, vertebrate collections; **NMNH**, National Museum of Natural History, Smithsonian Institution, Department of Paleobiology (formerly **USNM**, United States National Museum).

TESTUDINES Batsch 1788
PLEURODIRA Cope 1864
BOTHREMYDIDAE Baur 1891
BOTHREMYDIDAE INDET.
(Figs. 3A–C)

Specimen—CMM-V-4776, left epiplastron found by Melville Hurd.

Locality, horizon, and age—Found on the beach at the foot of the bluff west of Loyola Retreat, 1.7 miles north of Popes Creek in southern Charles County, Maryland; the color, density, and the presence of very fine silvery mica adhering to the bone surface all indicate that it came from the adjacent Woodstock Member (Bed A) of the Nanjemoy Formation; early Eocene (late Ypresian; within nannofossil zone NP12).

Description—CMM-V-4776, epiplastron broadly attached suturally to right epiplastron and hyoplastron, anterior portion of contact with the entoplastron shingled. Two sulcal grooves present on the external (ventral) surface. Anterior sulcal groove trends anteriorly; posterior sulcal groove trends more laterally than anteriorly.

Remarks—The shape of the left epiplastron is rather similar to that of both the bothremydid *Chedighaii* Gaffney, Tong & Meylan 2006 and the baenid *Baena* Leidy 1870. However, the reticulate pattern of grooves on the external surface is typical of bothremydids (e.g., Hay 1908, fig. 121) and the hypoplastral suture is transverse and somewhat anterolaterally directed as in bothremydids and not posterolaterally directed or pointed posteriorly as in baenids. Additionally, this specimen is large. It is more than twice the size of the epiplastra of adult early or middle Eocene *Baena* and, unlike in adult *Baena*, was not fused to its surrounding plastral bones (Hutchison 1984).

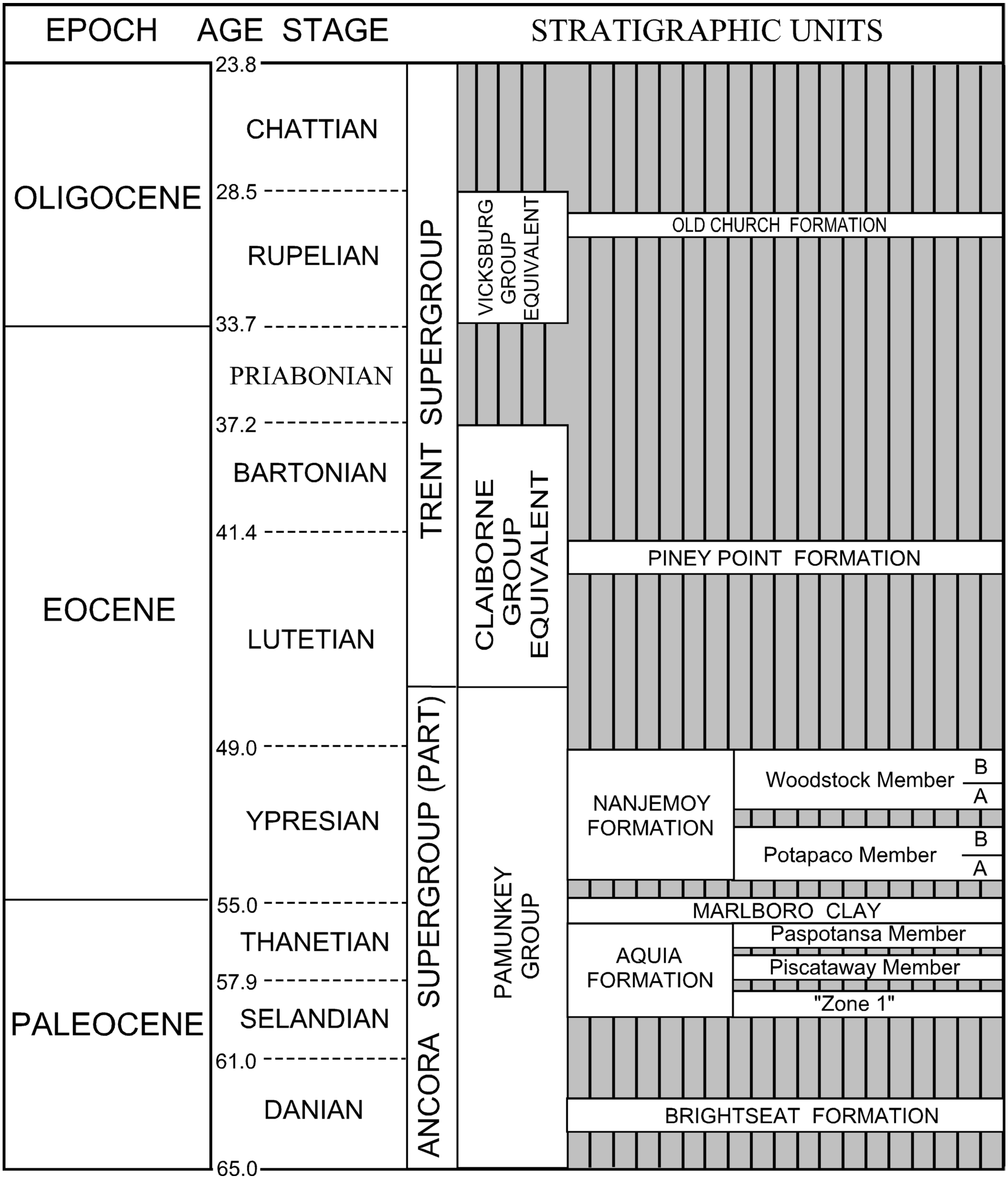

Figure 2. Stratigraphic column showing the ages and intervals of Paleogene strata in the Maryland and Virginia region and in nearby states.

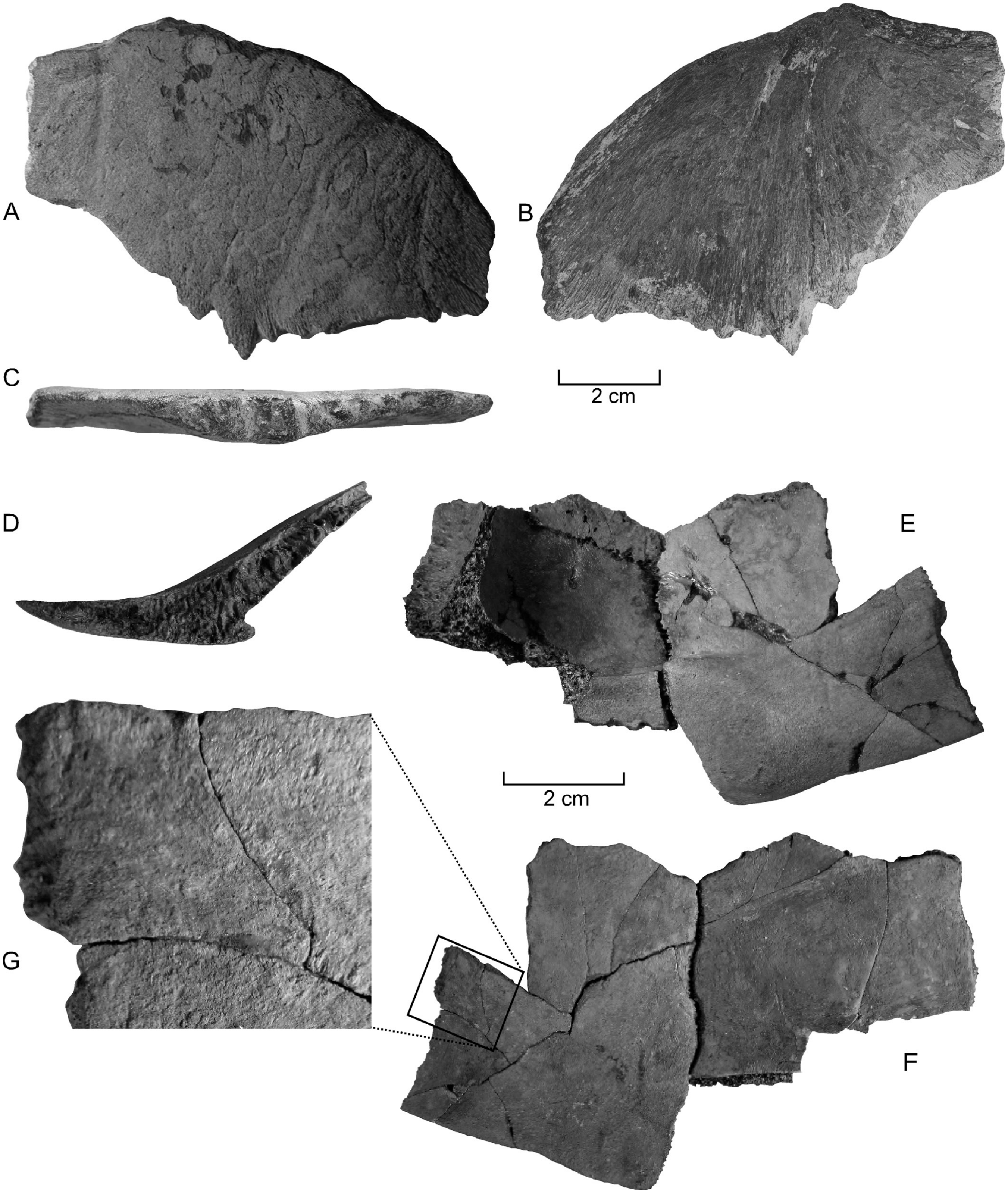

Figure 3. **A–C.** Bothremydidae indet., left epiplastron from bed A of the Woodstock Member of the Nanjemoy Formation of Maryland, CMM-V-4776. **A.** Ventral (external) view. **B**. Dorsal (internal) view. **C.** Posterior view. **D–G.** Bothremydinae indet., partial eighth and adjacent ninth peripheral from the Aquia Formation of Maryland, CMM-V-4762; **D**, anterior border of ninth peripheral; **E**, eighth (left) and ninth (right) peripherals in internal view; **F**, eighth and ninth peripherals in external view; **G**, detail of external surface of ninth peripheral.

Therefore, based on these features, this specimen is from a pleurodiran turtle and not a baenid. Although there is not enough material to allow assignment of this specimen to a specific genus or species of bothremydid turtle, it does show that bothremydid turtles persisted in the eastern United States through most or all of the early Eocene.

BOTHREMYDINAE Gaffney, Tong & Meylan 2006
GEN. ET SP. INDET.
(Figs. 3D–G)

Specimens—CMM-V-4762, associated eighth and ninth right peripherals, neither complete, found by Gary Grimsley.

Locality, horizon, and age—Found in the Blue Banks south of Liverpool Point, eastern shore of the Potomac River in Charles County, Maryland; “Zone 2” of the Piscataway Member of the Aquia Formation (Clark and Martin 1901); late Paleocene (early Thanetian).

Description—Eighth and ninth peripheral elements from a very low-arched carapace. Distal margins thin, elongated, and slightly upturned. Eighth peripheral bears a buttress for attachment to a plastral bridge. External (dorsal) surface without visible sulcal grooves, unsculptured except for a matte-like texture.

Remarks—These associated fragmentary eighth and ninth right peripherals (Figs. 3D–G) so far are the only record of this family from the Aquia Formation. The eighth peripheral is clearly attached to a plastral bridge, and this precludes assignment of this specimen either to the chelonioid turtles, for they lack a plastral bridge, or to a trionychid turtle, for they lack peripherals altogether. The only turtles known from the Paleocene of the eastern United States with thin and blade-like posterior peripherals, a plastral bridge, and a very low-arched shell are members of the Bothremydidae and “Macrobaenidae.” “Macrobaenids” have deeply impressed sulcal grooves on the peripherals, a distinctive surface texture, and a plastral bridge that is only ligamentous and not sutured. None of these characters are present on these specimens, so assignment to Bothremydidae is indicated. This specimen lacks the surface texture typical of bothremydid taphrosphyne turtles such as *Taphrosphys* Cope 1869b but it does have a matte surface texture similar to that seen in the late Paleocene specimens assigned by Hutchison and Weems (1998) to *Bothremys* Leidy 1865. It is possible that these specimens are from a taphrosphyne turtle with a deeply worn external surface, but this seems very unlikely. Gaffney et al. (2006) pointed out that assignment of South Carolina material to *Bothremys* by Hutchison and Weems (1998) is possible, but not certain, since no generically diagnostic elements have been found. In view of this, the specimen discussed here is assigned to Bothremydinae without generic or species designation.

CRYPTODIRA Cope 1868
EUCRYPTODIRA Gaffney 1975
“MACROBAENIDAE” Sukhanov 1964
Judithemys Parham & Hutchison 2003
Judithemys kranzi n. sp.
(Figs. 4–7)

Synonymy—*Osteopygis roundsi* (partem) Weems 1988.

Holotype—CMM-V-4755, slightly more than half of a carapace, nearly complete on its right side except for the first peripheral and in its medial region except for the nuchal and first and second neurals; on the left side only a fragment of the central and posterior portions of the carapace are preserved.

Type locality, horizon, and age—This specimen was recovered at a construction site in Fort Washington, west of Maryland Route 210, Prince Georges County, Maryland (in the vicinity of 38.7435 N, 77.0104 W); in a block of lime-cemented rock broken from an Aquia Formation hard-bed, very probably “Zone 3” or “Zone 5” of the Piscataway Member (Clark and Martin 1901); late Paleocene (early Thanetian).

Referred specimen—USNM 357710, left hyoplastron and hypoplastron, discussed and illustrated in Weems (1988).

Locality, horizon, and age—Found in the Blue Banks south of Liverpool Point, eastern bank of the Potomac River, Prince Georges County, Maryland; from “zone 2” of the lower Piscataway Member of the Aquia Formation (Clark and Martin 1901); late Paleocene (early Thanetian).

Etymology—The species is named for Dr. Peter Kranz, who recovered and donated the holotype.

Diagnosis—The deeply impressed sulcal grooves, the wide but only ligamentously connected plastral bridge, and the large size of *Judithemys kranzi* readily places it among the “Macrobaenidae.” Of the two North American genera in this family, *J. kranzi* differs from *O. emarginatus* in having only two suprapygals, a wide nuchal, a pygal that does not appear to be posteriorly elongated, and a hyoplastron with an external margin that shows a narrow outer anterior extension (Fig. 6). All of these traits are present in *Judithemys*. Compared to the two known species of *Judithemys* (Brinkman et al. 2010), *J. kranzi* differs from *J. sukhanovi* Parham and Hutchison 2003 in having a much more regularly elliptical-shaped carapace not much widened posteriorly, neurals much longer than wide, a seventh neural that is distinctly shortened anteroposteriorly, and much more elongate second and third vertebral scales. It differs from *J. backmani* (Russell 1934) in having a relatively wider nuchal, a relatively longer second vertebral scale, a relatively narrower fifth vertebral scale, and a sulcus on the eighth costal located near and along its posterior border and not near its anterior edge.

Description—The carapace is elliptical, longer than wide, with anterior border rounded and posterior border slightly scalloped at the lateral margins of the pygal (Fig. 5). The bone has an anastomosing surface texture and deeply impressed sulcal grooves. Nuchal much wider than long and apparently somewhat "T"-shaped. Neurals are longer than wide except for the seventh which is shortened and about as wide as long. Two suprapygals are present; the pygal is smaller and anteroposteriorly shorter than the adjacent peripherals. The vertebral scales are hexagonal, with the first being wide and short, the second being longer than wide, the third and fourth being about as long as wide, and the fifth wider than long.

Remarks—The pygal region is variable in "macrobaenids," so comparison of that region with other species, based only on a single specimen, is not instructive. These similarities and differences are summarized in Table 1. This specimen is the first reported occurrence of *Judithemys* in the eastern United States, though part of its plastron was previously illustrated by Weems (1988) and incorrectly assigned to *Osteopygis roundsi*.

AMERICHELYDIA Joyce, Parham & Gauthier 2004
KINOSTERNOIDEA Joyce, Parham & Gauthier 2004
"KINOSTERNOID B" Hutchison & Weems 1998
(Figs. 8A–H)

Specimens—CMM-V-4758, neural element found by Mike Folmer; CMM-V-4759, proximal end of two costals found by Ron Ison.

Locality, horizon, and age—All specimens were found along the Blue Banks on the east side of the Potomac River south of Liverpool Point, Charles County, Maryland. Deposits at this locality belong to "Zone 2" of the lower part of the Piscataway Member of the Aquia Formation (Clark and Martin 1901); late Paleocene (early Thanetian).

Description—Neural is hexagonal, thick, unkeeled and with a nearly smooth surface. Costals are thick proximally but thin away from the midline region. Sulcal grooves on one costal indicate generally quadratic vertebral scales.

Remarks—These specimens are very similar in size and morphology to the specimens of similar age described

Figure 4. Carapace of *Judithemys kranzi* n. sp., dorsal view, CMM-V-4755.

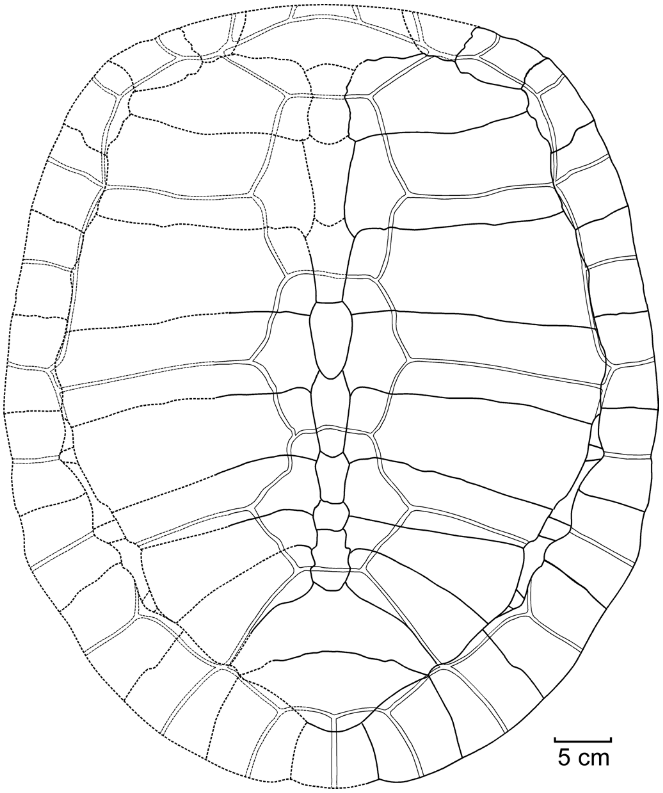

Figure 5. Restoration of the carapace of *Judithemys kranzi* n. sp. based on CMM-V-4755, dorsal view.

from South Carolina as "Kinosternoid B" by Hutchison and Weems (1998). The only difference from the South Carolina material is that there is no median ridge on the neural, but the Aquia neural apparently came from the anterior part of the shell which may not have had the ridge found on posterior neurals. The only other turtle

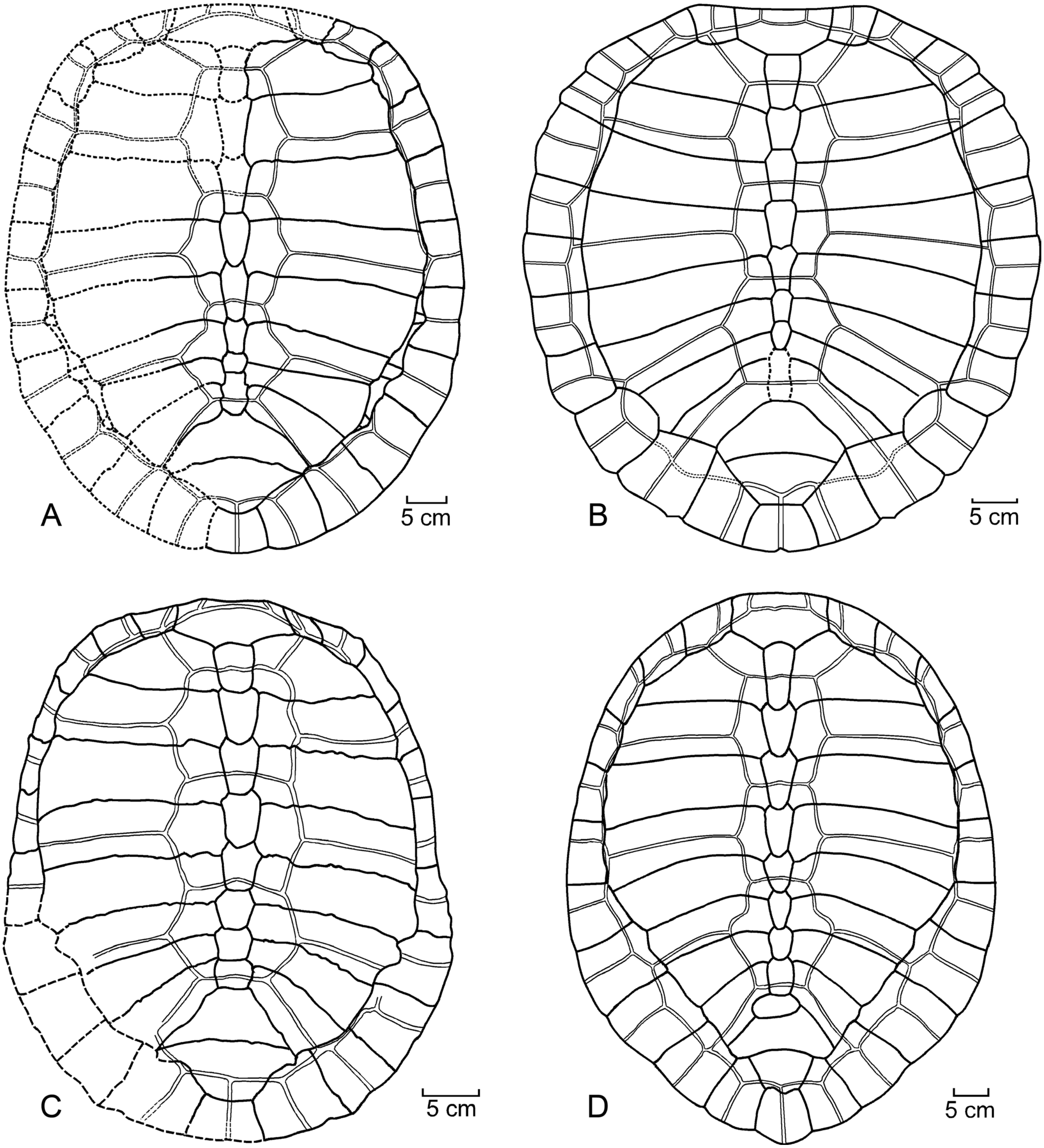

Figure 6. A–D. Comparison of carapaces in dorsal view. **A.** *Judithemys kranzi* n. sp., CMM-V-4755. **B.** *J. backmani* (early Paleocene; adapted from Parham & Hutchison 2003). **C.** *J. sukhanovi* (Late Cretaceous; adapted from Brinkman et al. 2010). **D.** *Osteopygis emarginatus* (early Paleocene; adapted from Hay 1908).

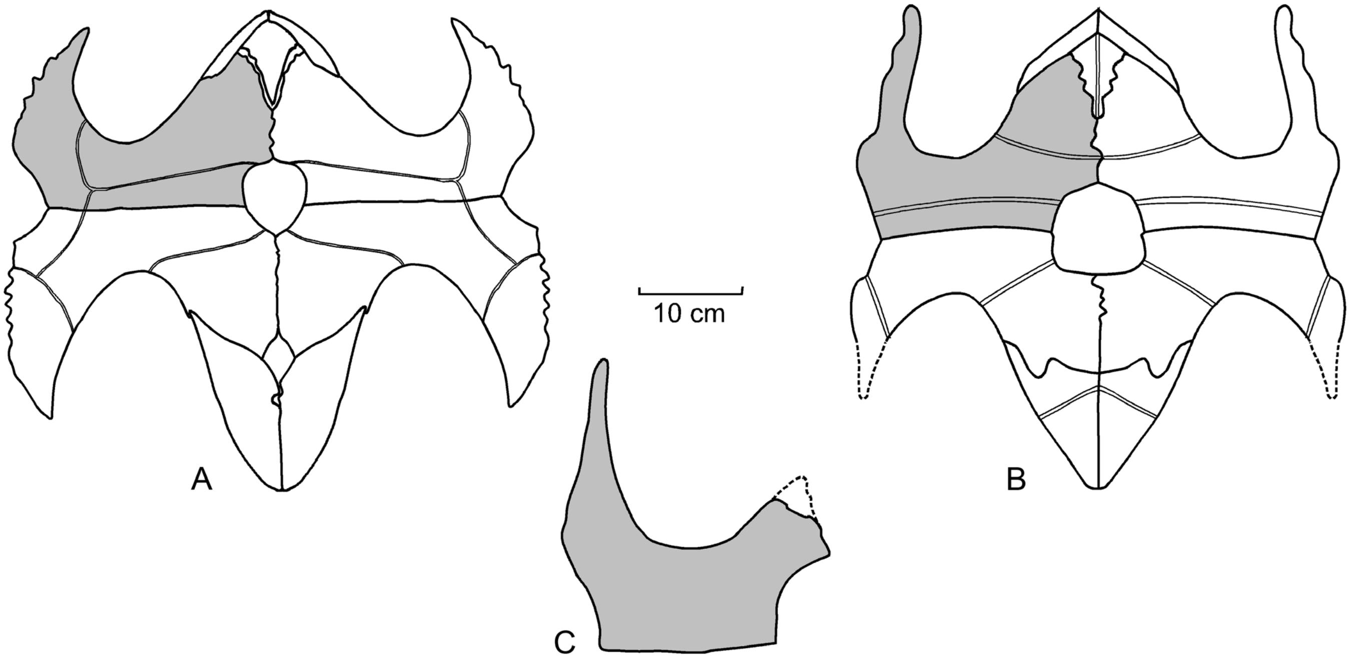

Figure 7. A–C. Comparison of the plastron of **(A)** *Osteopygis emarginatus* and **(B)** *Judithemys backmani* (right hyoplastron shaded) with the right hyoplastron of **(C)** *J. kranzi* n. sp. *Osteopygis emarginatus* adapted from Hay (1908), *J. backmani* adapted from Brinkman et al. (2010), *J. kranzi* adapted from Weems (1988).

Table 1. Distribution of shell characters among species of *Judithemys* and *Osteopygis emarginatus*.

	Judithemys sukhanovi	***Judithemys backmani***	***Judithemys kranzi***	***Osteopygis emarginatus***
Carapace proportions	Longer than wide	About as long as wide	Longer than wide	Longer than wide
Nuchal proportions	Width more than twice the length	Width less than twice the length	Width more than twice the length	Width less than twice the length
1st vertebral/ 2nd marginal contact	Corner	Corner	Corner	Broad
Suprapygals	2	2	2	3
Bridge peripherals	C-shaped	C-shaped	C-shaped	Triangular, massive
2st vertebral scale	Wider than long	About as long as wide	Longer than wide	Longer than wide
5th vertebral scale	Slightly wider than long	Much wider than long	Slightly wider than long	Slightly wider than long
Distally trending sulcus on 8th costal	Near middle of costal	Near anterior border of costal	Near posterior border of costal	Slightly behind middle of costal
Outer anterior extension of hyoplastron	Narrow	Narrow	Narrow	Wide
Central plastral fontanelles	Absent	Present	Present	Present

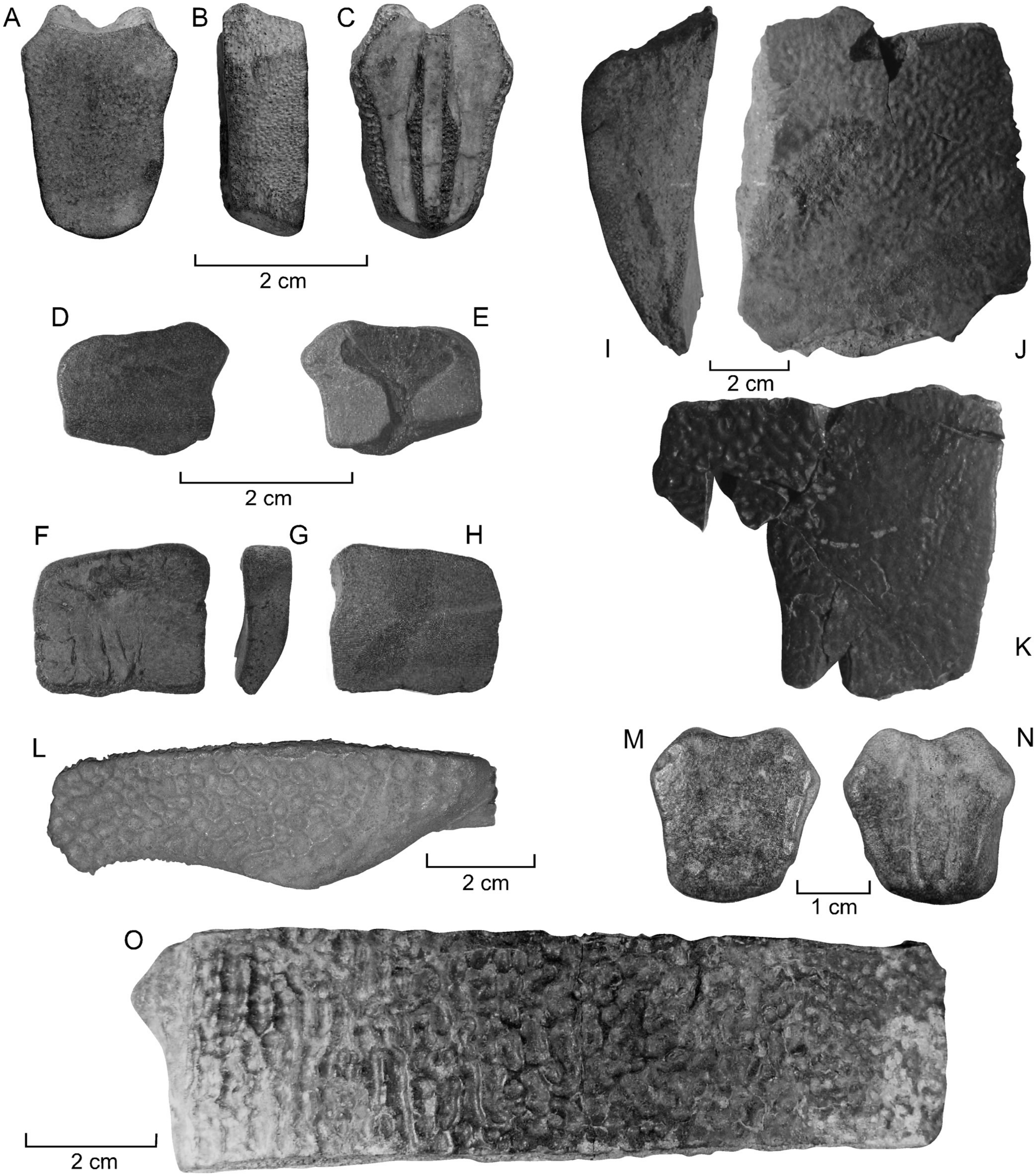

Figure 8. Kinosternoid and trionychioid turtles from the Aquia, Nanjemoy, and Piney Point Formations. **A–C.** Neural of kinosternoid B of Hutchison and Weems 1998, CMM-V-4758. **A**, dorsal (external) view; **B**, lateral view; **C**, ventral view. **D, E.** Proximal portion of a right costal of kinosternoid B of Hutchison and Weems 1998, CMM-V-4759. **D**, external view; **E.** internal view. **F–H.** Proximal portion of a right costal of kinosternoid B of Hutchison and Weems 1998, CMM-V-4759. **F**, internal view; **G**, anterior view; **H**, external view. **I, J.** Peripheral of *Allaeochelys* sp., CMM-V-4779. **I,** posterior view; **J,** dorsal view. **K.** Right hypoplastron of *Allaeochelys* sp. in ventral (external) view, CMM-V-4780. **L.** Seventh right costal of cf. *"Trionyx" halophilus* Cope in dorsal (external) view, CMM-V-4760. **M, N.** Neural of cf. *"Trionyx" halophilus* Cope, CMM-V-4761. **M,** dorsal view; **N,** ventral view. **O.** Third left costal of *"Trionyx" pennatus* in dorsal view, CMM-V-3283.

closely related to this form is *Agomphus*, but assignment to that genus is not indicated for several reasons. First, the Maryland and South Carolina material is consistently small in size compared to *Agomphus*. Second, the neural is much narrower than in *A. tardus* Wieland 1905. It is similar in shape to the neurals of "*A.*" *alabamensis* Gilmore 1919 a related species probably not properly referable to *Agomphus* (Hutchison and Weems 1998), but it does not have the wide and high median keel found in that species. Third, the thick costals of *Agomphus* do not thin rapidly away from the midline. Fourth, a low ridge, developed on the proximal portion of the costals distal to the sulcal grooves, is not found in *A. tardus*, and the low ridge on the Maryland and South Carolina material is weakly developed compared to the ridge in "*A.*" *alabamensis*.

TRIONYCHIA Hummel 1929
PLANETOCHELYIDAE Hutchison 2012
PLANETOCHELYS Weems 1988
Planetochelys savoiei Weems 1988

Specimen—USNM 412107, posterior half of carapace, described by Weems (1988).

Locality, horizon, and age—Found along the western bank of Aquia Creek at the base of "zone 2" of the lower Piscataway Member of the Aquia Formation (Clark and Martin 1901); late Paleocene (early Thanetian).

Remarks—Weems (1988) assigned this taxon to the family Sinemydidae Yeh 1963 but new material and more extensive descriptions of *Sinemys* Wiman 1930 (Brinkman and Peng 1993, Sukhanov 2000) have documented a suite of diagnostic features that do not support close relationship between *Sinemys* and *Planetochelys*. Hutchison (2012) has restudied the type specimen of *Planetochelys savoiei*, reinterpreted its suprapygal region, and described a new closely related species from the western United States, *P. dithyros* Hutchison 2012. Unlike the type specimen of *P. savoiei*, the new species includes the anterior portion of the carapace and plastron. The occasional presence in *P. dithyros* of extragular scales indicates that it is too primitive to be included within the chelydrid-testudinoid lineage and most likely lies near the adocid grade of trionychians (Hutchison 2012). *Planetochelys* has a number of specializations that show it to have been a terrestrial turtle that had evolved a carapace and plastron much like that of a "box turtle," even though it is not closely related to the emydid and kinosternid turtles that independently have evolved a plastral hinge to allow the shell to partly or wholly close. Because of its unique combination of primitive and derived features, *Planetochelys* is not particularly close to any other turtles and has been placed in its own family (Hutchison 2012).

ADOCIDAE Cope 1870
ADOCUS Cope 1868
Adocus sp.

Specimen—USNM 357834, a third right peripheral element, discussed in Weems (1988) and Hutchison and Weems (1998).

Locality, horizon, and age—Found at the Hampton Mall in Prince Georges County, Maryland, probably in the Brightseat Formation, early Paleocene (Danian).

Remarks—A peripheral of a non-marine turtle from the early Paleocene Brightseat Formation was considered by Weems (1988) to belong to *Agomphus* sp. because it showed no obvious surface sculpture. However, this specimen was reassigned to *Adocus* sp. by Hutchison and Weems (1998) because it does have a faint pitted surface texture that was largely obliterated before the specimen was buried. Therefore, it is *Adocus* that occurs in the Brightseat Formation and not *Agomphus*, though the presence of *Agomphus tardus* in the laterally equivalent Hornerstown Formation in New Jersey to the northeast implies that this taxon may yet be found in the Brightseat.

CARETTOCHELYIDAE Boulenger 1887
ALLAEOCHELYS Noulet 1867
Allaeochelys sp.
(Figs. 8I–K)

Specimen—CMM-V-4779, peripheral element found by Ron Ison; CMM-V-4780, fragment of right hypoplastron found by Bob Wiest.

Locality, horizon, and age—Both specimens came from outcrops of the Piney Point Formation along the Pamunkey River in eastern Hanover County, Virginia; middle Eocene (late Lutetian to early Bartonian).

Description—Peripheral is thick in cross-section, with pitted to vermiform sculpture on its external surfaces and a sutural border on its proximal end for attachment to a costal element. The hypoplastron is strongly constricted in its medial region and also has pitted to vermiform sculpture on its external surface. Neither element shows any evidence of sulci marking scale boundaries.

Remarks—The pitted to vermiform sculpture on these elements and the absence of evidence for sulci show them to pertain to Trionychia, but the presence of peripherals precludes assignment to the family Trionychidae Gray 1825. Therefore, this material pertains to the family Carettochelyidae. Only three genera of carettochelyids are known from North America: *Anosteira* Leidy 1871, *Pseudanosteira* Clark 1932, and *Allaeochelys*. The large size and the details of the sculpture both preclude assigning this material to *Anosteira* or *Pseudanosteira*, but in both regards it is fully comparable to *Allaeochelys*. Only one other occurrence of *Allaeochelys* has been reported from North America (Westgate 1989). It is interesting that the material was found in a middle Eocene estuarine setting in Texas that was similar to the shallow marine setting of the Piney Point Formation in Virginia. In contrast, *Anosteira* and *Pseudanosteira* seem to be restricted to nonmarine deposits of Eocene age in western North America and China (Hay 1908, Tong et al. 2010). *Allaeochelys* apparently did not survive in North America beyond the middle Eocene.

TRIONYCHIDAE Gray 1825

SUBFAMILY INDET.

"*Trionyx*" *halophilus* Cope 1869a

(Figs. 8L–N)

Specimens—CMM-V-4761, neural element found by Peter Kranz; CMM-V-4760, seventh right costal found by Michael Smigaj.

Locality, horizon, and age—The neural was found at the foot of the bluffs west of Fort Washington on the shore of the Potomac River, Prince Georges County, Maryland. The specimen probably came from the base of the Piscataway Member of the Aquia Formation (late Paleocene, early Thanetian), but it seems likely it was reworked from the Brightseat Formation (early Paleocene, Danian). The costal was found at a site along Central Avenue just east of Washington, D.C., in Prince Georges County, Maryland. The specimen came either from near the base of the Piscataway Member of the Aquia Formation (late Paleocene, early Thanetian) or from the Brightseat Formation (early Paleocene, Danian).

Description—Neural and costal both have a distinctive surface sculpture composed of rounded shallow pits separated by flat-topped interconnected ridges. Posterior border of costal abutted a relatively small eighth costal.

Remarks—There is little that can be gleaned from these specimens that would allow any detailed identification within the family Trionychidae. The relatively small size of the eighth costal, as indicated by its nested border with the seventh costal, is typical of trionychine turtles but also is found in some cyclanorbines. Therefore, no definitive subfamily placement can be made. The pitting pattern on the external surface of the bones is distinctly different from that of the described Aquia Formation trionychid species "*Trionyx*" *virginianus* Clark 1895 referred below to the genus *Aspideretoides* Gardner, Russell & Brinkman 1995 so this material pertains to a different taxon of trionychid turtle. The pattern on the surface of these bones is quite similar to that of "*Trionyx*" *halophilus* (Cope 1870, Hay 1908), which was described from Maastrichtian strata in Delaware (Baird and Galton 1981). *Aspideretoides* species (Gardner et al. 1995), *Axestemys puercensis* (Hay 1908), and *Oliveremys* Vitek 2011 have a somewhat similar pattern of pits. *Oliveremys* is not known to range below the middle Eocene and has not been reported from anywhere in eastern North America, so it is very unlikely that this material would pertain to that genus. *Axestemys* and *Aspideretoides* are known to range from the Upper Cretaceous into or through the Paleocene (Williamson and Lucas 1993, Hutchison and Holroyd 2003, Jasinski et al. 2011), so "*T.*" *halophilus* might pertain to one of these genera.

Unfortunately, the holotype material and the specimens described here are too fragmentary to assign to any genus with certainly, so the matter cannot be resolved. Therefore this material is referred to "*Trionyx*" *halophilus* for the sake of nomenclatural stability, while recognizing that the type material is not diagnosable and this species is a *nomen dubium*. It is possible that these specimens represent a turtle that survived into the very beginning of deposition of the Aquia Formation, but the total absence of any similar remains at any horizon above the very base of the Aquia Formation suggests that it is far more likely that these specimens originated in the Brightseat Formation and were reworked into the base of the immediately overlying Aquia Formation.

"*Trionyx*" *pennatus* Cope 1869a

(Fig. 8O)

Specimen—CMM-V-3283, third left costal found by William Counterman.

Locality, horizon, and age—This costal was found in the bluffs north of Popes Creek and south of the Loyola Retreat in southern Charles County, Maryland. The specimen came from the upper part (B) of the Woodstock Member, Nanjemoy Formation; early Eocene (Ypresian, NP 13).

Description—Costal elongate with no indication of sulcal grooves or any sutural border at its distal end for attachment to a peripheral element. Dorsal surface bears a coarse sculpture of pits and grooves, with pits predominating proximally and grooves predominating distally. Distal rib end protrudes beyond the costal only a short distance.

Remarks—The size, thickness, and external surface sculpture of this specimen are indistinguishable from material described by Cope (1869a) as "*Trionyx*" *pennatus*, which apparently came from the age-equivalent early Eocene Manasquan Formation in New Jersey. The type material from New Jersey, the specimen described here, and similar early Eocene material described from the Fisher/Sullivan site in Stafford County, Virginia (Weems 1999) almost certainly pertain to one and the same taxon because all of this material is very similar and also because no other early Eocene species of trionychid turtle has been reported from anywhere in the eastern United States. Although *Trionyx* Forskål 1775 was once widely used as a generic designation for American Cenozoic soft-shell turtle specimens, the name does not properly apply to any American material (Meylan 1987). At the same time, however, there are no characteristics preserved in this Nanjemoy material that could clearly establish what the correct generic designation is or even to which subfamily of trionychids it pertains. It is possible, but far from certain, that it pertains to the living genus *Apalone* Rafinesque 1832. For now, the established name "*Trionyx*" *pennatus* is retained with *Trionyx* in quotes for nomenclatural stability, while recognizing that the type material is not diagnosable and this species is a *nomen dubium*.

TRIONYCHINAE Gray 1825
ASPIDERETOIDES Gardner, Russell & Brinkman 1995
Aspideretoides virginianus (Clark 1895) n. comb.
(Figs. 9A–F, 10)

Synonymy—*Trionyx virginianus* Clark 1895, *Amyda*

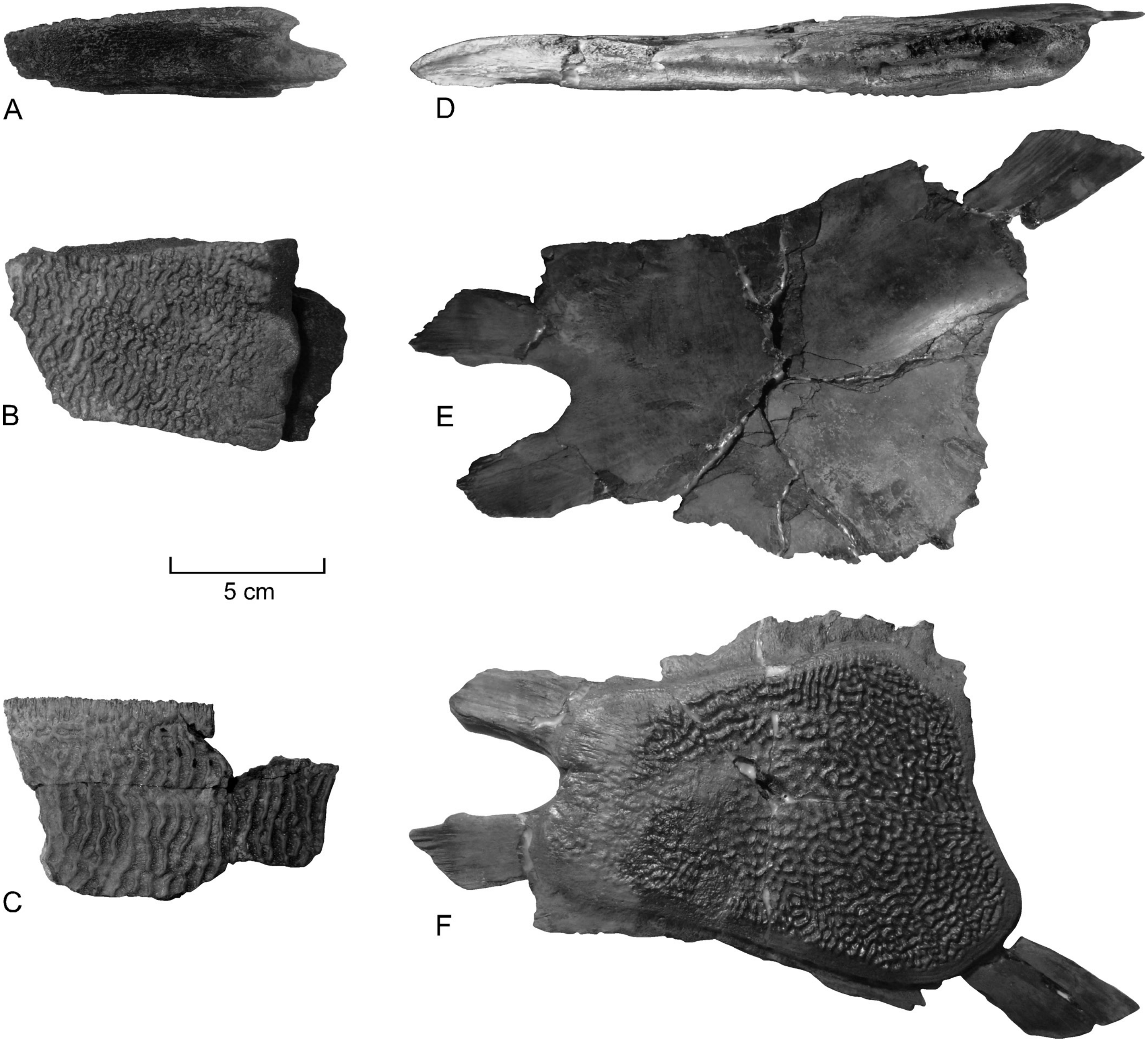

Figure 9. *Aspideretoides virginianus* from the Aquia Formation. **A, B.** Distal end of costal, CMM-V-4756. **A,** lateral view; **B,** dorsal view. **C.** Medial region of costal in dorsal view, CMM-V-4756. **D–F.** Right xiphiplastron, CMM-V-4768. **D,** medial view, dorsal side up; **E,** internal (dorsal) view; **F,** external (ventral) view.

virginiana (Lynn 1929), *Aspideretes virginianus* (Weems 1988).

Type species—*Aspideretoides virginianus* (Clark 1895).

Diagnosis–Costal plates up to 26 mm thick; sculpture consists of ridges and grooves oriented at right angles to the sutural borders; a few to many ridges cross the grooves, breaking them up into circular and elongate pits up to 5 mm in diameter (after Hay 1908).

Expanded diagnosis—Carapace elliptical in shape, longer than wide, adult specimens over 60 cm in length; neurals and costals very thick with a ridge and groove sculpture pattern oriented generally at right angles to sutural boundaries and generally broken up by ridges crossing the grooves into circular to elongate pits; preneural present. Plastron strongly reduced; xiphiplastron similar in shape to that of *Aspideretoides foveatus* but less elongated anteroposteriorly, posterior border concave rather than convex as in *A. foveatus*, and much larger.

Holotype—USNM-9354, fragments of two costal elements.

Hypodigm—USNM-11944, a largely complete carapace illustrated in Weems (1988); CMM-V-4756, a partial carapace found by Peter Kranz; CMM-V-4768, largely complete right xiphiplastron found by Gary Grimsley; CMM-V-4766, proximal portion of scapula found by Thomas G. Gibson.

Locality, horizon, and age—The type material came from the high bluffs between Potomac Creek and Aquia Creek along the southern shore of the Potomac River in Stafford County, Virginia, as did the nearly complete carapace described in Lynn (1929) and Weems (1988). The scapula fragment was found by Thomas G. Gibson

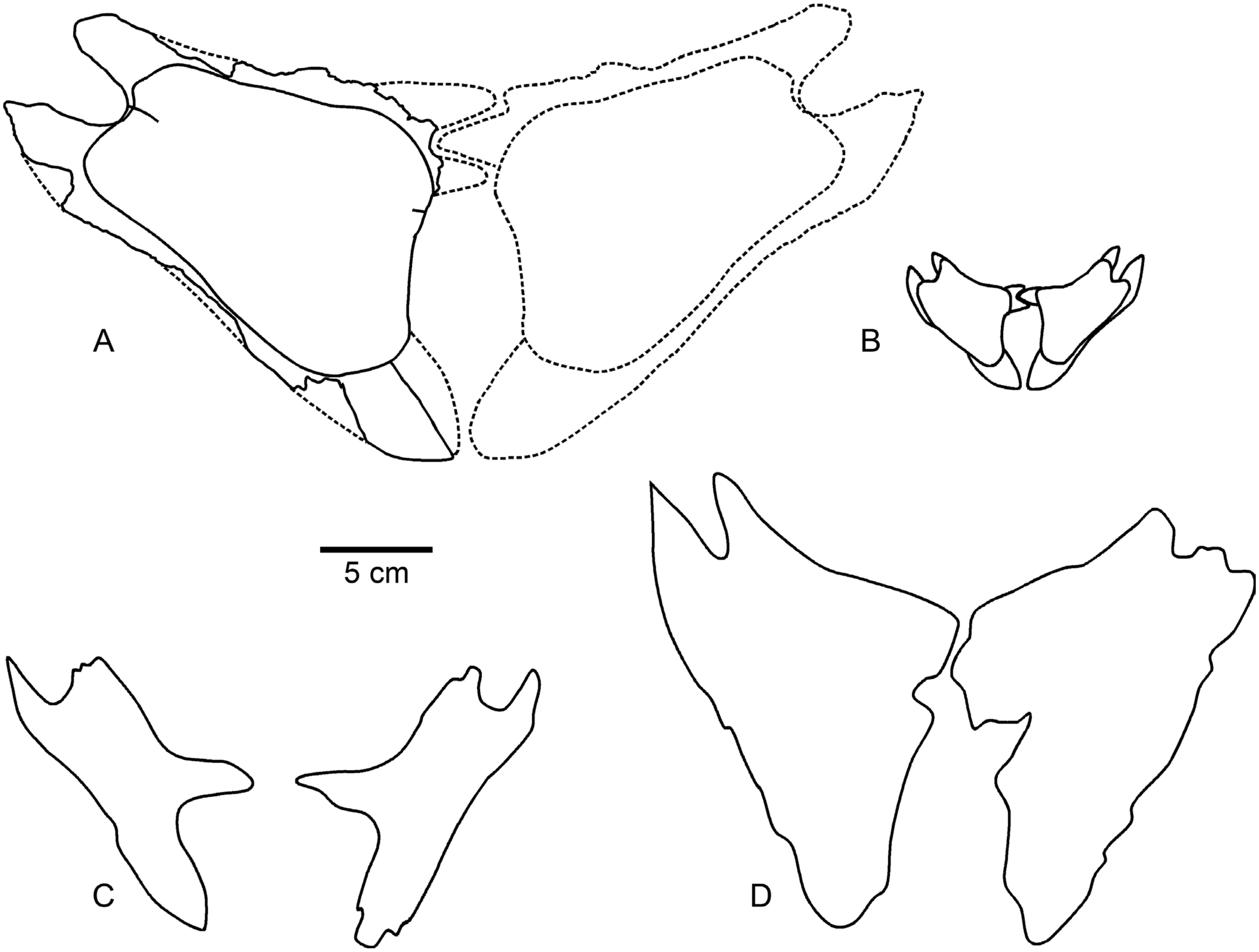

Figure 10. A–D. Xiphiplastra of **(A)** *Apideretoides virginianus* compared with the xiphiplastra of **(B)** *A. foveatus* (adapted from Gardner et al. 1995), **(C)** *Oliveremys uintaensis* (adapted from Vitek 2011), and **(D)** *Axestemys montinsana* (adapted from Vitek 2012).

in "Zone 4" of the Aquia Formation in these same bluffs. The right xiphiplastron was found in the Blue Banks south of Liverpool Point on the east bank of the Potomac River in "Zone 2" of the Aquia Formation, Charles County, Maryland. All of these specimens came from the lower part of the Piscataway Member of the Aquia Formation; late Paleocene (early Thanetian).

Remarks—Clark's "*Trionyx*" *virginianus* was referred by Weems (1988) to the genus *Aspideretes* because the carapace bears a large preneural element, which is present in that genus and not in the genus *Trionyx*. Since then, however, it has become apparent that the presence of a preneural is a primitive feature among the Trionychidae that has persisted in several quite different lineages, and that the genus name *Aspideretes* is applicable only to some Asian trionychines (Meylan 1987, Vitek 2012). Gardner et al. (1995) have erected the genus *Aspideretoides* to include Late Cretaceous to Early Cenozoic western American trionychine species that retain a preneural and also have similar and distinctive plastra. As discussed below, the discovery of a "*T.*" *virginianus* xiphiplastron that is very similar now makes it appropriate to assign this species to *Aspideretoides*.

The referred xiphiplastron clearly pertains to *Aspideretoides virginianus* because (1) it comes from an animal too large to be the enigmatic basal Aquia or pre-Aquia trionychid "*Trionyx*" *halophilus*, (2) its ridge and trough sculpture pattern is like that of *A. virginianus* and unlike the pitted pattern of "*T.*" *halophilus*, and (3) this xiphiplastron was found at a locality that has produced numerous carapace examples of "*A.*" *virginianus* and no examples of "*T.*" *halophilus*. For all of these reasons, this xiphiplastron can be confidently assigned to *A. virginianus*. Its discovery for the first time allows comparison with the plastra of other trionychids known from the Late Cretaceous and Early Cenozoic of North America.

North American Late Cretaceous and Cenozoic trionychids include representatives of both the subfamilies Plastomeninae Hay 1902 and Trionychinae. Most plastomenines have a preneural, but they also have a plastron that is much less reduced than in this species and most other trionychines; therefore referral to Plastomeninae is not indicated. Among Paleocene and Eocene trionychines, *Apalone* and *Oliveremys* differ from *A. virginianus* in that they both lack a preneural element. *Axestemys* is similar to *A. virginianus* in that it retains a preneural and attains a large size (greater than 60 cm), but it shows no close similarity in its xiphiplastra. The right xiphiplastron discussed here bears considerable resemblance to the xiphiplastra of *Aspideretoides* (Fig. 10), so reference of the species *virginianus* to the genus *Aspideretoides* is indicated. The detailed morphology of this xiphiplastron, however, is not identical to that of any known species of *Aspideretoides*, so the species name remains valid.

Although the holotype of *A. virginianus* is very fragmentary and not directly diagnosable, the supplementary material discussed here and in Weems (1988) does provide adequate information to allow a unique diagnosis. The large size of the supplementary xiphiplastron and the large size and exceptional thickness of the supplementary carapace specimens indicate that all of this material pertains to a very large trionychine turtle comparable in size to the turtle from which the holotype specimens came. The only other trionychid turtle that possibly has ever been found in the Aquia Formation is "*Trionyx*" *halophilus* which, as discussed above, more probably is only present in the basalmost Aquia Formation as material reworked from the immediately underlying Brightseat Formation. Even if "*T.*" *halophilus* did survive into the base of the Aquia Formation, however, it is a much smaller species than *A. virginianus* and has a distinctly different surface sculpture. Considering that all of the material assigned here to *A. virginianus* was found within a very restricted stratigraphic interval (lower Piscataway Member of the Aquia Formation) in outcrops less than ten miles apart, there is no reason to doubt that all of the large, thick-shelled trionychid specimens from the Piscataway Member of the Aquia Formation represent a single species.

The xiphiplastron of *A. virginianus* has a healed fracture which is discernable near its external and internal margins (shown in Fig. 10) but untraceable across its central region. This indicates that the xiphiplastron was fractured when the turtle was young, but the animal survived and its fracture healed almost entirely before the animal died.

CHELONIOIDEA Oppel 1811
DERMOCHELYIDAE Baur 1888
EOSPHARGIS Lydekker 1889a
Eosphargis insularis (Cope 1872)

Synonymy—*Lembonax insularis* Cope 1872, *Allopleuron insularis* Weems 1988, *Allopleuron insularis* Karl et al. 2012.

Specimen—USNM 359002, nuchal, first neural, right and left first and second peripherals, and left third peripheral, described in Weems (1988).

Locality, horizon, and age—Found in bluff between Aquia Creek and Potomac Creek, western bank of Potomac River, Stafford County, Virginia; nannofossils in the attached matrix indicate the specimen came from "zone 6," Piscataway Member of the Aquia Formation (Clark and

Martin 1901); late Paleocene (early Thanetian).

Remarks—Weems (1988) assigned to *Allopleuron insularis* the anterior portion of a large but lightly built carapace found in the late Paleocene (early Thanetian) Piscataway Member of the Aquia Formation. This Aquia carapace has a peculiar first peripheral that is sutured to the second peripheral on both its distal and internal sides so that it is completely out of contact with the costoperipheral fontanelle. This condition is characteristic of a species found in the age equivalent late Paleocene (early Thanetian) Vincentown Formation of New Jersey that Cope named *Lembonax insularis*. Cope included three species in the genus *Lembonax* Cope 1870: *L. polemicus* Cope 1870 which is the type species, *L. insularis* Cope 1872 and *L. propylaeus* Cope 1872. Unfortunately, the type species of *Lembonax* is a *nomen dubium* (Weems 1988) and cannot be adequately defined. Because of this, Weems (1988) chose to refer *Lembonax insularis* to the similar (but not identical) Late Cretaceous turtle genus *Allopleuron* Baur 1888 (type species *Allopleuron hoffmani* (Gray 1831)) as a new combination (*A. insularis*) and assigned *Allopleuron* to the Dermochelyidae. At that time, this assignment was in accord with the conclusion of Gaffney and Meylan (1988) and Hiramaya (1992) that *Allopleuron* was an aberrant protostegid or dermochelyid turtle. Somewhat later, however, Hirayama (1994) concluded that *A. hoffmani* was an aberrant pancheloniid turtle, and this placement has been followed since (Lapparent de Broin 2001, Karl 2007, Karl et al. 2012). In recent years two new species of *Allopleuron* have been named: *A. lipsiense* Karl 2007 from the early Oligocene of Germany and *A. qazaqstanense* Karl, Gröning, and Brauckmann 2012 from the early middle Eocene of Kazakhstan. These new records show that in Europe *Allopleuron* survived at least until the early Oligocene.

Significantly, the three European species assigned to *Allopleuron* (*A. hoffmani*, *A. qazaqstanense*, and *A. lipsiense*) all have a normal progression of peripheral elements away from the nuchal, a nuchal that is anteroposteriorly short, and a first neural that is as long as or longer than wide (Karl et al. 2012:164). This stands in marked contrast to the condition seen in "*A.*" *insularis* in which the second peripheral makes broad contact with the nuchal beneath the first peripheral so that the first peripheral is nested above the second peripheral-nuchal contact, the nuchal is relatively much narrower and more elongate, and the first neural is very wide. These are striking differences that clearly indicate that (1) "*A.*" *insularis* should not be referred to the European genus *Allopleuron* and (2) that *Allopleuron* henceforth should be considered to be an exclusively Eurasian genus.

It still seems likely that the material included in *Lembonax* represents a dermochelyid rather than a pancheloniid turtle. Referral of the species *Lembonax insularis* to *Eosphargis* is proposed because the early Eocene dermochelyid *Eosphargis gigas* (Owen) Lydekker 1889a also has a nuchal that is strongly indented anteriorly and because *Lembonax* occurs at a horizon equivalent in age to the oldest specimens of *Eosphargis* known from Denmark (Lapparent de Broin 2001). No skull or plastron material referable to *Lembonax insularis* has been found, so there is no way to perform a rigorous comparison between *L. insularis* and the two described European species of *Eosphargis*, *E. gigas* and *E. breineri* Nielsen 1959. In the absence of such material, there is no way to determine with certainty if "*A.*" *insularis* might be identical with *E. gigas* or *E. breineri*. Therefore, at least for now it seems most parsimonious to refer the long established and diagnosable species *Lembonax insularis* to *Eosphargis* as a third species, *Eosphargis insularis*.

Eosphargis breineri was described as an Eocene dermochelyid (Nielsen 1959), but it is now known to be latest Paleocene in age (Bonde 1987). Therefore this species most probably is age equivalent to the late Thanetian Paspotansa Member of the Aquia and somewhat younger than the early Thanetian source horizon of *E. insularis* in both New Jersey and Maryland. It remains possible that *E. breineri* is synonymous with *E. insularis*. Until such time as this can be tested in a meaningful way, however, they should remain as separate species of slightly different age and distinctly different provenance.

cf. *Eosphargis gigas* (Owen) Lydekker 1889a
(Figs. 11A–G)

Specimens—CMM-V-4777, a fragmentary nuchal element; CMM-V-4778, two fragmentary neurals, largely complete right hyoplastron, and proximal end of coracoid; all found by Gary Grimsley.

Locality, horizon, and age—All specimens were found near the base of the bluff on the Potomac River immediately west of Loyola Retreat, 1.7 mile north of Popes Creek in southern Charles County, Maryland; lower part of the Woodstock Member (Woodstock A) of the Nanjemoy Formation; early Eocene (Ypresian, nannofossil zone NP12).

Description—Nuchal deeply indented, with a pronounced knob on its ventral surface for attachment to the top of the neural spine of the first dorsal vertebra. Neural thin and wide, with a low but well developed midline ridge and a beveled lateral margin bearing only faint indications of suturing to the adjacent costals, peripherals about as

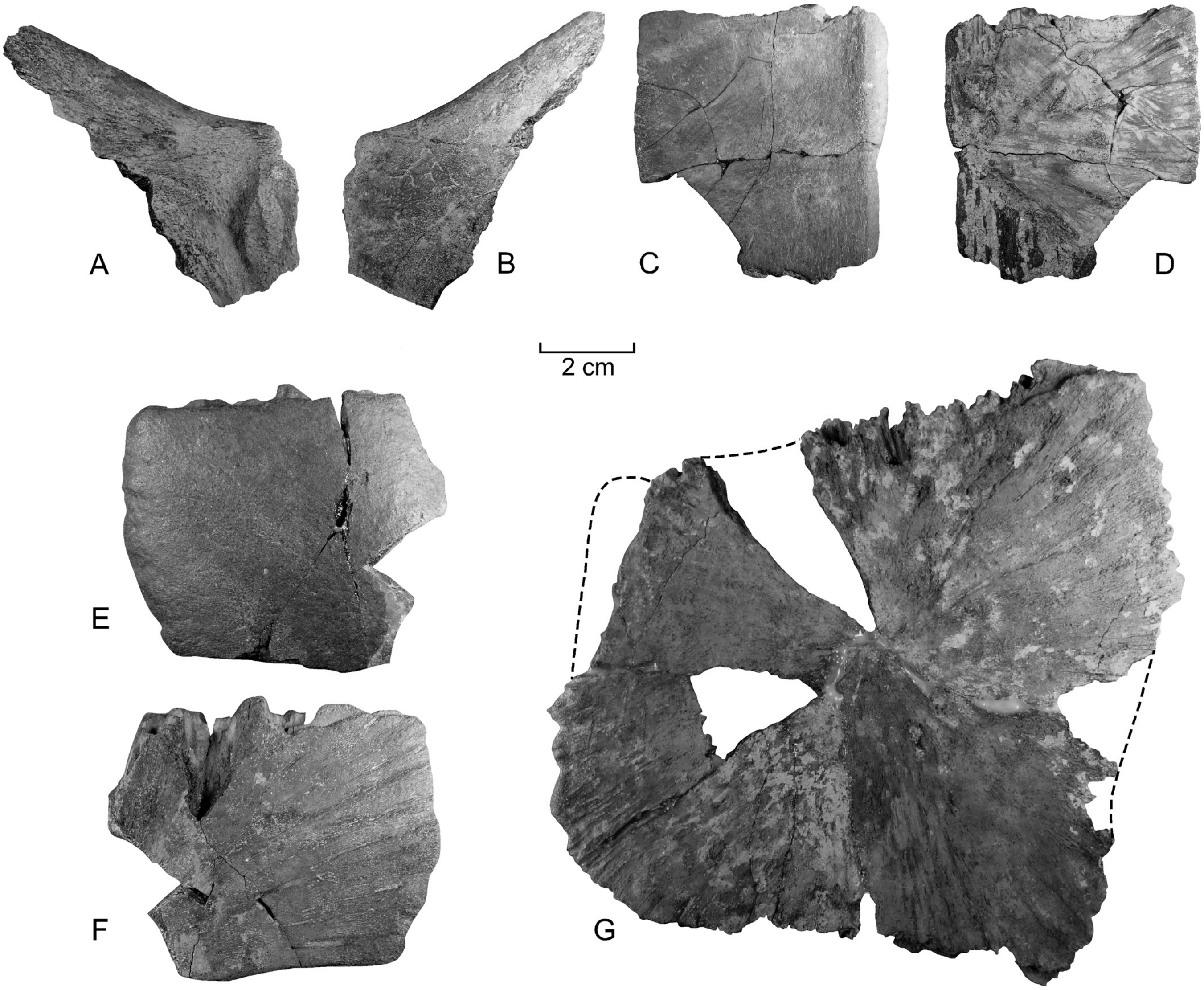

Figure 11. A–G. Fragments of carapace of cf. *Eosphargis gigas*. **A, B.** Right central region of nuchal, CMM-V-4777. **A,** ventral view; **B,** dorsal view. **C, D.** Lateral and central portion of a neural bearing a medial dorsal ridge near right broken border, CMM-V-4778. **C,** dorsal view; **D,** ventral view. **E, F.** Lateral region of a neural, CMM-V-4778. **E,** dorsal view; **F,** ventral view. **G.** Left hyoplastron in ventral (external) view, CMM-V-4778.

long as wide and roughly square-shaped with no sutural contact with the costals or any plastral element.

Remarks—These four bones belonged to a very large turtle with a much reduced carapace. The deep emargination of the nuchal, the medially ridged neurals that are wider than long, and the faint indication of a sutural attachment between the neurals and costals all indicate that this was a dermochelyid turtle. At one time two species of *Eosphargis* (*Eosphargis gigas* and *E. breineri*) were reported from the early Eocene of the North Atlantic region (Nielsen1959), but the stratigraphic horizon of *E. breineri* later was revised from early Eocene to latest Paleocene (Bonde 1987). Therefore only *E. gigas*, described by Owen (1880) from the early Eocene London Clay of England and also reported from the early Eocene of Belgium, presently represents the Dermochelyidae in the North Atlantic region in the early Eocene. A frontal from a dermochelyid skull, found in the Potapaco Member (Potapaco B) of the Nanjemoy Formation, was assigned by Weems (1999) to cf. *E. gigas* because it was fully comparable with that species but not really diagnostic. The remains reported here also are fully comparable with *E. gigas* but similarly are inadequate to be diagnostic. In the absence of any other described early Eocene dermochelyid species in the North Atlantic region, all of this material is provisionally assigned to *E. gigas* until such time as any other early

Eocene species is recognized in the North Atlantic region.

In the early Eocene of the North Atlantic region, no dermal ossicles have been found anywhere that could be assigned to one of the more advanced dermochelyid genera that had an epithecal shell mosaic (e.g., *Arabemys* Tong, Buffetaut, Thomas, Roger, Halawani, Memesh, and Lebret 1999, *Cosmochelys* Andrews 1919, *Psephophorus* von Meyer 1847 or *Dermochelys* de Blainville 1816). The oldest reported dermochelyid dermal plates in the southeastern United States are from the late Eocene Clinchfield Formation of Georgia (Parmley et al. 2006), but still older dermal plates have been found in the middle Eocene Cross Member of the Tupelo Bay Formation of South Carolina (material observed by author in the Charleston Museum collections). The oldest dermochelyid dermal plates from England are from the middle Eocene of Sussex (Lydekker 1889b), which is comparable in age to the oldest ossicles known from the southeastern United States. In the southern hemisphere, Albright et al. (2003) reported rather similar dermochelyid ossicles from Antarctica that might be as old as early Eocene but more probably are also middle Eocene in age. The only documented occurrence of dermochelyid ossicles older than middle Eocene are ossicles assigned to *Arabemys crassicutata* Tong et al. (1999). These were reported as being late Paleocene to early Eocene in age, but this age range is the maximum permissible. Based on the ranges of some of the co-occurring mollusks and the earliest known first occurrence of the teleost fish *Eotrigonodon* Weiler 1929 (Thomas et al. 1999), the most likely age is early Eocene. Even so, this still is the oldest known occurrence of dermochelyid ossicles, and these are distinctly more primitive in their morphology and osteology than dermal ossicles found in the middle Eocene. It therefore seems that the dermochelyid epithecal shell mosaic first evolved in the Arabian region of the Tethys Seaway but its bearers did not spread into the North Atlantic Ocean Basin and elsewhere until the middle Eocene.

PANCHELONIIDAE Joyce, Parham & Gauthier 2004
LOPHOCHELYINAE Zangerl 1953
LOPHOCHELYS Zangerl 1953
?*Lophochelys* sp.
(Figs. 12A–C)

Specimen—USNM 537787, associated right hyoplastron and hypoplastron found by Dave Bohaska.

Locality, horizon, and age—Hill behind Hampton Mall located near the intersection of Central Avenue and Interstate 95, Prince Georges County, Maryland; Brightseat Formation; early Paleocene (Danian).

Description—Hyoplastron and hypoplastron of small size (combined length about 4.5 cm) with a prominent low knob developed on each that lies away from the proximal end of each bone about one-fourth the distance toward the distal end. No sutural border developed medially or laterally; the mid-line fontanelle expands in its central region into a sub-rounded vacuity. Suture line on hypoplastron indicates xiphiplastra were narrow and located close to the midline. Hyoplastron and hypoplastron constricted antero-posteriorly at their mid-length to form a saddle-shaped concavity both anteriorly and posteriorly.

Remarks—The prominent low knobs on the external surface of the hyoplastron and hypoplastron are a distinctive characteristic that readily characterize this material as belonging to a lophochelyine pancheloniid. Lophochelyines were an abundant and diverse group of marine turtles

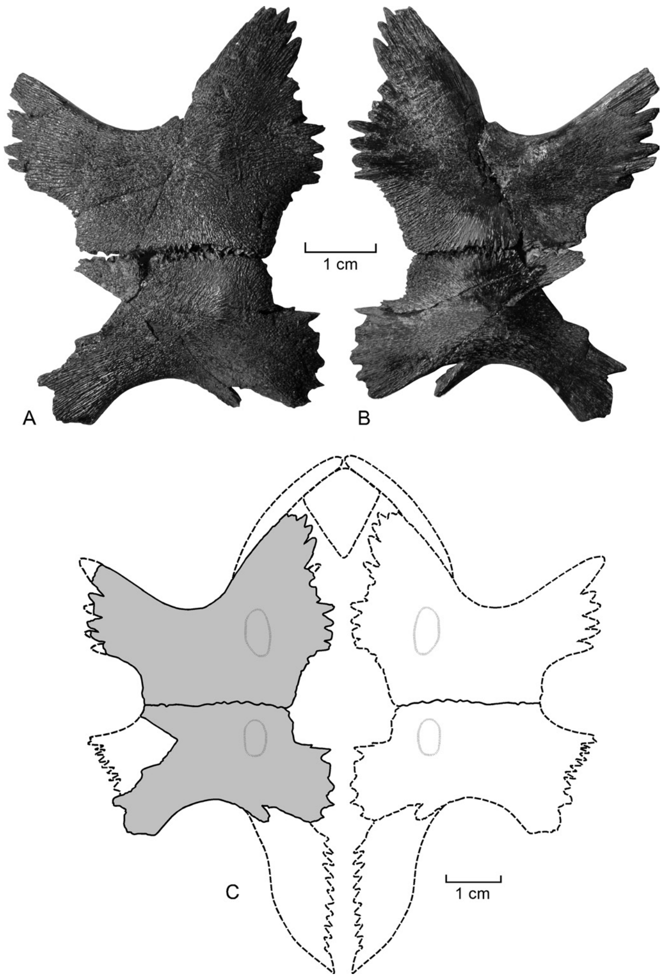

Figure 12. ?*Lophochelys* sp. plastron from the Brightseat Formation of Maryland. **A, B.** Associated hyoplastron and hypoplastron, USNM 537787. **A,** dorsal view; **B,** ventral view. **C.** Restoration of the plastron based on Fig. 13A; plastral knobs indicated by four dotted ellipses.

during the Late Cretaceous (Zangerl 1953), but they were decimated during the end-Cretaceous extinction event. Wood (1973) documented the persistence of one member of this group into the Paleocene of west-central Africa, part of a plastron too incomplete to assign to a genus. Moody (1980) has suggested that the early Eocene London Clay turtle *Neurochelys harvicensis* (Woodward 1830) also may belong to this group, but this conclusion has not been subsequently followed (Lapparent de Broin 2001).

The associated hyoplastron and hypoplastron described here constitute the first record of this group in the Paleogene of the Atlantic Coastal Plain. The lack of elongation in the distal part of the hyoplastron and hypoplastron is typical of juvenile primitive pancheloniids (Nicholls 1988); this characteristic and the very small size of these elements both suggest that this material represents an immature individual. It is likely that this specimen pertains to *Lophochelys*, which was a persistently small Late Cretaceous North American form, but the partial plastron described here is too incomplete to be certain of this so assignment to this genus is queried.

SUBFAMILY: INDET.

CATAPLEURA Cope 1868

Catapleura coatesi (Weems 1988)

(Figs. 13A–D, 14A–C)

Synonymy—*Dollochelys coatesi* Weems 1988, *Catapleura repanda* (partem) Hirayama 2006

Specimens—CMM-V-4764, second left costal found by Jason Osborn; CMM-V-4767, pygal found by Gary Grimsley; CMM-V-4765, neural found by Mark Bennett.

Locality, horizon, and age—Blue Banks south of Liverpool Point, Charles County, Maryland; "Zone 2" of the Piscataway Member of the Aquia Formation (Clark and Martin 1901); late Paleocene (early Thanetian).

Description—Left second costal, thin proximally (3 mm) thickening distally to moderately thin (5 mm), sulcal grooves discernable on dorsal surface. Anterior portion of distal end has sutures for attachment to an anterior peripheral; posterior portion forms the internal border of the anterior internal rim of the costoperipheral fontanelle. Nuchal hexagonal and only about 3 mm thick. Pygal attached to second suprapygal by only a narrow bridge of bone.

Remarks—Weems (1988) described this species and placed it in the genus *Dollochelys* Zangerl 1971. Since then, Hirayama (2006) concluded that *Dollochelys* is a junior synomym of *Catapleura*. This synonymy is accepted here. However, Hirayama also concluded that the three described species formerly in *Dollochelys* (*D. casieri* Zangerl 1971, *D. atlantica* (Zangerl 1953) and *D. coatesi*) are all essentially identical with *C. repanda* and thus are junior synonyms of that taxon. With this the present author disagrees. Many but not all of the features of *D. coatesi* are the same as in *C. repanda*, but a second specimen of *C. coatesi* illustrated here (Fig. 14A) indicates by the position of its sulcal grooves that there was only a very narrow vertebral scale as in the type specimen of *Catapleura coatesi* and quite different from the much wider vertebral scale characteristic of *C. repanda*. Since no specimen has been found with a vertebral scale width intermediate between these two species, available evidence still clearly favors these being distinctly different species. The fact that *C. coatesi* is found in the late Paleocene Aquia Formation, while the type material of *C. repanda* and *D. atlantica* both come from the early Paleocene Hornerstown Formation, further casts doubt on any likely synonymy of *C. coatesi* with *C. repanda* and instead suggests that *C. repanda* is probably ancestral to *C. coatesi*.

Catapleura sp.

(Figs. 13E-I)

Specimens–CMM-V-4774, proximal costal found by Gary Grimsley; CMM-V-4775, proximal costal found by Bob Wiest.

Locality, horizon, and age–Found in the bluff immediately west of Loyola Retreat, 1.7 miles north of Popes Creek; lower part (Bed A) of the Woodstock Member of the Nanjemoy Formation; early Eocene (Ypresian), within nannoplankton zone NP12.

Description–Costal thin with a smooth surface texture, average thickness about 4–5 mm and maximum thickness 7 mm over center of rib shaft. Proximal rib neck short and stout, with an elliptical rib head twice as wide as high.

Remarks–These costals are far too large to belong to *Tasbacka* Nessov 1987 or *Puppigerus* Cope 1870. They are quite similar to the costal elements of *Catapleura* and *Euclastes* Cope 1867, but differ from *Euclastes* in being exceptionally thin. It seems likely that they pertain to the same taxon Weems (1999) called ?*Dollochelys* sp. from

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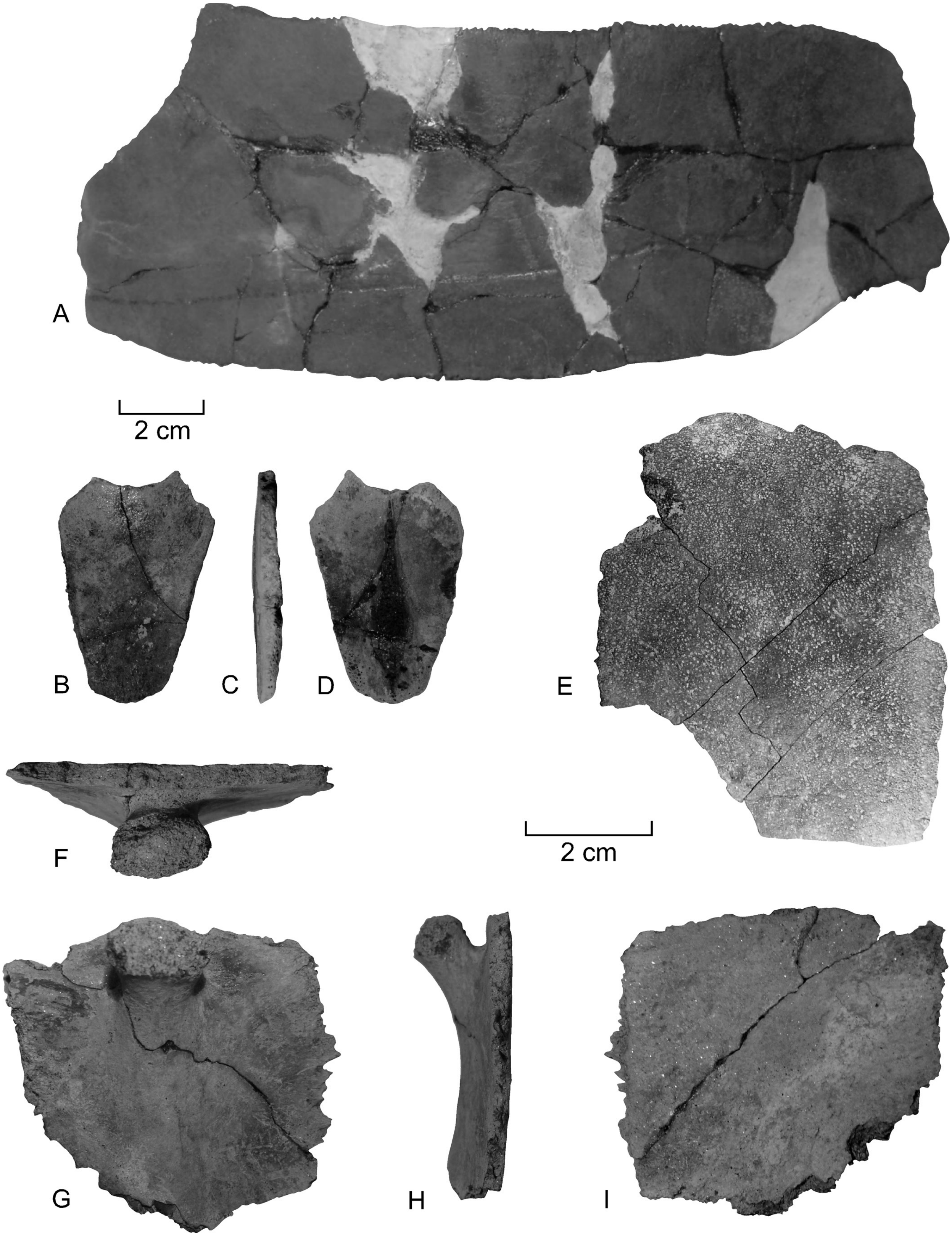
► **Figure 13. A–I.** Carapace elements of *Catapleura*. **A.** Second left costal of *Catapleura coatesi* in dorsal view, CMM-V-4764. **B–D.** Fourth neural of *Catapleura coatesi*, CMM-V-4765. **B,** dorsal view; **C,** lateral view; **D,** ventral view. **E.** Proximal costal of *Catapleura* sp., dorsal view, CMM-V-4774. **F–I.** Proximal costal of *Catapleura* sp., CMM-V-4775. **F,** proximal view; **G,** ventral view; **H,** anterior view; **I,** dorsal view.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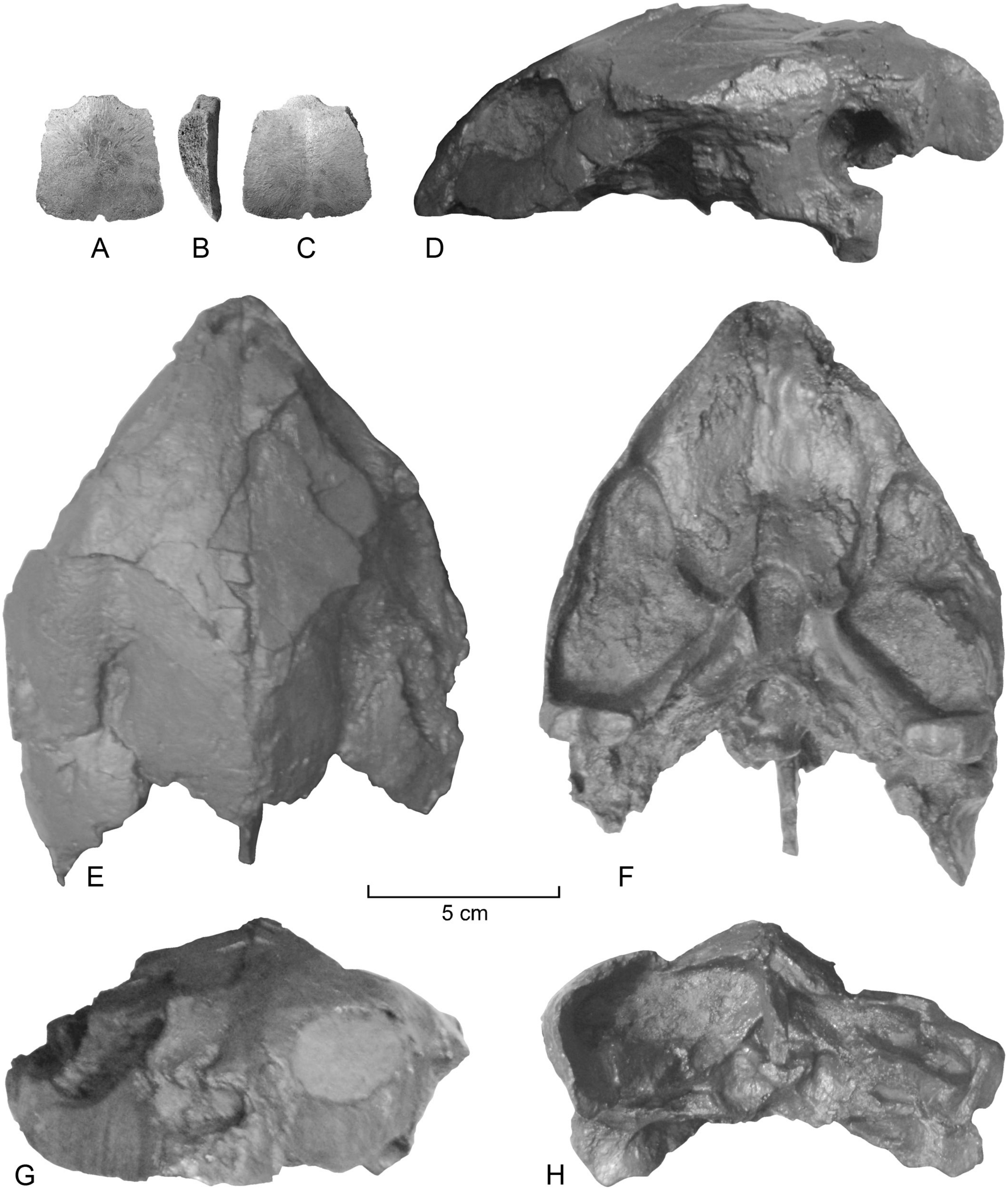

Figure 14. A–C. Pygal element of *Catapleura coatesi,* CMM-V-4767; **A,** dorsal view; **B,** lateral view; **C,** ventral view. **D–H.** Skull cast of *Euclastes roundsi*, CMM-V-4825. **D,** lateral view; **E,** dorsal view; **F,** ventral view; **G,** anterior view; **H,** posterior view.

the early Nanjemoy Formation (bed B of the Potapaco Member) at the Fisher/Sullivan site in Stafford County, Virginia. At neither the Fisher/Sullivan site nor at the bluffs around Popes Creek have even fragments of the highly specialized and diagnostic premaxillaries or dentaries of *Euclastes* been found, which argues against the presence of that genus at any of the collected Nanjemoy localities. These costal fragments could pertain to some as yet undescribed taxon, but in the absence of evidence for this they are referred for now to *Catapleura*, with which they are fully comparable. In any case, these specimens document the presence of a second pancheloniid turtle in addition to *Puppigerus* from the Woodstock Member of the Nanjemoy Formation (discussed below).

EUCLASTES Cope 1867

Euclastes wielandi (Hay 1908)

Synonymy–*Lytoloma angusta*? (partem) Wieland 1904, *Lytoloma wielandi* Hay 1908, *Osteopygis borealis* Hay 1908 (partem), *Erquelinnesia molaria* Hay 1908, *Osteopygis emarginatus* (partem) Zangerl 1953, *Osteopygis emarginatus* (partem) Weems 1988, *Osteopygoides priscus* Karl, Tichy & Ruschak 1998, *Euclastes priscus* Lynch & Parham 2003 (partem) *Euclastes wielandi* Parham 2005 (partem).

Specimen–USNM 412113, palate composed of premaxillaries, maxillaries, and vomer, described in Weems (1988).

Locality, horizon, and age–Found at Hampton Mall, Prince Georges County, Maryland; Brightseat Formation; early Paleocene (Danian).

Remarks–A pair of fused premaxillaries and maxillaries from the Brightseat Formation in Prince Georges County, Maryland were assigned by Weems (1988) to *Osteopygis emarginatus* following the taxonomy current at that time. Since then, Parham (2005) has demonstrated that only carapace and plastral material assigned to *O. emarginatus* properly belongs to that taxon, which belongs in the "Macrobaenidae." Skull material that had been assigned to *O. emarginatus* does not belong to that species and instead belongs to a pancheloniid turtle, *Euclastes wielandi*. Therefore, the Brightseat skull fragment has been taxonomically reassigned to *E. wielandi* and the Pancheloniidae.

Euclastes roundsi (Weems 1988)

(Figs. 14D-H, 15)

Synonymy–*Osteopygis roundsi* (partem) Weems 1988, *Osteopygis wielandi* (partem) Lynch & Parham 2003, *Osteopygis wielandi* (partem) Parham & Pyenson 2010.

Holotype–USNM 412108, crushed and slightly exploded skull imbedded in a nodule.

Referred specimen–Cast of largely complete skull (CMM-V-4825); original in the collection of Mel Gulotta who found the specimen.

Locality, horizon, and age–Holotype found in a bluff along the Pamunkey River upriver from U.S. Highway 301, Hanover County, Virginia; basal Piscataway Member of the Aquia Formation; late Paleocene (early Thanetian). Referred specimen found in the Blue Banks south of Liverpool Point, Charles County, Maryland; "Zone 2," Piscataway Member, Aquia Formation (Clark and Martin 1901); late Paleocene (early Thanetian).

Description–Cranium slightly longer than wide, snout narrow but rounded and not elongate. Dorsally, parietals cover nearly half of the skull roof; supraoccipital does not extend beyond the parietals as far rearward as the squamosal horns. Ventrally, a secondary palate is well developed, with both narrow premaxillaries and vomer elongated back to half way across the suborbital vacuities and with maxillary-palatine flanges extending even farther back to either side and terminating in a small contribution to the palate by the pterygoids.

Remarks–The species *Osteopygis roundsi* was described by Weems (1988) and assigned to the genus *Osteopygis*. Since then, Parham (2005) has established that the concept of *O. emarginatus* had become a chimera with a pancheloniid skull improperly associated with a "macrobaenid" shell and skeleton. He concluded that the postcranial material should remain *O. emarginatus* but that the skull should be assigned to *Euclastes wielandi*. Thus, the holotype skull of "*O.*" *roundsi* was referred to *Euclastes* (Lynch and Parham 2003). The paratype postcranial shell elements of *E. roundsi* now are referred to *Judithemys kranzi* n .sp. The excellent skull cast of *E. roundsi* illustrated here (Figs. 14D-H) was made by Billy Palmer for the Calvert Marine Museum. The suture boundaries of the skull elements can be readily seen on both the original and the cast (Figs. 15A, B). This specimen, by far the best example of this species yet found, differs considerably from the holotype (Fig. 15E) in that the nasals and vomer of the new specimen are much narrower than in the holotype, the contribution of the pterygoids to the secondary palate is smaller, and the vomer lacks a strong midline ridge. This perhaps could indicate that two durophagous pancheloniid species are present in the Aquia, but both skulls are almost identical in absolute size and ecologically it seems very unlikely for two closely related species to be present in the same area at essentially the same time. With only two skulls of *E. roundsi* available for study, it is impossible to determine the range of individual variability that existed

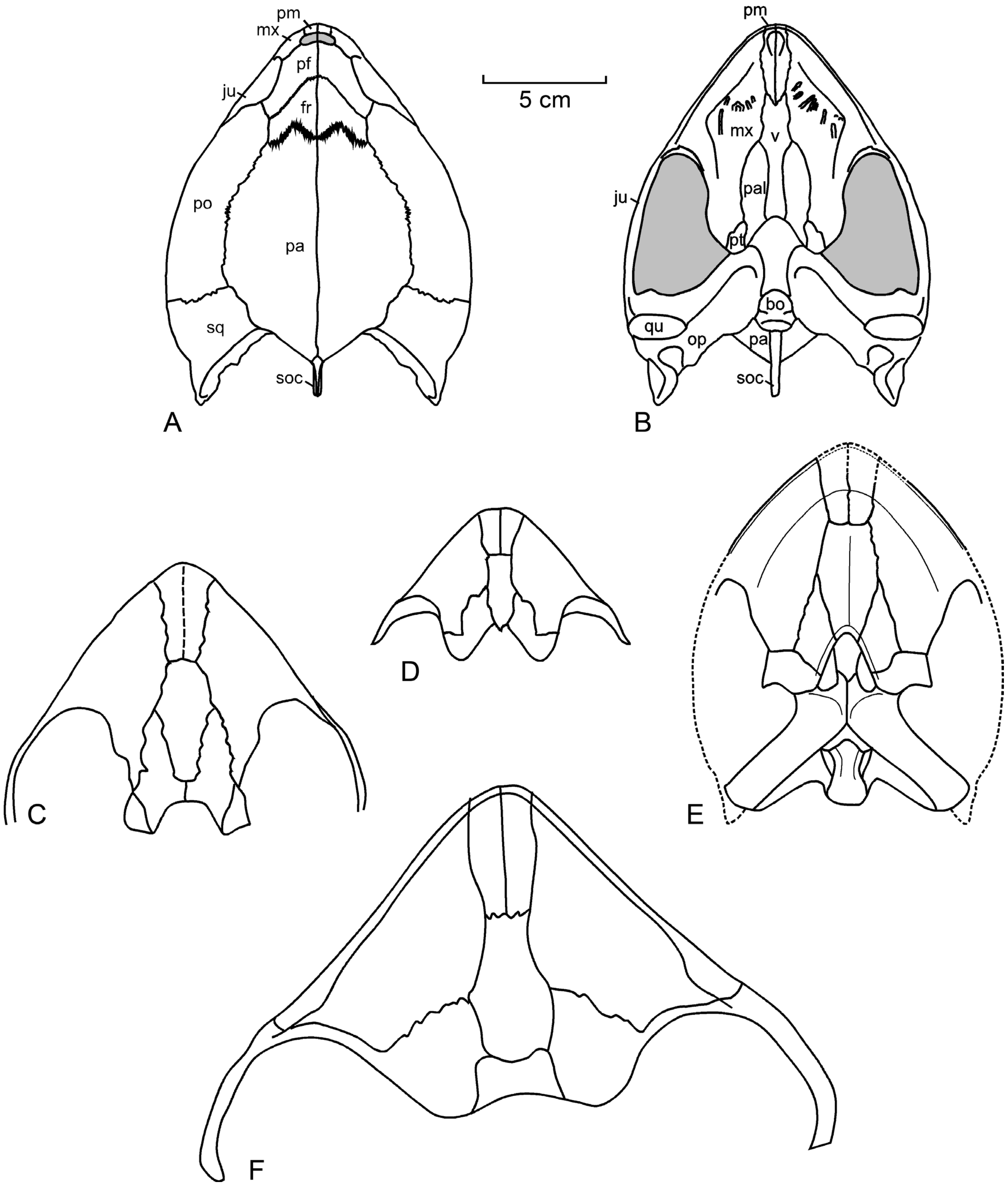

Figure 15. A–B. Restoration of *Euclastes roundsi* skull based on cast shown in Fig. 14. **A**, dorsal view**;** **B**, ventral view. **C–F.** Comparative views of the palatal region of the skulls of *Erquelinnesia gosseleti* **(C),** *Euclastes wielandi* **(D)**, *Euclastes roundsi* **(E)**, and *Euclastes platyops* **(F)**. All are modified from Parham (2005, fig. 3) except the holotype of *E. roundsi* **(E)** which is modified from Weems (1988, fig. 13). Abbreviations: **bo**, basioccipital; **fr**, frontal; **ju**, jugal; **mx**, maxilla; **op**, opisthotic; **pa**, parietal; **pal**, palatine; **pf**, prefrontal; **pm**, premaxilla; **po**, postorbital; **pt**, pterygoid; **qu**, quadrate; **soc**, supraoccipital; **sq**, squamosal; **v**, vomer.

in the secondary palates of these turtles. However, it is significant that Zangerl (1971) described considerable differences in skulls of the closely related turtle *Erquelinnesia gosseleti* (Dollo 1886) and suggested that these differences may reflect sexual dimorphism similar to that seen in the modern alligator snapping turtle (*Macrochelys temmincki* (Troost in Harlan 1835). Therefore it seems best to consider the two available skulls of *E. roundsi* from the Aquia Formation as examples of a single species with a markedly variable palate region, possibly due to sexual dimorphism but otherwise with the same skull morphology. The secondary palate of both specimens of *E. roundsi* are much longer than the secondary palate of *E. wielandi* (Fig. 15), and the premaxillaries and vomer also are much longer and narrower than in *E. wielandi*. These consistent and marked differences between the length of the palate region and constituent bones of *E. wielandi* and *E. roundsi* refutes the suggestion by Lynch and Parham (2003) and Parham and Pyenson (2010) that these two species are synonymous, though in all likelihood *E. roundsi* descended from *E. wielandi*. The secondary palate of the slightly younger (late Thanetian) species *E. platyops* Cope 1867 is much wider than in *E. roundsi*, and *E. platyops* also seems to have attained a much larger size. The palate of *E. gosseleti* is more similar to *E. roundsi* in its size and proportions than the palates of the other described species, but a striking difference is that the palatines of *E. gosseleti* enclose the vomer posteriorly unlike in any of the other species (Parham 2005, fig. 3). No carapace material referable to *Euclastes* has been identified so far from the Aquia Formation, but it would presumably be similar to the carapace of the closely related turtle *E. gosseleti* (Fig. 16).

TASBACKA Nessov 1987
Tasbacka ruhoffi (Weems 1988) n. comb.
(Fig. 16)

Synonymy–*Catapleura ruhoffi* Weems 1988.

Specimen–USNM 358865, disarticulated partial skeleton consisting of the fused dentaries, nuchal, right and left first peripherals, right and left second peripherals, right third peripheral, fifth, sixth and ninth left peripherals, eleventh right peripheral, parts of second costal, sixth right costal, first neural, part of fourth neural, eighth neural, and first suprapygal, described in Weems (1988).

Locality, horizon, and age–West bank of roadcut, Indian Head Road near Piscataway Creek, Prince Georges County, Maryland; Piscataway Member of the Aquia Formation; late Paleocene (early Thanetian).

Remarks–The turtle described by Weems (1988) as *Catapleura ruhoffi* later was discussed by Tong and Hirayama (2002), who strongly implied but did not explicitly state that the species should be referred to the genus *Tasbacka*. The first costal of *T. ruhoffi* is quite similar to that of *Catapleura* in that its external border is much longer than its internal border. This is due to the fact that the sutures along the anterior border of the first costals are strongly angled outward from the rim of the shell carapace (away from the midline) and not oriented normal to the carapace rim as is typical in pancheloniid turtles. This unusual conformation was why Weems (1988) referred the species to that genus. However, it is now apparent that in this regard the first costal of *T. ruhoffi* also is very similar to that of *Tasbacka*, and in all other diagnosable characters the similarity with *Tasbacka* is greater. Therefore, assignment to *Tasbacka* is accepted here. Tong and Hirayama (2002) correctly reported the age and stratigraphic horizon of *T. ruhoffi*, but they erroneously placed the type locality in the "Pamunkie [Pamunkey] River Bluffs, Virginia;" the type specimen actually is from Prince Georges County, Maryland. Tong and Hirayama (2002) thought that, in characters that can be compared between the two taxa, *T. ruhoffi* is very similar to *T. aldabergeni* except that *T. aldabergeni* has a more strongly developed symphyseal ridge on its dentary (Nessov 1987). It is also true, however, that the nuchal of *T. aldabergeni* has a much shallower anterior concavity (width:depth ratio = 14) than the nuchal of *T. ruhoffi* (width:depth ratio = 7), and the seventh to ninth neurals of *T. ruhoffi* are keeled while the seventh to ninth neurals of *T. aldabergeni* are unkeeled (compare fig. 2 of Nessov 1987 with fig. 18 of Weems, 1988). Therefore, even though both species are referable to *Tasbacka*, they appear to be distinctly different. *T. aldabergeni* was described from the late Paleocene of Kazakhstan and a third species, *T. ouledabdounensis* Tong and Hirayama 2002 has been described from the late Paleocene of Morocco (Tong and Hirayama 2002), so *Tasbacka* seems to have dispersed widely in the early or middle Paleocene and then developed into distinctly different populations in central Asia, north Africa, and the eastern United States. It seems likely that some population of late Paleocene *Tasbacka* was the ancestor of the early Eocene species *Puppigerus camperi* (Gray) Moody.

PUPPIGERUS Cope 1870
Puppigerus camperi (Gray 1831)
(Figs.17A–F)

Specimens—CMM-V-4769, proximal and central part of fourth right costal found by Bob Wiest; CMM-V-4770; right premaxillary found by Bob Wiest; CMM-V-4771, fragmentary nuchal found by Gary Grimsley;

CMM-V-3322, fragmentary nuchal found by Bill Counterman; CMM-V-4773, central and distal portion of right hyoplastron found by George Fonger.

Locality, horizon, and age—All found in the bluff immediately west of Loyola Retreat, 1.7 miles north of Popes Creek, Charles County, Maryland; lower part (Bed A) of the Woodstock Member, Nanjemoy Formation; early Eocene (Ypresian) within nannoplankton zone NP12.

Description—Hyoplastron wide with a long external border extending far anteriorly but lacking any sutural border with the carapace, costals thin and lacking external sculpture, premaxillary forms narrow forward snout with a well-developed secondary palate.

Remarks—These remains and others of similar size are the most commonly found fragments of turtle in the Woodstock Member of the Nanjemoy; they are found in both the lower and upper beds A and B. They are not perceptibly different in size or morphology from skeletal material of *Puppigerus camperi* described and illustrated by Moody (1974) from the London Clay, which is equivalent in age to the Nanjemoy. This species has been reported from the lower member of the Nanjemoy, based on fused elongate dentaries with a prominent shelf (Weems 1999), so it is not surprising to find it in the upper member as well. Curiously, although *Eosphargis* and *Puppigerus* are found both in the Nanjemoy Formation and the London Clay, other London Clay marine turtles (*Neurochelys* Moody 1980, *Argillochelys* Lydekker1889a and *Eochelone* Dollo 1903, Moody 1996, Lapparent de Broin 2001) have not been found in the Nanjemoy.

PROCOLPOCHELYS Hay 1908
Procolpochelys charlestonensis Weems & Sanders 2014
(Fig. 18A)

Specimen—CMM-V-4781, costal found by Robert E. Weems.

Locality, horizon, and age—Found in place about a foot above the basal contact at the base of the low bluff outcrop at Northbury, northwestern New Kent County, Virginia on the south bank of the Pamunkey River; Old Church Formation; late early Oligocene (late Rupelian, lower nannofossil zone NP24).

Description—Distal two-thirds of a costal element

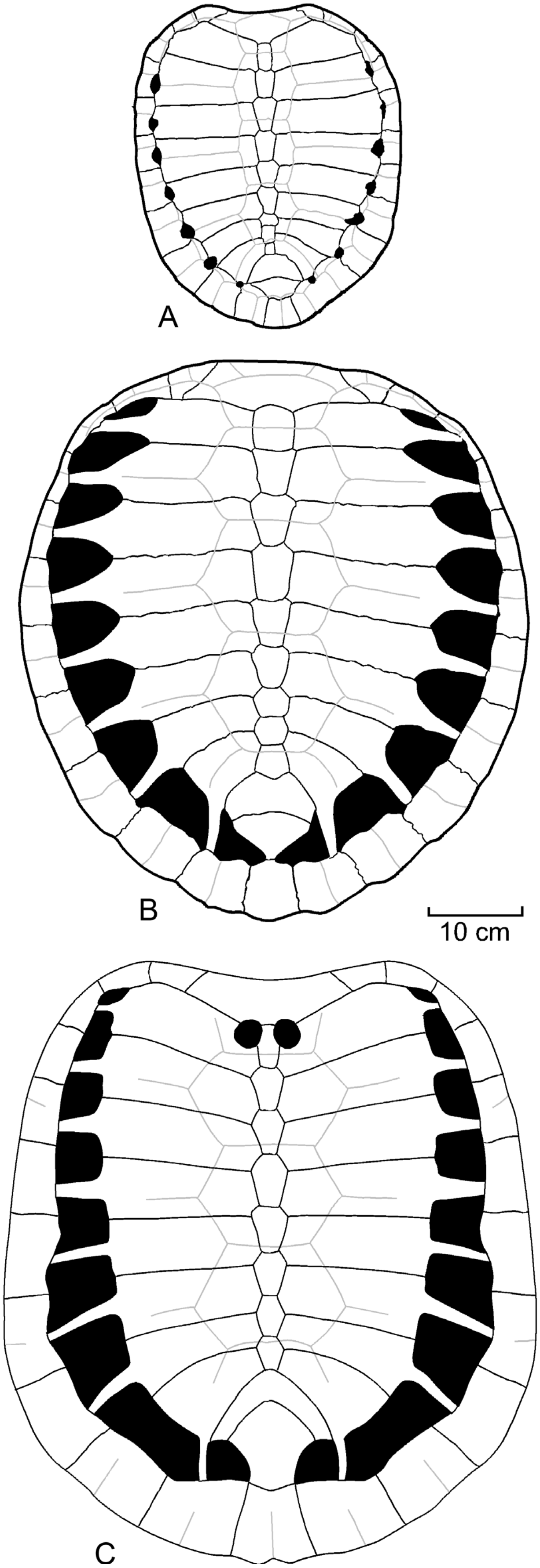

Figure 16. A–C. Comparison of the carapace in Paleocene pancheloniid turtles. **A**, *Tasbacka* after Nessov (1987); B, *Catapleura* after Hirayama (2006); **C**, *Erquelinnesia* after Zangerl (1971). *Erquelinnesia* is the closest relative to *Euclastes* for which the carapace is well known.

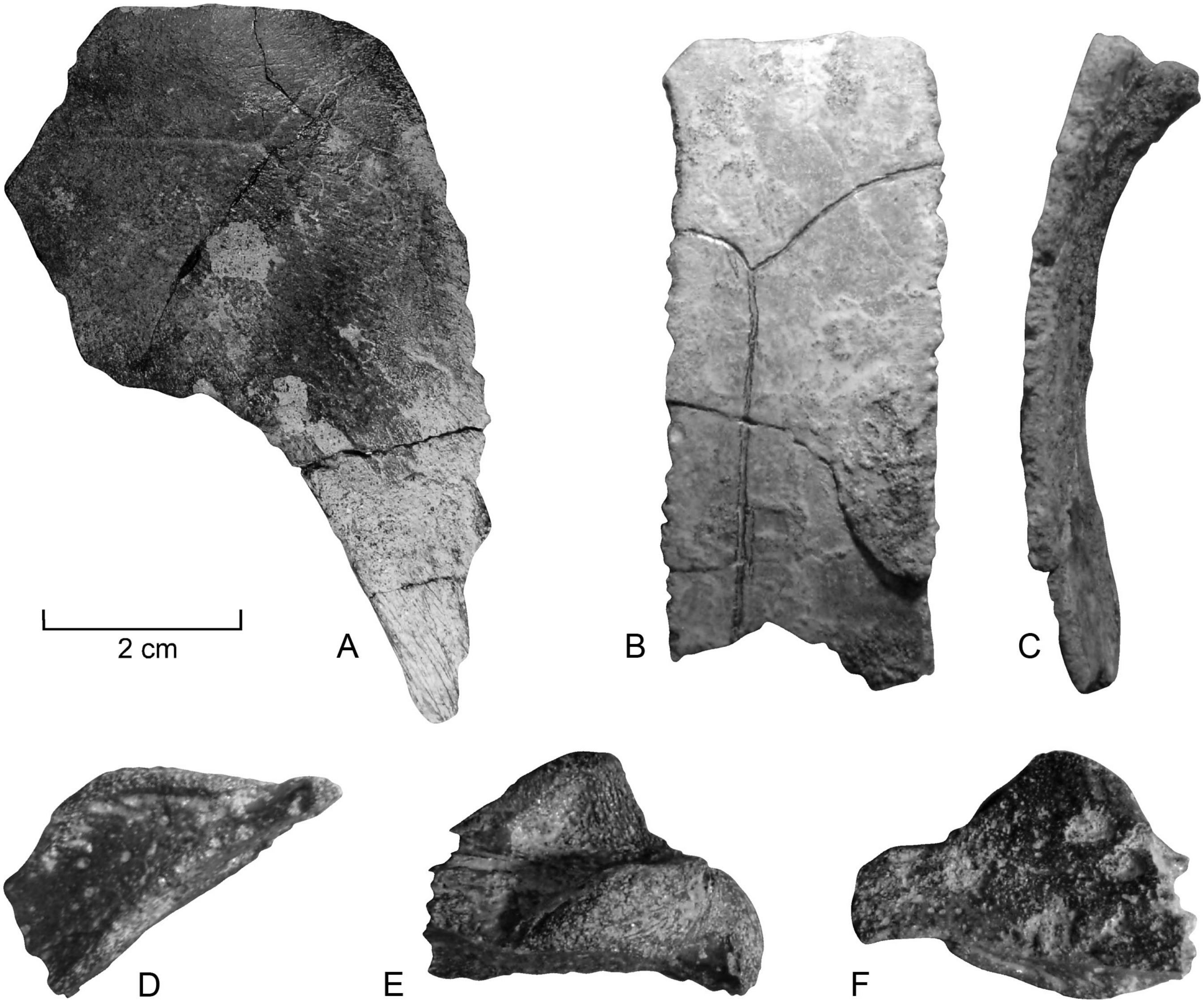

Figure 17. A–F. *Puppigerus camperi* carapace and skull elements from the Woodstock Member of the Nanjemoy Formation. **A.** Left hypoplastron in ventral view, CMM-V-4773. **B, C.** Fourth right costal, CMM-V-4769. **B,** dorsal view; **C,** anterior view. **D-F.** Left premaxilla, CMM-V-4770. **D,** ventral view; **E,** internal view; **F,** external view.

lacking any trace of surface sculpturing.

Remarks—This costal is quite similar in its proportions to the costals of *Procolpochelys charlestonensis*, known from the early Chattian Chandler Bridge Formation near Charleston, South Carolina. The Old Church specimen is smaller than the type of *P. charlestonensis* and relatively somewhat thinner, but this is typical of juvenile specimens of *Procolpochelys*. The absence of sculpturing precludes assignment to *Ashleychelys* Weems & Sanders 2014 or *Carolinochelys* Hay 1923 which are the only other pancheloniid genera known from the Oligocene of South Carolina. The presence of a juvenile *P. charlestonensis* in Virginia supports the suggestion of Weems and Sanders (2014) that *Procolpochelys* nested north of the Charleston, South Carolina region, because only adult specimens have been found in the Charleston area.

ASHLEYCHELYS Weems & Sanders 2014
Ashleychelys palmeri Weems & Sanders 2014
(Fig. 18B)

Specimen—CMM-V-4782, neural found by Gary Grimsley.

Locality, horizon, and age—Found on the beach at the base of the low bluff outcrop at Northbury, northwestern New Kent County, Virginia on the south bank of the Pamunkey River; Old Church Formation; late early Oligocene (late Rupelian, nannofossil zone NP24). Along this part of the bluff, only the Old Church is exposed.

Description—Narrow hexagonal-shaped neural with a low longitudinal keel and sculpturing typical of *Ashleychelys*.

Remarks—This isolated neural is quite similar in shape, size, thickness and pattern of sculpturing to neurals of *Ashleychelys palmeri*, known from the Late Rupelian Ashley and early Chattian Chandler Bridge formations near Charleston, South Carolina. The elongate shape, low longitudinal keel, and characteristic sculpturing are typical of *Ashleychelys*.

CAROLINOCHELYS Hay 1923

Carolinochelys wilsoni Hay 1923

(Figs. 18C–D)

Specimen—CMM-V-4783, neural found by Ron Ison; CMM-V-4784, neural found by Jason Osborne.

Locality, horizon, and age—Along the banks of the Pamunkey River where it forms the boundary between New Kent and King William counties, Virginia; Old Church Formation; late early Oligocene (late Rupelian, lower nannofossil zone NP24).

Description—Neurals hexagonal in shape, flat and without a medial longitudinal keel, bearing sculpture characteristic of *Carolinochelys*.

Remarks—These isolated neurals are quite similar in shape, size, thickness and pattern of sculpturing to neurals of *Carolinochelys wilsoni*, known from the Late Rupelian Ashley and early Chattian Chandler Bridge formations near Charleston, South Carolina. The lack of a medial longitudinal keel precludes their assignment to *Ashleychelys*, which has a somewhat different pattern of sculpturing, and their hexagonal shape and the presence of sculpturing precludes assignment to *Procolpochelys*.

DISCUSSION AND CONCLUSIONS

The species comprising the turtle fauna in each of the Paleogene formations in Maryland and Virginia are found exclusively in that unit and in no younger or older unit (Fig. 19). Therefore, the turtles in each unit are stratigraphically useful for correlating strata both between outcrops within these units and with units in other parts of the Atlantic Coastal Plain.

The Brightseat/Hornerstown non-marine turtle fauna includes *Osteopygis*, *Agomphus, Adocus* sp. and "*Trionyx*" *halophilus*, all endemic to the southeastern United States. These four taxa all survived the end-Cretaceous extinction event in the eastern United States, persisted through the early Paleocene, but did not survive into the late Paleocene. Their early Paleocene (Danian) survival in the eastern United States may be due to the persistence into the Paleocene of the Cannonball Sea across the Western Interior region, which separated eastern from western North America throughout the first five million years of the Paleocene (Boyd and Lillegraven 2011). The continued presence of this seaway probably prevented any early Paleocene influx of new turtle taxa from western North America into the eastern region. Once that seaway withdrew, however, three genera of non-marine turtles that occur in western North America (*Planetochelys*, *Judithemys*,

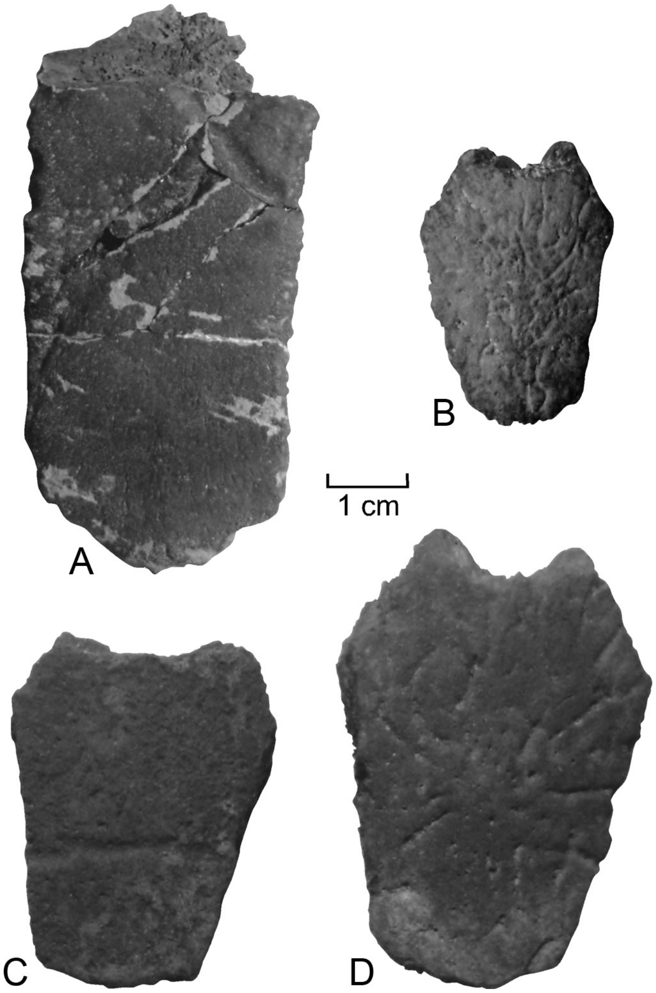

Figure 18. A–D. Carapace elements of *Procolpochelys*, *Ashleychelys*, and *Carolinochelys* from the early Oligocene Old Church Formation of Virginia. **A.** *Procolpochelys charlestonensis*, distal end of a costal in dorsal view, CMM-V-4781. **B.** *Ashleychelys palmeri*, neural in dorsal view, bearing characteristic sculpture and a faint longitudinal mid-line ridge, CMM-V-4782. **C.** *Carolinochelys wilsoni*, posterior neural in dorsal view, bearing characteristic sculpture, a sulcal groove, and lacking a longitudinal mid-line ridge, CMM-V-4783. **D.** *Carolinochelys wilsoni*, anterior neural in dorsal view, bearing characteristic sculpture and lacking a longitudinal mid-line ridge, CMM-V-4784.

and *Aspideretoides*) appear abruptly in the late Paleocene Aquia Formation and the four earlier endemic species disappear. This suggests that western North American non-marine turtles began to move into eastern North

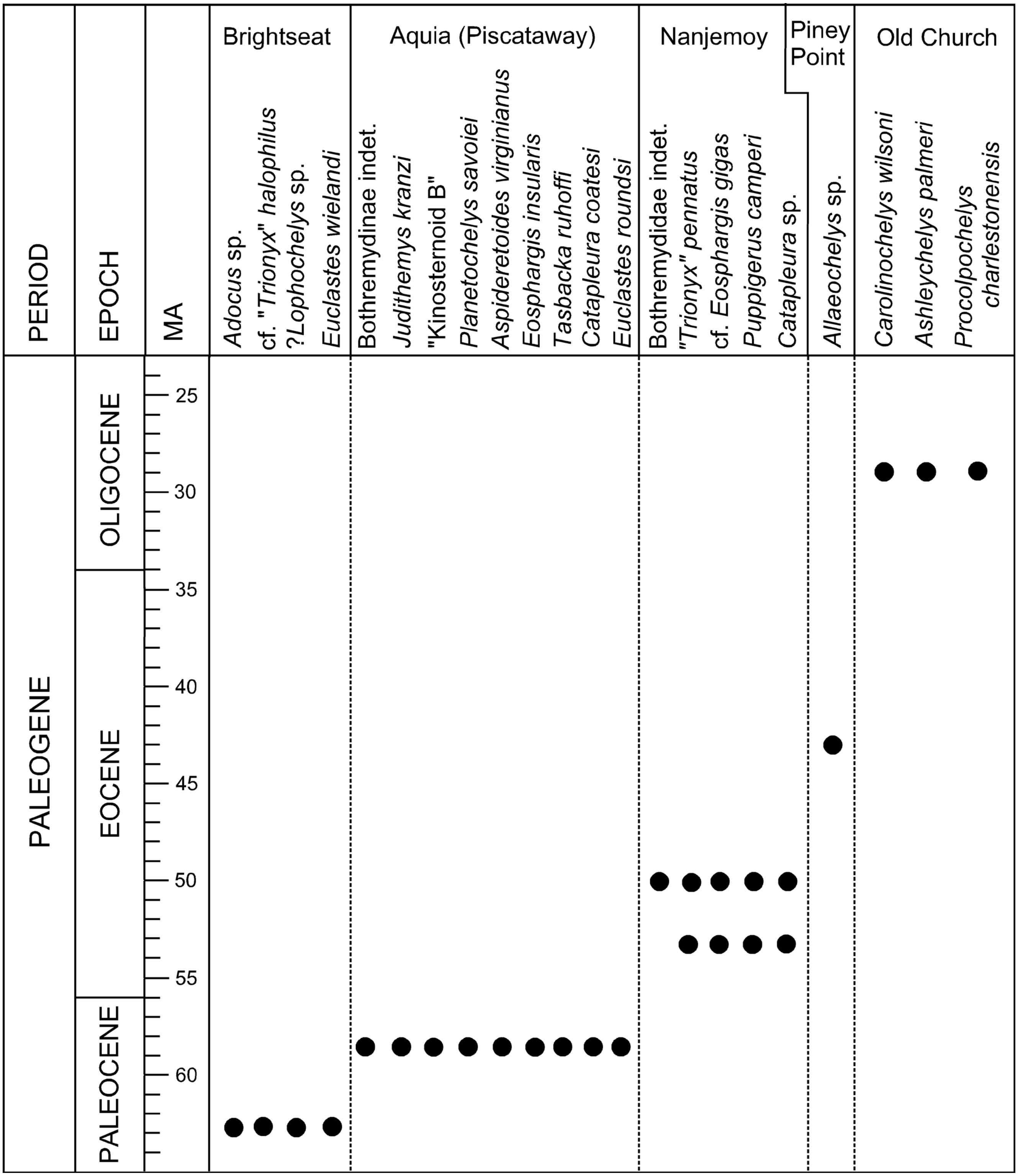

Figure 19. Stratigraphic range chart showing the horizons of occurrence for turtle remains in the Paleogene strata of Maryland and Virginia. The two tiers of occurrences in the Nanjemoy correspond to the lower Potapaco Member (Potapaco B) assemblage described by Weems (1999), and an overlying Woodstock Member assemblage described in this paper.

America by the late Paleocene, outcompeting many endemic forms and displacing them.

Sparse nondiagnostic remains of kinosternoid turtles are known from the late Paleocene of the southeastern United States, including the oldest record of the family Kinosternidae (Hutchison and Weems 1998). After this, there is no record of this group in eastern North America north of Florida throughout the Eocene and Oligocene, so the Paleogene history of the eastern American kinosternids remains obscure. The Paleogene record for testudinoid turtles is even more sparse, including only aquatic testudinoid remains from the late Eocene of Georgia (Parmley et al. 2006) and a partial carapace of *Gopherus* Rafinesque 1832 from the early Oligocene of South Carolina (Weems and Sanders 2014).

Unlike the terrestrial and other strongly fluvial taxa, trionychine turtles remained strongly endemic throughout the entirety of the Paleocene. After that, nothing taxonomically useful is known concerning eastern American trionychids during the Eocene and Oligocene. The carettachelyine *Allaeochelys*, typically a European and North African turtle, appears briefly in the middle Eocene but then disappears from the southeastern United States. *Allaeochelys* is known in North America only from the Gulf and Atlantic coastal plains, and this contrasts with the Rocky Mountain region where different middle Eocene carettochelyine turtles occur, *Anosteira* and *Pseudanosteira*. Thus the middle Eocene carettochelyine faunas of the western and eastern United States were distinctly different.

The marine turtle faunas follow a rather different trend. The early Paleocene genera *Euclastes* and *Catapleura* persist into the late Paleocene, where they are joined by *Tasbacka* (which also occurs in Eastern Europe and North Africa) and the large dermochelyid turtle *Eosphargis* (which also occurs in Europe). In the early Eocene *Eosphargis* persisted, *Tasbacka* appears to have been replaced by the closely related genus *Puppigerus*, and *Catapleura* also seems to have persisted into the early Eocene.

Euclastes has not been found in the early Eocene Nanjemoy Formation in the Maryland or Virginia regions. *Euclastes platyops* Cope 1867 was reported from the Eocene of New Jersey (Rapp 1944), but this age is wrong because the limestone lithology reported with the type specimen (Hay 1908) is only compatible with parts of the Vincentown Formation. In 1944 the Vincentown was considered to be early Eocene, but it is now dated as late Paleocene (late Thanetian, nannofossil zones NP8 and NP9; Gibson et al. 1993). This unit therefore correlates with the upper (Paspotansa) member of the Aquia Formation, which is younger than the Piscataway Member that has yielded specimens of *E. roundsi* but still older than Eocene. Therefore, *Euclastes* is not known to survive beyond the Paleocene-Eocene boundary in the eastern United States.

Curiously, although several examples of the carettochelyine turtle *Allaeochelys* have been found in the marine, middle Eocene Piney Point Formation, no marine turtles are known from that unit. By the mid-Oligocene, when marine turtles are again found, three entirely new pancheloniid genera have appeared, *Ashleychelys*, *Carolinochelys*, and *Procolpochelys* (Weems and Sanders 2014). No dermochelyid ossicles are yet known from the Old Church, but the equivalent units in South Carolina (the Ashley and immediately overlying Chandler Bridge formations) have yielded remains of three kinds of dermochelyids that are being described by Roger Wood. None of the Oligocene pancheloniid genera seems likely to have descended from the earlier marine turtles of this region (Weems and Sanders 2014), so a complete pancheloniid faunal turnover apparently happened in this region somewhere between the middle Eocene and the mid-Oligocene, possibly around the time of the cooling event that accompanied the beginning of widespread Antarctic glaciation at the beginning of the Oligocene.

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