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The Geology and Vertebrate Paleontology of Calvert Cliffs, Maryland, USA

Edited by
Stephen J. Godfrey

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ABSTRACT

Godfrey, Stephen J., editor. The Geology and Vertebrate Paleontology of Calvert Cliffs, Maryland, USA. *Smithsonian Contributions to Paleobiology*, number 100, iv + 274 pages, 93 figures, 63 body restoration images, 11 tables, 2018.—The last comprehensive review of the fossil vertebrates from the Miocene of Calvert Cliffs was published more than 100 years ago. This volume is a collection of papers that updates some of the geological features of Calvert Cliffs and provides reviews of the fossil biota that include representatives from the following taxonomic groups: chondrichthyans (chimaeras, shark, skates, and rays), actinopterygians (ray-finned fishes), crocodilians (crocodiles), and sirenians (sea cows). Peter Vogt, Ralph E. Eshelman, and Stephen J. Godfrey document how the 20–40 m [65–130 ft] high Calvert Cliffs along the western shore of the Chesapeake Bay continue to yield insights into 18–8 MYA (Miocene) geology, marine and terrestrial vertebrate fauna, and the origin and evolution of Chesapeake Bay and Calvert Cliffs up to the present. These exposures rank high among the best-known fossiliferous deposits of any age. Bretton W. Kent describes the cartilaginous fish (the chondrichthyan) fauna, consisting of 54 species—3 chimaeras (ratfishes), 39 sharks, and 12 skates and rays—a fauna rich in large macrophagous sharks and large neritic rays. In an addendum to Kent's chapter, he and David J. Ward describe a new species of giant thresher shark with serrated teeth. Giorgio Carnevale and Stephen J. Godfrey present an account of the 38 actinopterygian taxa known from osteological remains and a diverse otolith assemblage of at least 55 taxa. These actinopterygians show an affinity for well-oxygenated muddy and sandy substrates dominated primarily by shallow-water species characteristic of the inner shelf and secondarily by epipelagic taxa. Robert E. Weems details the crocodilians referable to the tomistomine *Thecachampsa*. The closest living relative is *Tomistoma schlegelii*, the false gharial of Southeast Asia. Two species are present: *Thecachampsa sericodon* and *T. antiquus*. These tomistomines are found in shallow marine coastal deposits, indicating that they inhabited coastal waters. Daryl P. Domning reports that fossils of the Miocene marine fauna include rare sirenians of the family Dugongidae. Three taxa are known: the halitheriine dugongid *Metaxytherium crataegense*, the dugongine dugongid *Nanosiren* sp., and another dugongine, aff. *Corystosiren*. The St. Marys Formation contains remains that may be referable to *Metaxytherium floridanum*, but confirmation awaits the discovery of more complete specimens.

Cover image: Calvert Cliffs at Warrior's Rest Sanctuary; view looking north. These 12–15 million-year-old sediments from the Miocene epoch comprise the upper portion of the Calvert Formation and the overlying Choptank Formation. Photo by Stephen J. Godfrey.

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Contents

INTRODUCTION by <i>Stephen J. Godfrey</i>	1
1 Calvert Cliffs: Eroding Mural Escarpment, Fossil Dispensary, and Paleoenvironmental Archive in Space and Time <i>Peter Vogt, Ralph E. Eshelman, and Stephen J. Godfrey</i>	3
2 The Cartilaginous Fishes (Chimaeras, Sharks, and Rays) of Calvert Cliffs, Maryland, USA <i>Bretton W. Kent</i>	45
Addendum <i>Bretton W. Kent and David J. Ward</i>	157
3 Miocene Bony Fishes of the Calvert, Choptank, St. Marys, and Eastover Formations, Chesapeake Group, Maryland and Virginia <i>Giorgio Carnevale and Stephen J. Godfrey</i>	161
4 Crocodilians of the Calvert Cliffs <i>Robert E. Weems</i>	213
5 Fossil Sirenia (Mammalia) of the Miocene Chesapeake Group, Eastern United States <i>Daryl P. Domning</i>	241
INDEX	267

Miocene Bony Fishes of the Calvert, Choptank, St. Marys, and Eastover Formations, Chesapeake Group, Maryland and Virginia

Giorgio Carnevale^{1} and
Stephen J. Godfrey²*

ABSTRACT. Bony fishes are relatively common in the Miocene deposits of the Chesapeake Group. In the past three decades, intensive collecting has resulted in the accumulation of a large number of bony fish remains. Thirty-eight actinopterygian taxa, based on fossil bones, are now known from the Chesapeake Group. A diverse otolith assemblage of at least 55 taxa has also been reported. The reduced size of many of the otoliths is probably related to their juvenile nature. Such an abundance of juveniles suggests that the Salisbury Embayment represented a nursery ground for most of the Miocene. The fish taxa recognized in the deposits of the Chesapeake Group show a clear general affinity for well-oxygenated muddy and sandy substrates. The assemblages are dominated primarily by shallow-water fishes characteristic of the inner shelf and secondarily by epipelagic taxa. Benthopelagic fishes characteristic of the outer shelf and upper slope are nearly absent in the Calvert Formation (exceptions are *Brotula* sp. and *Lopholatilus ereborensis*). The common occurrence of open-ocean taxa (billfishes, tunas, wahoos) in the Calvert, Choptank, and Eastover Formations suggests that deposition took place in the distal portions of the inner shelf. Overall, the ichthyofaunal composition is consistent with the sedimentary and paleontological record, which evidences a general regressive trend from the Calvert to the St. Marys Formations, representing a gradual shallowing within the Salisbury Embayment. The fish assemblages of the Chesapeake Group exhibit a modern aspect, with most of the taxa belonging to genera or higher categories that currently occur in the northwestern Atlantic, including along the coasts of Maryland and Virginia.

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INTRODUCTION

Miocene deposits of the Middle Atlantic Coastal Plain include a series of remarkably fossiliferous interbedded siliciclastic deposits that extensively crop out with spectacular exposures in the Chesapeake Bay area in Maryland and Virginia. These richly fossiliferous deposits have attracted the attention of North American paleontologists since the nineteenth century (e.g., Conrad, 1830, 1842; Darton, 1891; Harris, 1893), providing the basis for stratigraphic subdivision and correlation of the Neogene Chesapeake Group (see Shattuck, 1904). Multiple systems of stratigraphic subdivision have been used to define the sedimentary units of the Miocene deposits of the Chesapeake Group, including the zones (Harris, 1893; Shattuck, 1904), members (Gernant, 1970), depositional sequences (e.g., Kidwell, 1984, 1988, 1989, 1997), depositional events (e.g., Ward, 1992), and beds (Ward and Andrews, 2008). Kidwell (1988) pointed out that the Miocene siliciclastic deposits of the Chesapeake Group provide rare, direct evidence for coastal sediment sinks during marine transgression. Stratigraphic and taphonomic evidence suggests that fossil concentrations in these Miocene units can be interpreted as stratigraphically condensed records of a suite of transgressive shallow marine to paralic environments (Kidwell, 1989). In the Maryland-Virginia area, the Neogene deposits of the Chesapeake Group directly overlie Paleogene units. The Miocene sedimentary units of the Chesapeake Group include the Calvert, Choptank, St. Marys, and Eastover Formations separated from each other by relatively short temporal gaps, spanning the Aquitanian, Burdigalian, Langhian, Serravallian, and Tortonian stages (see Vogt et al., this volume). Overall, the Miocene deposits of the Chesapeake Group record the gradual shallowing within the Salisbury Embayment, a landward extension of the Baltimore Canyon Trough bounded by the Norfolk High on the south and by the South Jersey High on the north (Poag, 1979). Within the Salisbury Embayment, maximum water depth and fully marine inner to middle shelf conditions occurred during deposition of the Calvert, Choptank, and Eastover Formations, whereas deposition of the St. Marys Formation took place during the transition from open marine shelf conditions to tidally influenced low-salinity muddy coastal environments (e.g., Ward and Blackwelder, 1980; Kidwell, 1989).

Bony fishes are relatively abundant in the Miocene deposits of the Chesapeake Group. However, these remains have not been properly investigated, resulting in a largely incomplete and underestimated diversity (see Kimmel and Purdy, 1984). Fossil bony fish remains were first documented from the deposits of the Chesapeake Group by Cope (1867), who cursorily reported the presence of isolated sphyraenid teeth in the Maryland Miocene. Two years later, he described (Cope, 1869) the sciaenid *Pogonias multidentatus* on the basis of a single upper pharyngeal plate from the Miocene deposits of Nomini Cliffs, Westmoreland County, Virginia. Subsequently, Leidy (1873a,b,c) described the sturgeon *Acipenser ornatus* and the wrasse *Protautoga conidens*

from the Miocene of Virginia. Eastman (1904) produced the first systematic account of the fish remains of the Miocene of Maryland, describing teeth of the barracuda *Sphyraena speciosa* from the Calvert Formation, as well as of gadid and sciaenid saccular otoliths from the St. Marys Formation. Hussakof (1908) discussed and illustrated the type specimen of *Pogonias multidentatus* in his catalog of types and illustrated fossil fishes housed in the American Museum of Natural History. Smith (1909) presented new material of this species from the Miocene of Maryland, providing additional morphological evidence to support its separate specific status. In 1917, Berry described the sailfish *Istiophorus calvertensis* on the basis of an incomplete rostrum collected from Tar Bay, Virginia, in the argillaceous beds assigned to the Calvert Formation and more recently referred to the Eastover Formation (Kimmel and Purdy, 1984; Fierstine, 1998). Berry (1932) documented the presence of isolated teeth belonging to the sparid genus *Lagodon* from the St. Marys Formation, and Lynn and Melland (1939) presented a well-preserved neurocranium with associated otolith from the Calvert Formation that they assigned to *Felichthys stauroforus*. Blake (1940) described the albuloid *Paralbula dorisiae* on the basis of an eroded dental plate collected at Plum Point from deposits of the Calvert Formation. In his monographic review of the Tertiary fish faunas of the eastern and central United States, Leriche (1942) listed seven taxa from the Miocene deposits of the Chesapeake Group (*Acipenser ornatus*, *Arius* sp., *Sphyraena speciosa*, *Pogonias multidentatus*, *Protautoga conidens*, Gadidae indet., and Sciaenidae indet.). Dante (1953) reviewed the sciaenid otolith previously illustrated by Eastman (1904), together with additional material from the Calvert Formation, and described *Sciaenops eastmani*. Kimmel and Purdy (1984) provided a brief overview of the fish faunas of the Calvert and Eastover Formations, listing at least 12 taxa. Weems (1985) analyzed the ocean sunfish genera *Mola* and *Ranzania* from the Calvert and Choptank Formations. More recently, Müller (1999) presented a broad analysis of the otolith assemblages of the whole Chesapeake Group. Moreover, a number of new species were described from the St. Marys Formation, including the stargazer *Astroscopus countermani* by Carnevale et al. (2011), the channel catfish *Ictalurus countermani* by Lundberg and Luckenbill (2012), and the needlefish *Belone countermani* by de Sant'Anna et al. (2013). Finally, Carnevale and Godfrey (2014) described the skeletal remains and possible trace fossils of the tilefish *Lopholatilus ereborensis* from the Calvert Formation.

Extensive geological and paleontological explorations of the Miocene deposits of the Chesapeake Group in the last three decades have resulted in the accumulation of a vast collection of bony fish remains primarily housed in the Calvert Marine Museum (CMM), Solomons, Maryland, and the Department of Paleobiology of the National Museum of Natural History (USNM), Smithsonian Institution, Washington, D.C. This chapter briefly describes and illustrates the diversity of Miocene bony fishes of the marine and paralic siliciclastic deposits of the Chesapeake Group and discusses their paleoenvironmental significance. The taxonomic classification and nomenclature used, unless otherwise

noted, follow Nelson (2006). Many of the taxa described herein would benefit from a more detailed examination. Furthermore, it is our hope that this chapter will prompt collectors to show their fish finds to qualified researchers and that this will stimulate additional research into this remarkable ichthyofauna.

SYSTEMATIC DESCRIPTIONS

CLASS OSTEICHTHYES HUXLEY, 1880

SUBCLASS ACTINOPTERYGII COPE, 1887

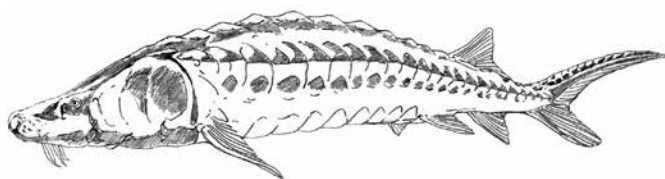
SERIES CHONDROSTEI MÜLLER, 1844

ORDER ACIPENSERIFORMES BERG, 1940

FAMILY ACIPENSERIDAE BONAPARTE, 1831

Gen. et sp. indet.

FIGURE 3.1A,B



Sturgeon – Acipenseridae

REFERRED MATERIAL. CMM-V-98, partially complete lateral scute; CMM-V-99, partially complete right post-temporal and fragments of skull roofing bones; CMM-V-100, dorsal dermal bony scute (Figure 3.1A); CMM-V-265, partially complete lateral scute; CMM-V-279, fragments of skull roofing bones; CMM-V-289, lateral scute; CMM-V-1417 (Figure 3.1B), lateral scute; CMM-V-1907, dorsal scute; CMM-V-1997, partially complete left cleithrum and two isolated lateral scutes and fragments of dermal scutes; CMM-V-2068, partially complete dermal scute; CMM-V-2140, partially complete dermal scute; CMM-V-2439, partially complete dermal scute; CMM-V-2577, partially complete dermal scute; CMM-V-2597, partially complete dermal scute; CMM-V-2612, partially complete ventral scute; CMM-V-2767, partially complete lateral scute; CMM-V-2913, extensively fragmented skull roofing bones; CMM-V-3785, eight isolated dermal scutes; CMM-V-3938, two isolated partially preserved dermal scutes; CMM-V-3953, partially complete dermal scute; CMM-V-3985, partially complete lateral scute; CMM-V-4104, partially complete left supracleithrum; CMM-V-4126, two isolated partially complete dermal scutes;

CMM-V-4234, partially complete dermal scute; CMM-V-4250, partially complete left clavicle and three isolated dermal scutes; CMM-V-4299, partially complete right opercle; CMM-V-4312, four isolated dermal scutes; CMM-V-4423, dorsal scute; CMM-V-4530, partially complete dermal scute; USNM 25880, fragments of dermal bones; USNM 438665, partially complete lateral scute; USNM uncataloged, fragmentary skull roofing bones and two isolated dermal scutes and five isolated partially complete lateral scutes.

HORIZON. Calvert, Choptank, St. Marys, and Eastover Formations.

REMARKS. The material consists of isolated, thick, and often fragmented dermal bones, including skull roofing and pectoral girdle elements and, more frequently, dermal bony scutes (Figure 3.1A,B). These dermal bones exhibit a strongly ornamented outer surface and a nearly smooth inner surface.

Overall, the available Miocene acipenserid material from the Chesapeake Group has not revealed any genus- or species-level diagnostic feature, thereby precluding a detailed taxonomic identification. Leidy (1873b) described the species *Acipenser ornatus* on the basis of a lateral scute from the Calvert Formation, Virginia (see also Leriche, 1942); the type specimen described and illustrated by Leidy is now considered lost (Purdy et al., 2001). In a recent revision of the North American fossil record of the Acipenseridae, Hilton and Grande (2006) demonstrated that there are no diagnostic characters that differentiate the type material of this fossil species from other acipenserids, thereby rendering *Acipenser ornatus* a nomen dubium.

Sturgeons are anadromous and occur in the shallow waters of the continental shelf, commonly near the mouth of rivers. They are bottom feeders, mostly on benthic invertebrates and small fishes.

SERIES NEOPTERYGII REGAN, 1923

DIVISION GINGLYMODI COPE, 1872

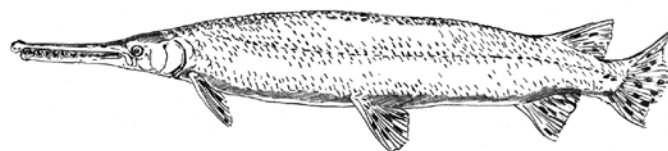
ORDER LEPISTOSTEIFORMES HAY, 1929

FAMILY LEPISTOSTEIDAE CUVIER, 1825

Genus *Lepisosteus* Linnaeus, 1758

Lepisosteus sp.

FIGURE 3.1C-E



Gar – *Lepisosteus* sp.

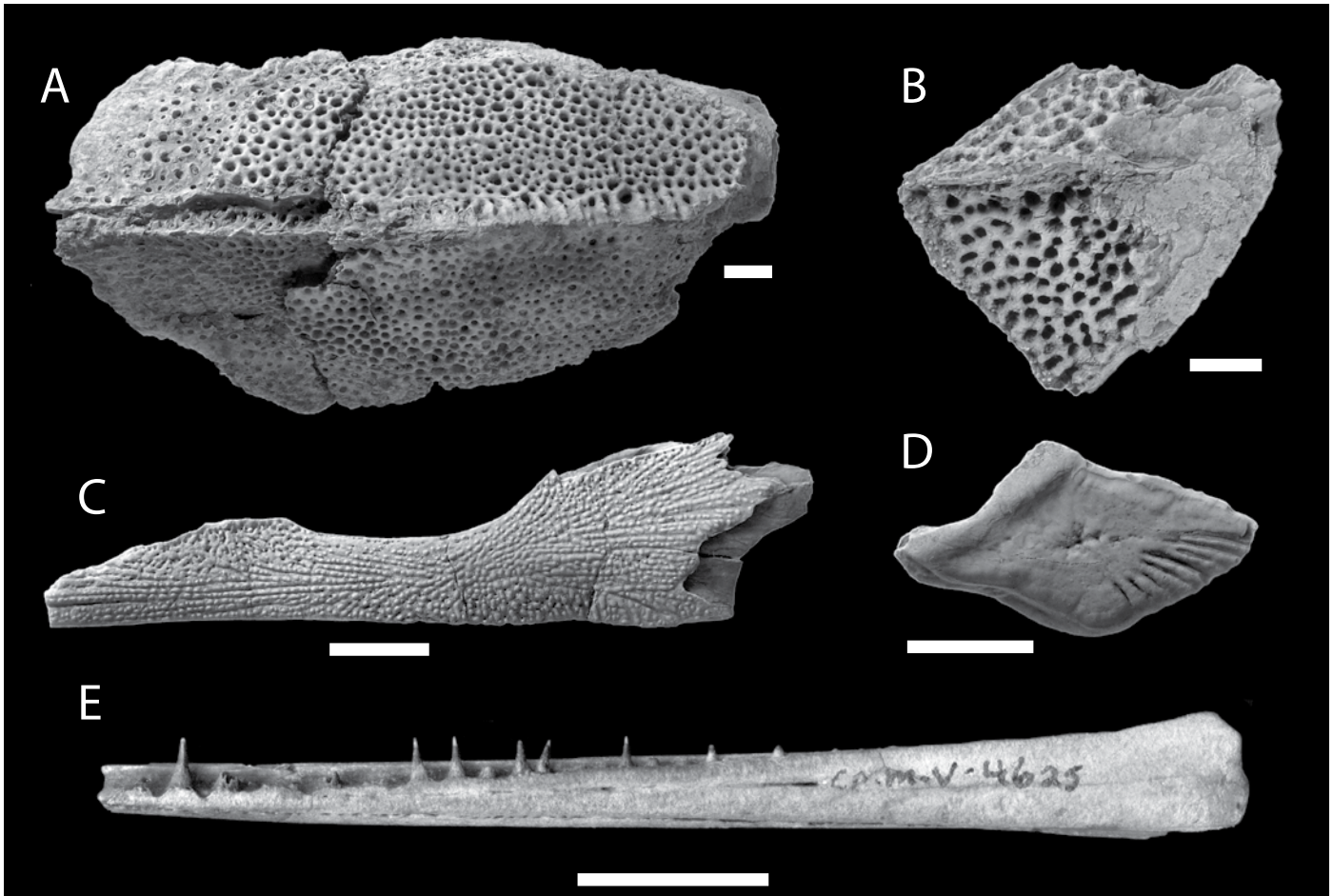


FIGURE 3.1. (A) CMM-V-100, Acipenseridae gen. et sp. indet., dorsal dermal bony scute in dorsal view. (B) CMM-V-1417, Acipenseridae gen. et sp. indet., right lateral dermal bony scute in lateral view. Anterior to right. (C) CMM-V-3137, *Lepisosteus* sp., right frontal in dorsal view. Anterior to left. (D) CMM-V-3992, *Lepisosteus* sp., ganoid scale, external view. Anterior to left. (E) CMM-V-4625, *Lepisosteus* sp., right dentary in medial view. Specimens lightly coated with sublimed ammonium chloride. Scale bars equal 10 mm.

REFERRED MATERIAL. CMM-V-3137, partially complete right frontal (Figure 3.1C); isolated scales CMM-V-97, CMM-V-362, CMM-V-3079, CMM-V-3135, CMM-V-3278, CMM-V-3575, CMM-V-3992 (Figure 3.1D), CMM-V-4625, partial left dentary (Figure 3.1E); USNM uncataloged, isolated scales.

HORIZON. St. Marys Formation.

REMARKS. An incomplete, narrow (measurable frontal width to length ratio = 0.24), and finely sculptured right frontal (Figure 3.1C), an incomplete extremely slender right dentary (Figure 3.1E), and 10 isolated rhomboid ganoid scales (Figure 3.1D) possibly belonging to a single individual are referred to the family Lepisosteidae. Within Lepisosteidae, the genus *Lepisosteus* is characterized by the lowest values of the ratio between frontal width to length (0.21–0.28; Grande, 2010); because of

the incompleteness of the available frontal, it is reasonable to hypothesize that the calculated value was certainly originally lower than 0.24, thereby suggesting that the fossil remains from the St. Marys Formation pertain to the genus *Lepisosteus*.

Gars are freshwater and estuarine ambush predators that feed primarily on smaller fishes.

DIVISION HALECOSTOMI REGAN, 1923

SUBDIVISION HALECOMORPHI COPE, 1872

ORDER AMIIFORMES HAY, 1929

FAMILY AMIIDAE BONAPARTE, 1838

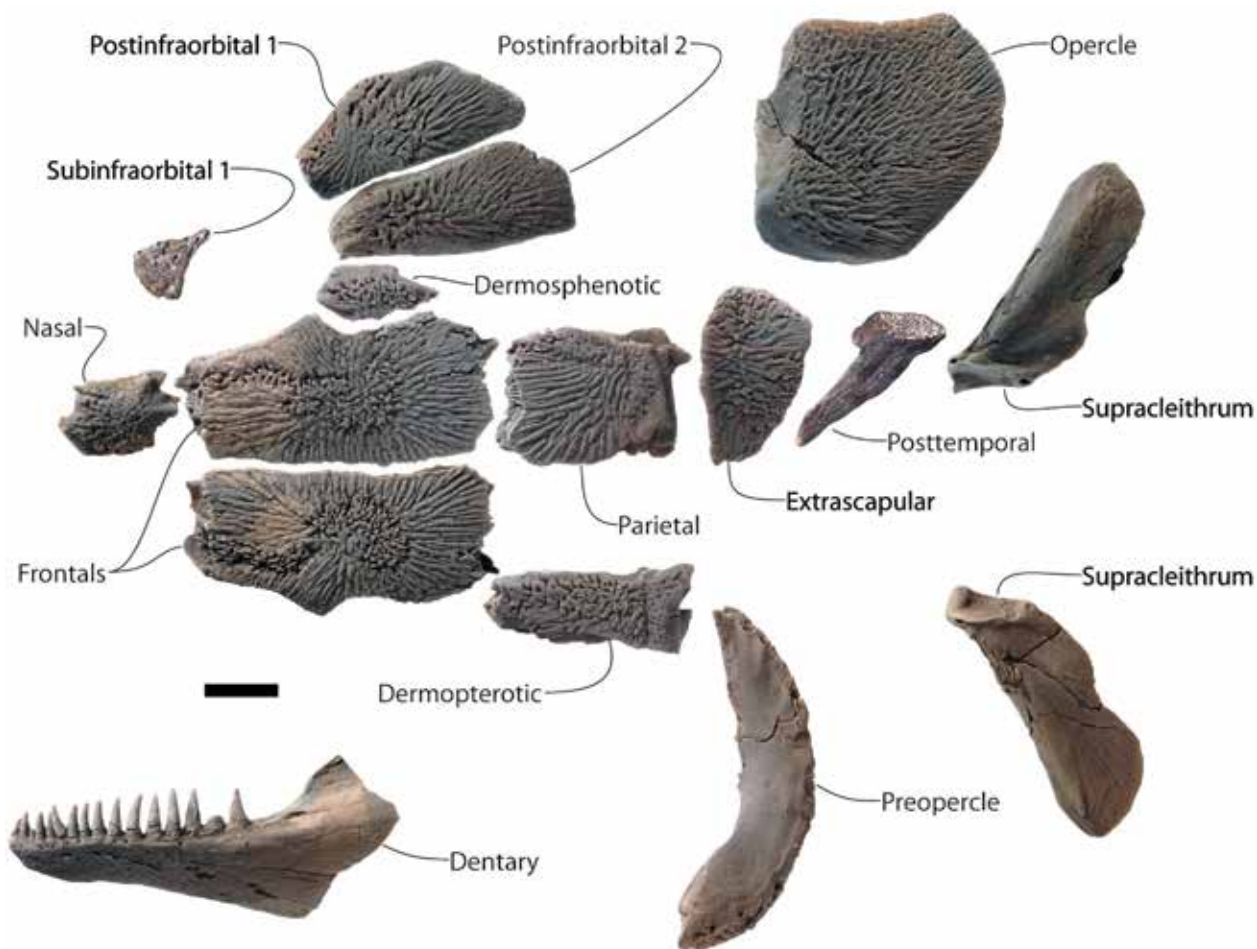
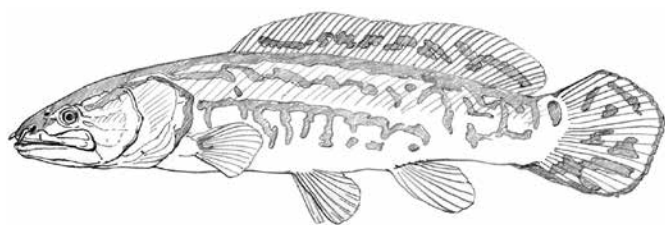


FIGURE 3.2. CMM-V-3134, *Amia* cf. *calva* disarticulated partial skull (flattened into the dorsoventral plane; elements variously shown in dorsal or lateral view). Anterior to left. Not all cranial bones preserved are included here. Specimen lightly coated with sublimed ammonium chloride. Scale bar equals 10 mm.

Genus *Amia* Linnaeus, 1766

Amia cf. *calva* Linnaeus, 1766

FIGURE 3.2



Bowfin – *Amia* cf. *calva*

REFERRED MATERIAL. CMM-V-3134 (Figure 3.2), well-preserved isolated bones from a single individual, including left and right frontals, right parietal, right dermosphenotic, right dermopterotic, right extrascapular, right posttemporal, left lachrymal, left antorbital, left nasal, a single left postinfraorbital (io4), two right postinfraorbitals (io4 + io5), right subinfraorbital, left preopercle, right opercle, right hyomandibula, right metapterygoid, left branchiopercle, left branchiostegal ray, left and right supracleithra, partially complete left cleithrum, a single abdominal centrum, and a single scale.

HORIZON. St. Marys Formation.

REMARKS. The available material consists of 25 bones belonging to a single individual (Figure 3.2). Most of the bones are extensively sculptured on their outer surfaces and are nearly identical to the corresponding ones of the extant bowfin *Amia*

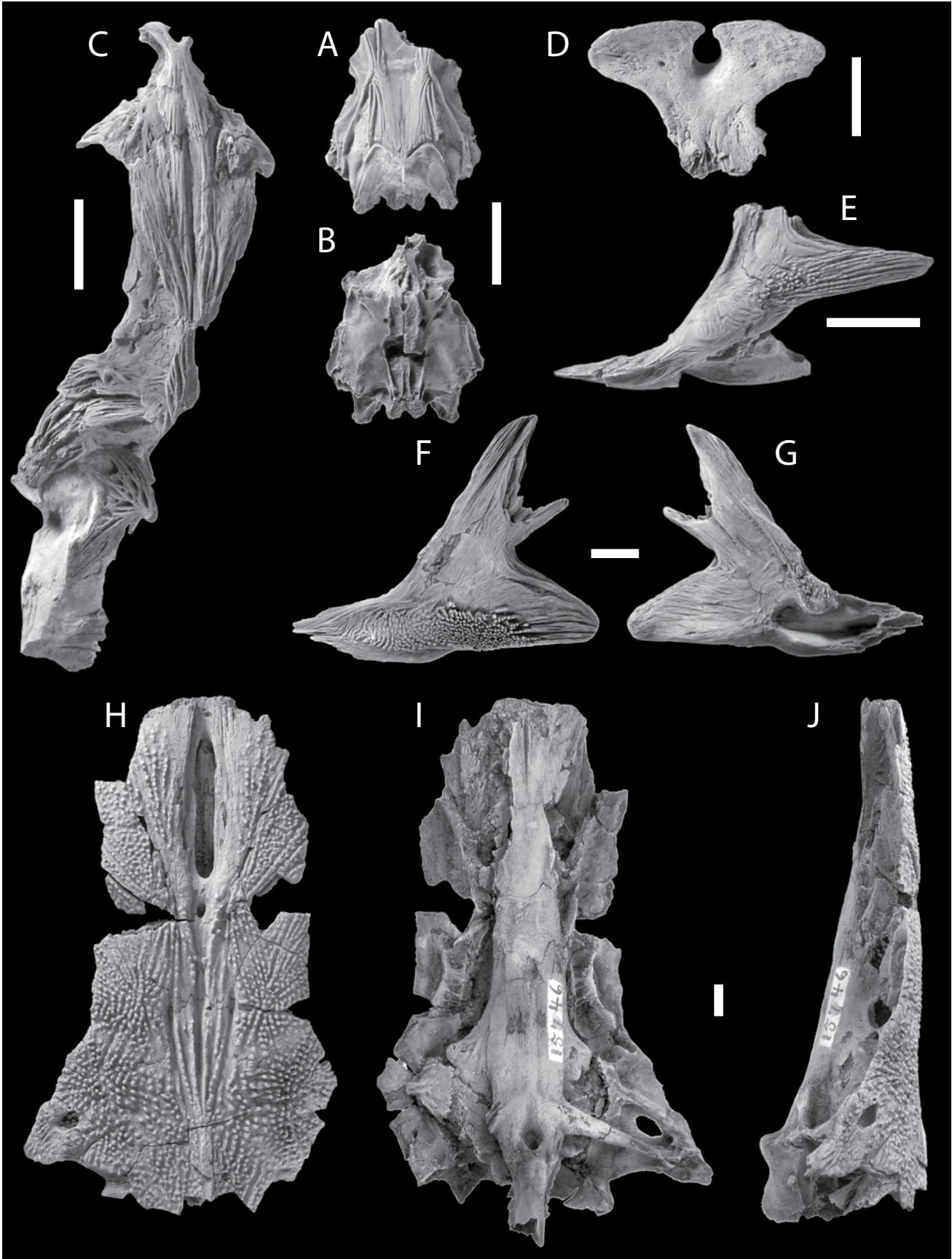


FIGURE 3.3. (*Facing page*) (A, B) CMM-V-3070, *Alosa* sp., partial neurocranium in dorsal and ventral views, respectively. Anterior to top of page. (C) CMM-V-3282, *Ictalurus countermani*, holotype, nearly complete neurocranium in dorsal view. Anterior to top of page. (D) CMM-V-3318, *Ictalurus countermani*, paratype, partial mesethmoid. Anterior to top of page. (E) CMM-V-3282, *Ictalurus countermani*, holotype, left cleithrum and coracoid bones in lateral view. (F, G) CMM-V-3207, *Ictalurus countermani*, paratype, left cleithrum in lateral and medial views, respectively. (H–J) USNM 15746, *Ariopsis stauroforus*, holotype, neurocranium in dorsal, ventral, and left lateral views, respectively. Anterior to top of page. Specimens lightly coated with sublimed ammonium chloride. Scale bars equal 10 mm.

calva. Unfortunately, because the skull is not complete, we could not confirm generic-level diagnostic characters (i.e., pointed teeth on coronoids and vomers, parasphenoid tooth patch being long and narrow, and possession of 75–82 preural centra; Grande and Bemis, 1998). Nevertheless, the great similarity of the fossil bones illustrated herein to those of the bowfin suggests a similar generic assignment. As far as the attribution at the species level is concerned, considering that the material from the St. Marys Formation includes two right postinfraorbital bones, of which the upper is evidently larger than the lower, which is in accordance with the species diagnosis provided by Grande and Bemis (1998), it is possible to tentatively refer CMM-V-3134 to the living species of bowfin.

Bowfins inhabit swampy, vegetated lakes and rivers of eastern North America. They are voracious and opportunist feeders subsisting on insects, crustaceans, fishes, and amphibians.

SUBDIVISION TELEOSTEI MÜLLER, 1846

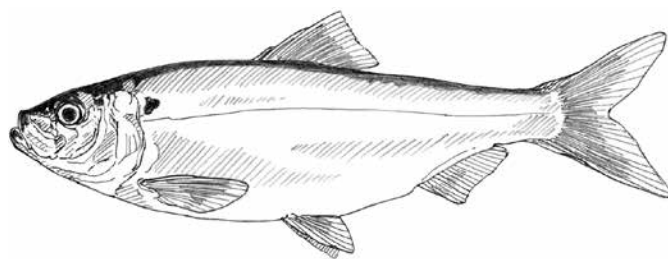
ORDER CLUPEIFORMES BLEEKER, 1859

FAMILY CLUPEIDAE CUVIER, 1817

Genus *Alosa* Linck, 1790

***Alosa* sp.**

FIGURE 3.3A,B



Shad – *Alosa* sp.

REFERRED MATERIAL. CMM-V-3070 (Figure 3.3A,B), partially complete neurocranium; CMM-V-3405, partially complete neurocranium.

HORIZON. St. Marys Formation.

REMARKS. The available material consists of two incomplete neurocrania lacking most of the orbital and ethmoid portions (Figure 3.3A,B). The general external outline of the neurocrania, particularly the relative development and mutual position of the epioccipitals; the broad and perpendicularly oriented transverse processes of the sphenotics; ornamentation of the frontals; and the morphology of pterotics, prootics, and intercalars are consistent with those of certain species of the clupeid genus *Alosa* (see Svetovidov, 1964). Despite a close similarity to the extant *Alosa sapidissima*, the fragmentary nature of the material does not allow for a more detailed taxonomic attribution.

Shad of the genus *Alosa* are anadromous planktivores that feed primarily on small arthropods, fish eggs, and algae. They are very common in nearshore waters but also occur in depths of more than 200 m.

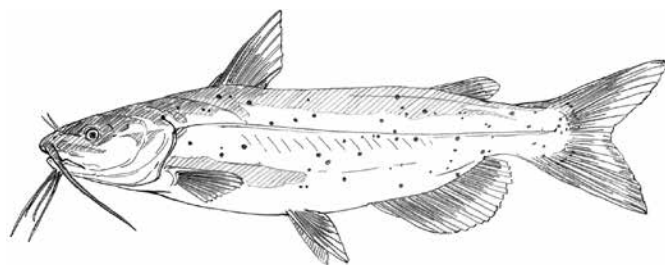
ORDER SILURIFORMES CUVIER, 1817

FAMILY ICTALURIDAE GILL, 1861

Genus *Ictalurus* Rafinesque, 1820

***Ictalurus countermani* Lundberg & Luckenbill, 2012**

FIGURE 3.3C–G



Catfish – *Ictalurus countermani*

HOLOTYPE. CMM-V-3282, nearly complete neurocranium with articulated Weberian complex (Figure 3.3C), left supracleithrum, left pectoral girdle (Figure 3.3E), pectoral-fin spine, and two abdominal vertebrae.

PARATYPES. CMM-V-3207, left cleithrum (Figure 3.3F,G); CMM-V-3316, right premaxilla; CMM-V-3318, mesethmoid (Figure 3.3D).

REFERRED MATERIAL. CMM-V-3319, dorsal-fin spine.

HORIZON. St. Marys Formation.

REMARKS. A few isolated bones and a nearly complete neurocranium belonging to a single individual are assigned to the extant genus *Ictalurus*. Placement within the family Ictaluridae is justified by the presence of three of the four putative synapomorphies of this family as proposed by Lundberg (1970) and subsequently discussed by Grande and Lundberg (1988). The synapomorphies include (1) the possession of a large and smooth temporal fossa bounded by the adductor muscle scar that develops from the lateral edge of the frontal to the occipital region involving the sphenotic, pterotic, supraoccipital, and posttemporo-supracleithrum; (2) a posttemporo-supracleithrum with an anterior process (=subpterotic process of Lundberg, 1970, 1982) that articulates with the ventral surface of the outer pterotic wing; (3) the position of the exit of the infraorbital canal from the frontal located well anterior to the frontal-sphenotic joint; and (4) the lack of vomerine teeth. The outline of the neurocranial bones, cleithrum, and pectoral-fin spine cannot be distinguished in the fossil and extant species of the genus *Ictalurus* (see Lundberg, 1970, 1975). More particularly, the available material shows at least some of the synapomorphies of the genus *Ictalurus* defined by Lundberg (1982): a superficial part of the supraoccipital ornamented with longitudinal grooves and ridges, the absence of the spine located along the lateral margin of the sphenotic, lateral ethmoid wings curved downward, an enlarged optic foramen, and a ventral keel of the coracoid that is elongated, nearly reaching the coracoid symphysis. According to Lundberg and Luckenbill (2012), *Ictalurus countermani* exhibits four synapomorphies of the *I. punctatus* group (channel catfish): the transverse crest of the supraoccipital being tilted obliquely backward and expanded onto the base of the supraoccipital process; the parasagittal crest of the supraoccipital being narrow and rounded; the horizontal shelves of the orbitosphenoid being reduced in width; and the posterior process of the cleithrum being strongly ornamented with at least moderately coarse tubercles.

Ictalurus countermani is unique within the *I. punctatus* group in having a low, obtusely angular sphenotic process developed at midlength along the sphenotic margin; a posterior cleithral process deep at its base, with an exceptionally coarse tuberculate ornamentation; and a pectoral-fin spine shaft that is broad, dorsoventrally depressed, and lenticular in cross section with ridged and dentate anterior and posterior margins, anterior dentations that are evenly spaced and relatively large, and posterior dentations that are relatively small in size (see Lundberg and Luckenbill, 2012).

Catfishes of the genus *Ictalurus* inhabit streams, rivers, creeks, ponds, and lakes and rarely enter brackish waters. They feed on a wide variety of prey items, including worms, mollusks, insects, crustaceans, fishes, and small mammals.

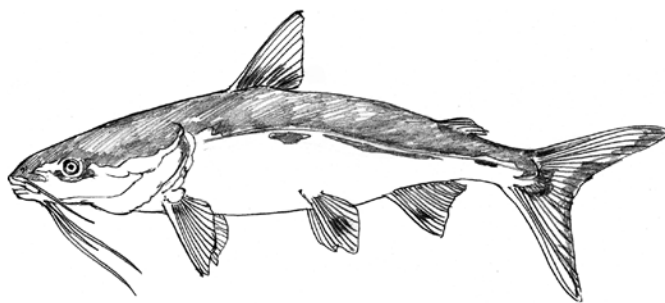
FAMILY ARIIDAE BLEEKER, 1862

Genus *Ariopsis* Gill, 1861

REMARKS. In a recent phylogenetic study of the family Ariidae, Kailola (2004) considered the genus *Ariopsis* as valid, characterized by two distinct geographic components, one American and the other typical of Australia and New Guinea. Marceniuk and Menezes (2007) included the species of this genus within the limits of the genus *Sciades*. Ferraris (2007) interpreted the two geographic components hypothesized by Kailola (2004) as separate genera, with the American species included in *Ariopsis* and those of the Australia–New Guinea region placed in *Neoaricus*.

Ariopsis stauroforus (Lynn & Melland, 1939)

FIGURE 3.3H–J



Catfish – *Ariopsis stauroforus*

- 1939 *Felichthys stauroforus* Lynn & Melland, pp. 14–20, figs. 1–3.
- 1975 *Arius stauroforus* (Lynn & Melland) – Lundberg, p. 3.
- 1984 *Arius felichthys* – Kimmel & Purdy, pl. 1, fig. 5.
- 1999 *Arius stauroforus* (Lynn & Melland) – Muller, p. 77, fig. 27.
- 2001 *Bagre stauroforus* (Lynn & Melland) – Purdy, Schneider, Applegate, McLellan, Meyer, & Slaughter, p. 165.
- 2007 *Felichthys stauroforus* Lynn & Melland – Ferraris, p. 32.
- 2012 cf. *Ariopsis felis* – Lundberg & Luckenbill, p. 8, fig. 23.

HOLOTYPE. USNM 15746, a partially complete neurocranium and a left lapillus (utricular otolith; Figure 3.3H–J).

REFERRED MATERIAL. CMM-V-3317, complete dorsal-fin spine (see Lundberg and Luckenbill, 2012); USNM 336490, partial neurocranium; USNM 336491, partial pectoral-fin spine; USNM 542405, partial neurocranium lacking the anterior portion of the orbital and ethmoid regions.

HORIZON. Calvert Formation.

REMARKS. Lynn and Melland (1939) presented a detailed description of the type specimen that was interpreted to be closely related to the extant hardhead catfish *Ariopsis felis*. Subsequently, Kimmel and Purdy (1984) presented a partial neurocranium that they referred to the sea catfish genus *Arius*.

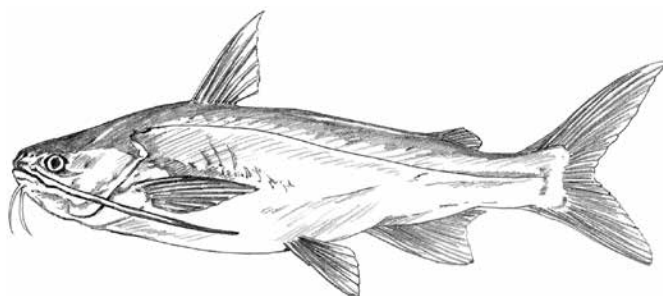
The analysis of the type and other material has evidenced several diagnostic features of the family Ariidae (see Acero and Betancur, 2007), including an extremely developed lapillus, relatively swollen otic capsules, a well-developed ventral process of the basioccipital, and a well-developed foramen (=temporal fossa of Acero and Betancur, 2007) between the posttemporo-supracleithrum, extrascapula, and pterotic. The well-defined aortic canal on the basioccipital and the absence of the anterior nuchal plate clearly support its inclusion within the subfamily Ariinae (see Acero and Betancur, 2007). Among the new-world genera of the subfamily Ariinae, the overall physiognomy of the fossils is consistent with that of certain species of the genus *Ariopsis*. More specifically, the neurocranium exhibits a close similarity to those characteristics of the extant *Ariopsis felis*, from which they differ in having a larger parasphenoid, a wider medial groove of the neurocranium that originates from the center of the supraoccipital, and enlarged anterior and posterior cranial fontanels.

Extant sea catfishes of the genus *Ariopsis* inhabit coastal marine and brackish environments and, to a lesser degree, large and medium rivers, where they are found in turbid waters over muddy bottoms. They feed mainly on invertebrates and small fishes.

Genus *Bagre* Cloquet, 1816

Bagre sp.

FIGURE 3.4A,B



Catfish – *Bagre*

REFERRED MATERIAL. USNM 542406, articulated skeleton consisting of an incomplete neurocranium lacking the ethmoid and most of the orbital regions, and part of the left pectoral girdle (including the pectoral-fin spine), the median nuchal plate, and the dorsal-fin spine (Figure 3.4A,B).

HORIZON. Calvert Formation.

REMARKS. The outer surface of the cranial bones and cleithrum is extensively sculptured. The morphology of the skull roofing bones, the overall outline of the neurocranium and

cleithrum, the relative development of the postcleithral process of the cleithrum, the presence of transverse ridges with one or two peaks along the anterior margin of the dorsal-fin spine (see Purdy et al., 2001), the subrectangular morphology of the supraoccipital bone, the overall morphology of the median nuchal plate, and the size and shape of the foramen (=temporal fossa of Acero and Betancur, 2007) between the posttemporo-supracleithrum, extrascapula, and pterotic are extremely similar to those of the species of the catfish genus *Bagre*, to which the material documented herein is tentatively referred.

Sea catfishes of the genus *Bagre* mainly inhabit marine habitats around the mouths of rivers but also inhabit brackish estuaries with high salinities. They prefer muddy bottoms and feed primarily on benthic invertebrates and small fishes.

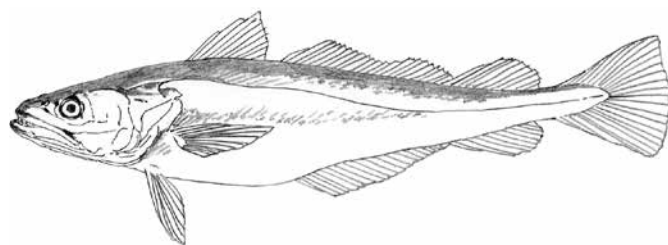
ORDER GADIFORMES GOODRICH, 1909

FAMILY MERLUCCIIDAE GILL, 1884

Genus *Merluccius* Rafinesque, 1810

Merluccius sp.

FIGURE 3.4C–F



Hake – *Merluccius* sp.

REFERRED MATERIAL. CMM-V-3488, nearly complete left mandible (Figure 3.4E,F); CMM-V-4492, partially complete right premaxilla (Figure 3.4C,D); USNM uncataloged, partially complete right dentary.

HORIZON. St. Marys Formation.

REMARKS. The premaxilla has a short, nearly vertical ascending process and a robust articular process with a rounded dorsal profile (Figure 3.4C). The alveolar process is long and straight, with two rows of large teeth. The dentary is greatly elongate and bears two rows of conical pointed teeth with lingually recurved tips; the teeth of the labial row are more firmly attached to the dentary than those of the lingual row, which are not preserved in the specimen; a deep groove extends for most of the length of the dentary along its ventrolateral surface. The anguloarticular is laminar, with a short and narrow coronoid process (Figure 3.4E,F).

The morphology of the premaxilla and mandibular bones is consistent with that of the genus *Merluccius*. In particular,

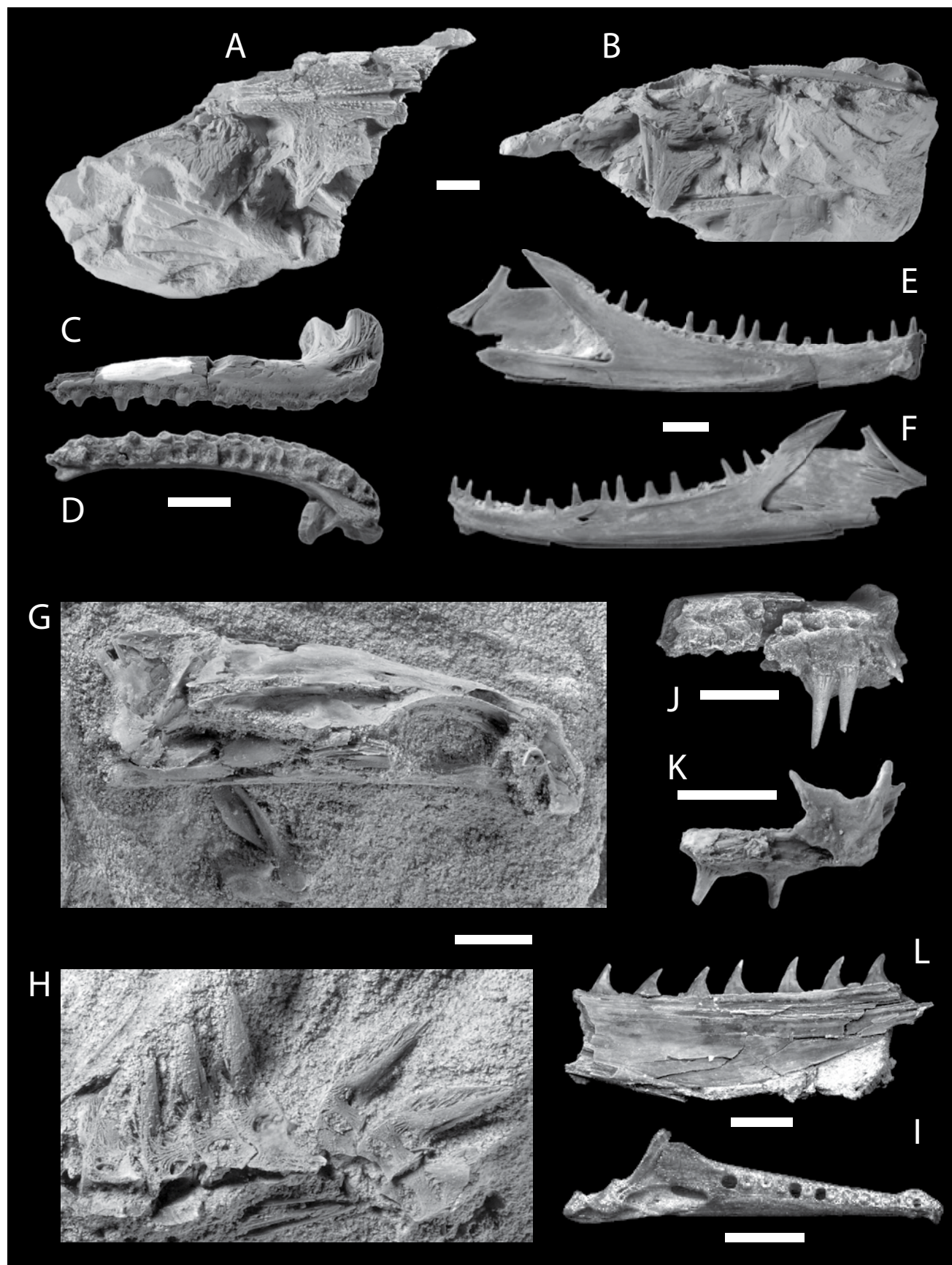


FIGURE 3.4. (*Facing page*) (A, B) USNM 542406, *Bagre* sp., partial articulated skeleton in dorsal and ventral views, respectively. (A) Anterior to right. (B) Anterior to left. (C, D) CMM-V-4492, *Merluccius* sp., right premaxilla in lateral and ventral views, respectively. (E, F) CMM-V-3488, *Merluccius* sp., left mandible in medial and lateral views, respectively. (G) CMM-V-4637, *Brotula* sp., neurocranium in right lateral view. Anterior to right. (H) CMM-V-4637, *Brotula* sp., abdominal vertebrae in left lateral view. (I) CMM-V-2509, *Opsanus* sp., partial left mandible, medial view. (J) CMM-V-839, *Lophius* sp., partial right premaxilla in medial view. (K) USNM 24865, *Lophius* sp., palatine in lateral view. (L) CMM-V-4628, *Lophius* sp., partial left dentary in lateral view. Anterior to left. Specimens lightly coated with sublimed ammonium chloride. Scale bars equal 10 mm.

the arrangement of the premaxillary teeth in two rows is typical of that genus (see Inada, 1981; Howes, 1991). Within the genus *Merluccius*, the identification at the species level is based primarily on the morphology of selected osteological structures (hyomandibula, sagitta, urohyal) that are not observable in the available material.

Hakes are marine demersal fishes recorded at depths of 1 to 400 m. They are often abundant on sandy grounds. Hakes are voracious predators of fishes and crustaceans.

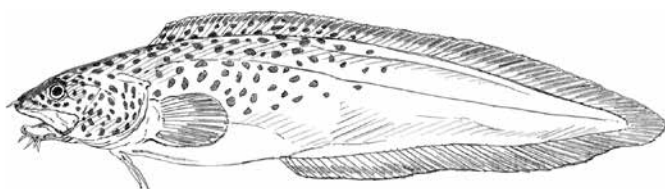
ORDER OPHIDIIFORMES BERG, 1937

FAMILY OPHIDIIDAE RAFINESQUE, 1810

Genus *Brotula* Cuvier, 1829

***Brotula* sp.**

FIGURE 3.4G–H



Brotulas – *Brotula* sp.

REFERRED MATERIAL. CMM-V-4637, partially complete articulated skeleton (Figure 3.4G,H).

HORIZON. Calvert Formation.

REMARKS. The single available specimen consists of a partially complete, articulated skeleton represented by a well-preserved neurocranium and fragmentary skull bones, 11 abdominal vertebrae, and fragments of what appear to be pleural ribs and epineural bones.

The neurocranium is elongate and tubular, its length approximately three times its maximum depth (Figure 3.4G). The ethmoid region is very short. The orbit is oblong. The skull roof is smooth except for a low crest developed in the temporal region of the frontal. The vomer prominently projects ventrally. The mesethmoid consists of a stout, nearly vertical and laterally compressed

bony lamina. The lateral ethmoid bears a laterally directed flange. The frontals are the largest bones of the skull roof. The parietal is subtriangular in outline. The supraoccipital extends posteriorly into a very low, laterally compressed crest. The parasphenoid and basioccipital are very robust and thickened.

The vertebral centra are massive and subquadrangular, bearing large bladelike parapophyses (Figure 3.4H). The bases of the neural arches are greatly expanded. The lateral surfaces of the centra, neural arches, and parapophyses are extensively ornamented with small deep pits and delicate ridges.

The morphological features of the neurocranium (general proportions and the structure of the frontals, supraoccipital crest, parasphenoid, and vomer) and the architecture and ornamentation of the abdominal vertebrae are extremely similar to those of the bearded brotula *Brotula barbata* (e.g., Patterson and Rosen, 1989: fig. 8). The specimen is referred herein to an indeterminate species of the genus *Brotula*; because of its incompleteness, it is preferable to use the open nomenclature until more complete articulated skeletons become available.

Brotulas are benthopelagic, inhabiting marine waters to depths of more than 600 m, but are common on the continental shelf on muddy and sandy bottoms. Brotulas feed primarily on fishes and crustaceans, mainly crabs.

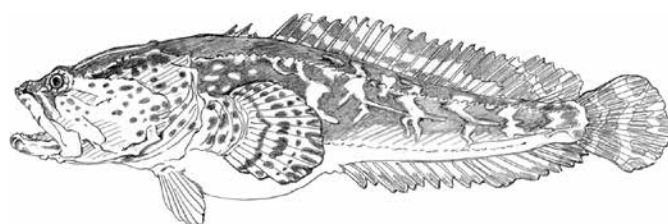
ORDER BATRACHOIDIFORMES GOODRICH, 1909

FAMILY BATRACHOIDIDAE JORDAN & EVERMANN, 1898

Genus *Opsanus* Rafinesque, 1818

***Opsanus* sp.**

FIGURE 3.4I



Toadfish – *Opsanus* sp.

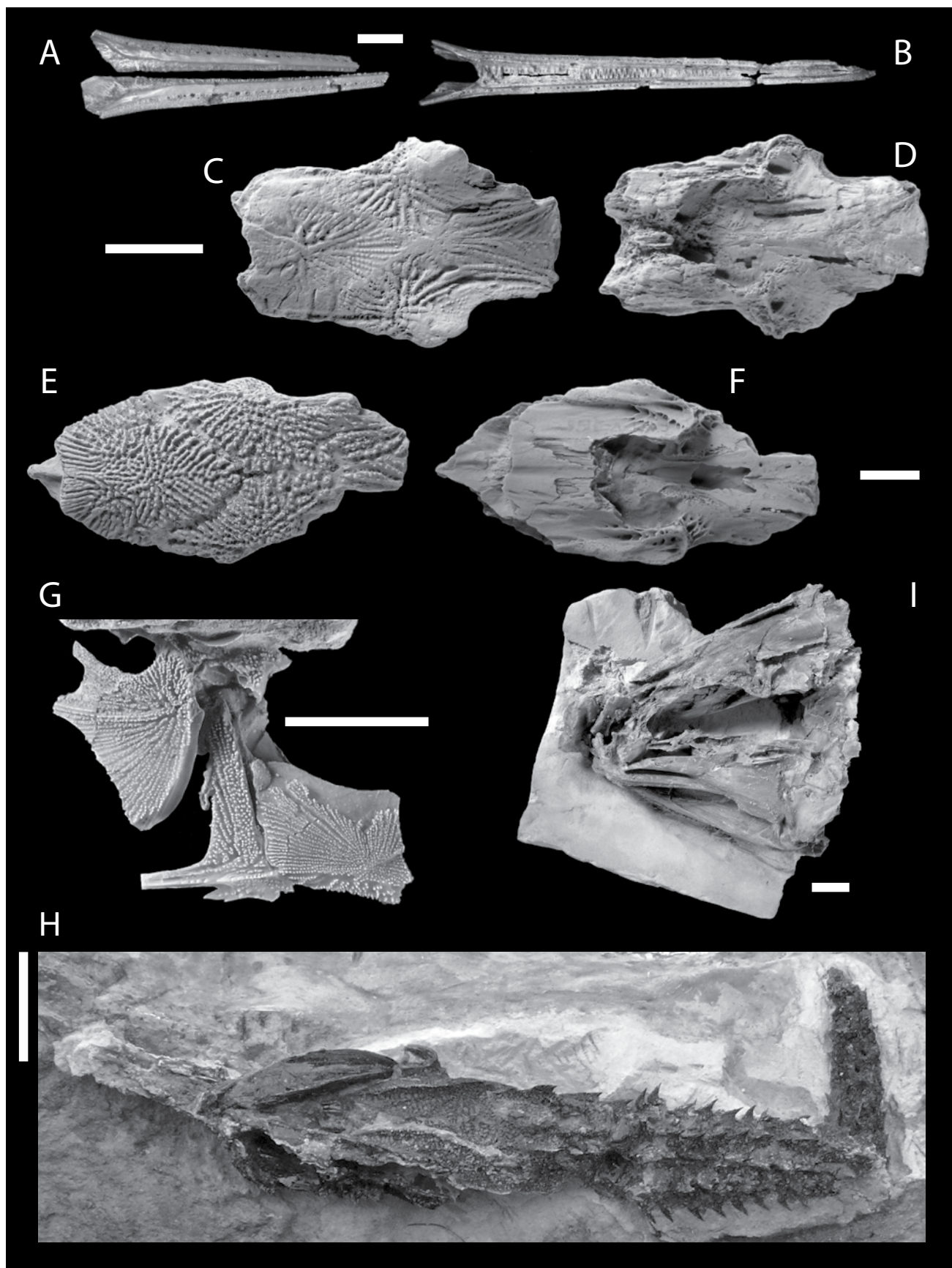


FIGURE 3.5. (*Facing page*) (A, B) CMM-V-3695, *Belone countermani*, holotype, articulated partial premaxillae and dentaries, respectively, in occlusal views. Anterior to right. (C, D) CMM-V-2006, *Prionotus* sp., partial neurocranium in dorsal and ventral views, respectively. Anterior to left. (E, F) CMM-V-2195, *Prionotus* sp., partial neurocranium in dorsal and ventral views, respectively. Anterior to left. (G) CMM-V-4631, *Prionotus* sp., left infraorbitals and preopercle and opercle. Anterior to left. (H) CMM-V-4535, Agonidae gen. et sp. indet.; nearly complete articulated skeleton in ventral view. Anterior to left. (I) USNM 542411, *Morone* sp., partial head skeleton in left lateral view. Anterior to left. Specimens lightly coated with sublimed ammonium chloride. Scale bars equal 10 mm.

REFERRED MATERIAL. CMM-V-2509, partially complete left mandible (Figure 3.4i).

HORIZON. Choptank Formation.

REMARKS. A single left mandible documents the presence of the toadfish genus *Opsanus* in the Miocene deposits of the Chesapeake Group. The dentary is elongate and slender, with a single row of rounded sockets that extends for most of its length. In the symphyseal region, some supernumerary teeth are irregularly arranged in an additional row. The anguloarticular is characterized by a thick ridge along its lateral side and a well-developed, obliquely oriented coronoid process. The dorsal margin of the joint between the dentary and the coronoid process of the anguloarticular is characterized by a rounded profile (see Greenfield et al., 2008).

The mandible cannot be distinguished from those of the extant oyster toadfish *Opsanus tau*. However, additional comparative information is necessary for a more detailed identification of the material.

Toadfishes of the genus *Opsanus* occur primarily inshore at depths up to 50 m on rocky bottoms and close to reefs. According to Thomson et al. (1978), some species of this genus migrate offshore during cold weather. Toadfishes are voracious predators that feed primarily on worms, crustaceans, and fishes.

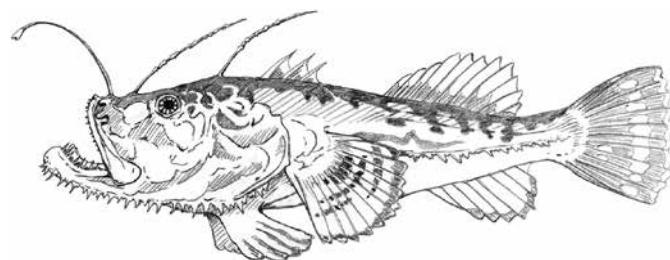
ORDER LOPHIIFORMES GARMAN, 1899

FAMILY LOPHIIDAE RAFINESQUE, 1810

Genus *Lophius* Linnaeus, 1758

***Lophius* sp.**

FIGURE 3.4J-L



Lophiid Anglerfish – *Lophius* sp.

REFERRED MATERIAL. CMM-V-839, partially complete right premaxilla (Figure 3.4J); CMM-V-1363, partially complete right premaxilla and right dentary associated with a vertebral column of *Thunnus* sp.; CMM-V-2777, isolated teeth; CMM-V-4624, partially complete right premaxilla; CMM-V-4628, partially complete left dentary (Figure 3.4L); CMM-V-4629, partially complete left dentary; USNM 24865, left and right dentaries and a right palatine (Figure 3.4K); USNM uncataloged, partially complete right premaxilla.

HORIZON Calvert, St. Marys, and Eastover Formations.

REMARKS. All the available bones are incomplete and only moderately well preserved. The large and robust caniniform teeth with shallow vertical grooves at their bases, as well as the posterior triangular teeth of the outer row of the dentary, exhibit the attachment structure (ankylosis and fibrous hinge) typical of the genus *Lophius* (see Kerebel et al., 1979). The bifid anterior head of the palatine also supports the assignment to the genus *Lophius* (see Carnevale and Pietsch, 2012).

Lophiid anglerfishes of the genus *Lophius* are benthic and inhabit different substrates at depths ranging from the shoreline to greater than 600 m, where they feed on fishes and invertebrates.

ORDER BELONIFORMES BERG, 1937

FAMILY BELONIDAE BONAPARTE, 1837

Genus *Belone* Cuvier, 1816

***Belone countermani* de Sant'Anna, Collette, & Godfrey, 2013**

FIGURE 3.5A,B



Needlefish – *Belone countermani*

HOLOTYPE. CMM-V-3695, articulated partially complete premaxillae and dentaries belonging to a single individual (Figure 3.5A,B).

HORIZON. St. Marys Formation.

REMARKS. De Sant'Anna et al. (2013) provided a detailed description of this specimen, the only fossil belonid known from the Maryland Miocene. The premaxillae are delicate and elongate (Figure 3.5A). There are two series of premaxillary teeth; the teeth of the inner series are arranged into a single row of relatively large conical elements, whereas those of the outer series consist of a dense band of very small accessory teeth that reach the lateral margin of the bone. The dentaries are slender and elongate, characterized by a thickened symphyseal portion and a moderately thin rostral end. The contralateral dentaries articulate through strong symphyseal interdigitation (Figure 3.5B; de Sant'Anna et al., 2013: fig. 6); however, this interdigitation does not extend up to the anterior tip of the mandible. Sockets document the presence of a single row of teeth of varying sizes in the rostral region; these teeth are associated with a dense series of numerous tiny accessory villiform elements posteriorly and a single outer series of accessory teeth in the symphyseal region (de Sant'Anna et al., 2013: figs. 4, 5).

The dentition of *Belone countermani* most closely resembles that of *B. belone*, an extant needlefish that inhabits the Mediterranean Sea and eastern North Atlantic Ocean (Collette and Parin, 1970; de Sant'Anna et al., 2013). Although they are similar, morphological differences warrant placement in separate species. With so little fossil material known of *B. countermani*, there is a high probability that additional finds will add significantly to our understanding of its morphology.

The garfish *B. belone* inhabits the brackish, shallow marine and oceanic biotopes of the eastern North Atlantic and Mediterranean, where it feeds on small fishes, mostly clupeoids.

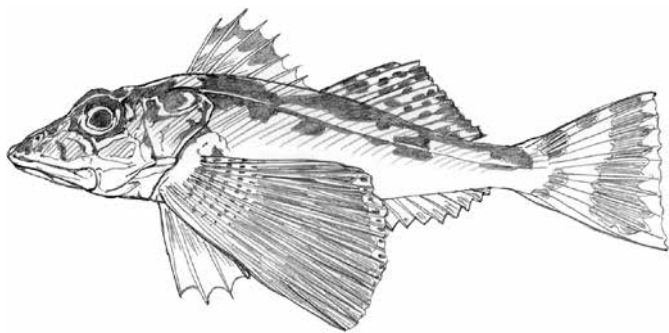
ORDER SCORPAENIFORMES GARMAN, 1899

FAMILY TRIGLIDAE RISSO, 1926

Genus *Prionotus* Lacépède, 1801

Prionotus sp.

FIGURE 3.5C–G



Sea Robin – *Prionotus* sp.

REFERRED MATERIAL. CMM-V-2006, partially complete neurocranium (Figure 3.5C,D); CMM-V-2195 (Figure 3.5E,F), partially complete neurocranium; CMM-V-3408, partially complete lachrymal; CMM-V-4337, partially complete neurocranium; CMM-V-4338, partially complete neurocranium; CMM-V-4631, left infraorbitals and preopercle and opercle (Figure 3.5G).

HORIZON. Calvert and St. Marys Formations.

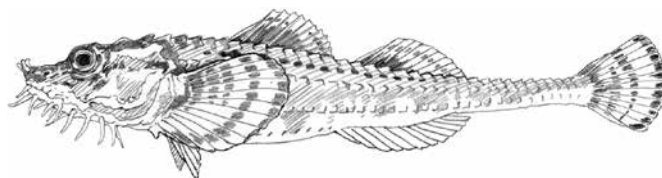
REMARKS. The available material consists exclusively of cranial remains (Figure 3.5C–G). The outer sides of the bones exhibit the elaborate sculpturing pattern characteristic of the members of the family Triglidae (e.g., Allis, 1909; Carnevale, 2008). The neurocrania are always represented by the orbital-ethmoid region, which includes the median mesethmoid, paired nasals, lateral ethmoids, and the anterior part of the frontals (Figure 3.5C–F). The neurocranial architecture and the morphological structure of the opercular bones (Figure 3.5G), as well as the external ornamentation pattern of the bones, fit very well with those of the sea robins of the genus *Prionotus*. A more detailed taxonomic identification is not possible without additional and more complete specimens.

Sea robins of the genus *Prionotus* are marine demersal inhabitants of the continental shelf down to about 200 m, where they feed primarily on worms, mollusks, and crustaceans. *Prionotus* species often enter brackish waters.

FAMILY AGONIDAE SWAINSON, 1839

Gen. et sp. indet.

FIGURE 3.5H



Poacher – Agonidae

REFERRED MATERIAL. CMM-V-4535, nearly complete articulated skeleton partially embedded in sediment (Figure 3.5H).

HORIZON. St. Marys Formation.

REMARKS. A recently discovered nearly complete articulated skeleton documents the presence of the family Agonidae in the deposits of the Little Cove Point Member of the St. Marys Formation (Figure 3.5H). The fossil is still partially embedded in sediment, and its detailed anatomical and systematic analysis is currently in progress using computer tomography. The general morphology of the fossil, with a slender body tapering to the caudal peduncle and covered with thick bony plates bearing a strong blunt retrorse spine arising from the center,

unambiguously supports its assignment within the family Agonidae (see Kanayama, 1991).

Agonids inhabit the sandy and rocky bottoms of the shallow marine biotopes of the northern Pacific, North Atlantic, North Sea, and the Patagonian region, where they feed on crustaceans and other benthic invertebrates.

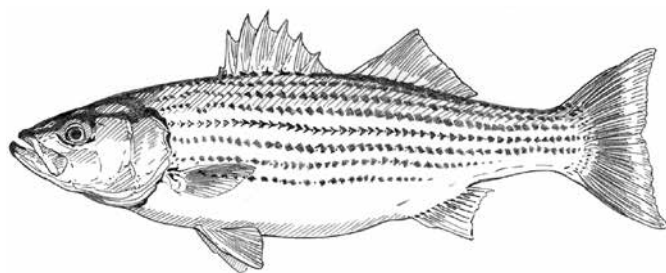
ORDER PERCIFORMES BLEEKER, 1859

FAMILY MORONIDAE FOWLER, 1907

Genus *Morone* Mitchill, 1814

Morone sp.

FIGURE 3.5i



Bass – *Morone* sp.

REFERRED MATERIAL. USNM 542410, partially complete head skeleton; USNM 542411, partial head skeleton (Figure 3.5i).

HORIZON. Calvert Formation.

REMARKS. The available material includes two partial skulls collected from the Calvert Formation. The excellent preservation of these specimens allows for the observation of a number of anatomical features that clearly evidence their affinity with the extant species of the genus *Morone*. In particular, the general outline of the neurocranium, the irregular configuration of the transverse lateral process of the sphenotic, the delicate subtriangular anterior process arising from the anterodorsal margin of the mesethmoid, the morphology of the jaw and suspensorial bones, the large bands of small premaxillary and dentary teeth, and the posterior enlarged laminar flange at the angle formed by the convergence of the horizontal and vertical arms of the preopercle are extremely similar to those of the extant striped bass *Morone saxatilis* (see Woolcott, 1957). However, the complete absence of characters of the axial skeleton, as well as of any morphometric or meristic features, does not allow for an unambiguous taxonomic interpretation at the specific level.

Basses of the genus *Morone* are anadromous and extremely common in shallow coastal waters and brackish biotopes. They enter rivers to spawn mostly during the spring. Fishes of the genus *Morone* are voracious and opportunistic predators that feed on a variety of fishes and invertebrates.

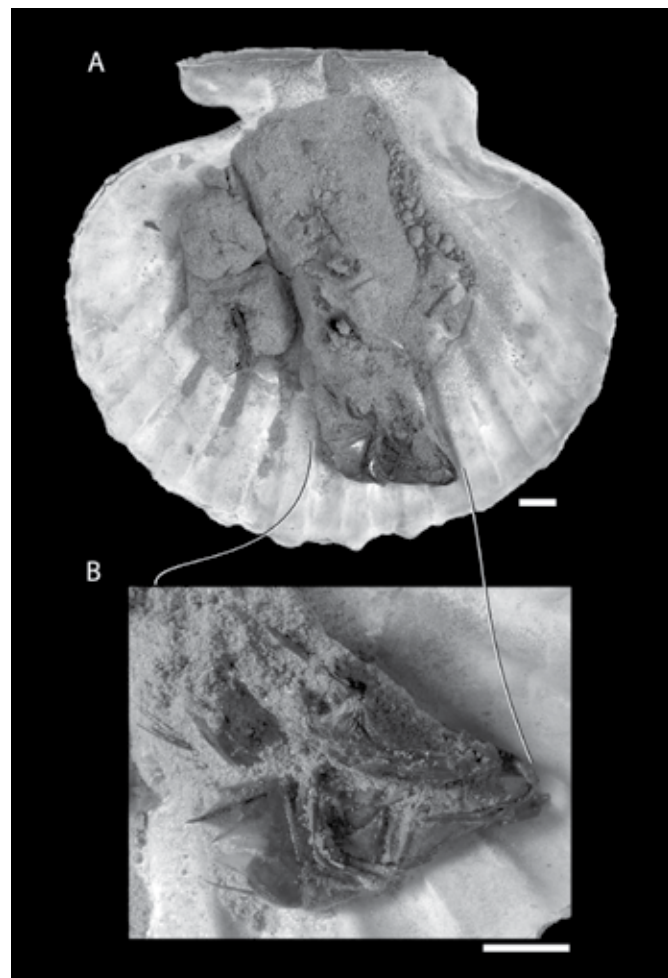


FIGURE 3.6. CMM-V-4622, Serranidae, gen. et sp. indet. (A) Partial articulated skeleton preserved inside joined valves of a Miocene scallop shell, *Chesapeakea nefrens*. (B) Enlarged view of skull in right lateral view. Anterior to right. Scale bars equal 10 mm.

FAMILY SERRANIDAE SWAINSON, 1839

Gen. et sp. indet.

FIGURE 3.6

REFERRED MATERIAL. CMM-V-4622, partially complete articulated skeleton preserved inside joined valves of a *Chesapeakea* (Figure 3.6).

HORIZON. Choptank Formation.

REMARKS. Although a large part of the skeleton is still embedded in the sediment, it is possible to observe the skull roof, both lower jaws, the right suspensorium, and the opercular complex (Figure 3.6). The preopercle is ornamented

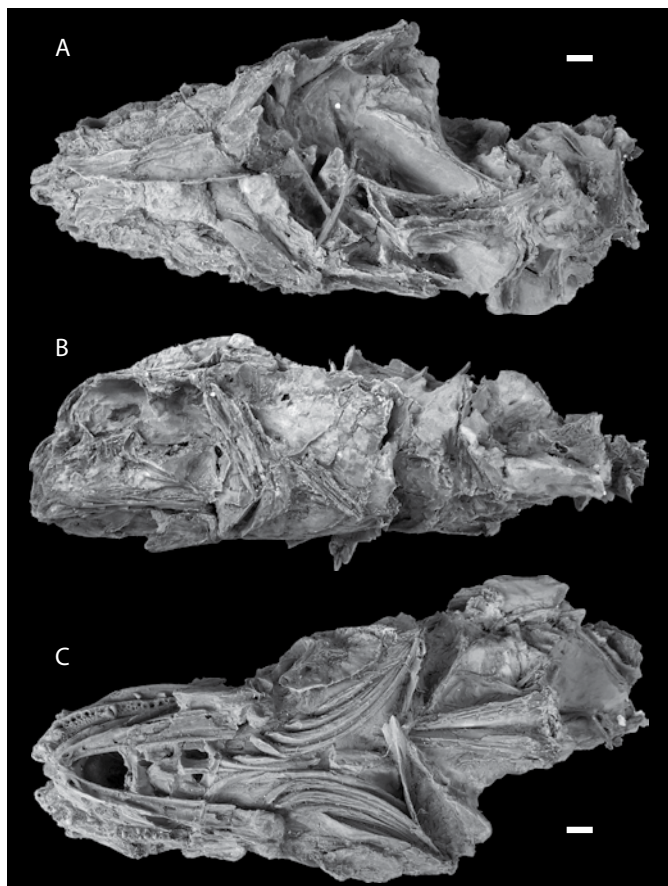


FIGURE 3.7. (A–C) USNM 467782, *Lopholatilus ereborensis*, holotype, nearly complete well-preserved skull and partial axial skeleton in dorsal, left lateral, and ventral views, respectively. Specimen is lightly coated with sublimed ammonium chloride. Scale bars equal 10 mm.

with fine serrations along the posterior margin of the vertical arm and by short, strong spines along the ventral margin of the horizontal arm and at the corner formed by the confluence of the two arms (Figure 3.6B). The opercle has three spines along its posterior margin, of which the central spine represents the distal end of the median horizontal ridge that originates from the articular surface for the opercular process of the hyomandibula.

The serrated posterior and ventral margins of the preopercle and the presence of three spines along the posterior margin of the opercle are clearly indicative of the family Serranidae (see Johnson, 1983). A more detailed identification of the fossil is not possible because of its inadequate preservation.

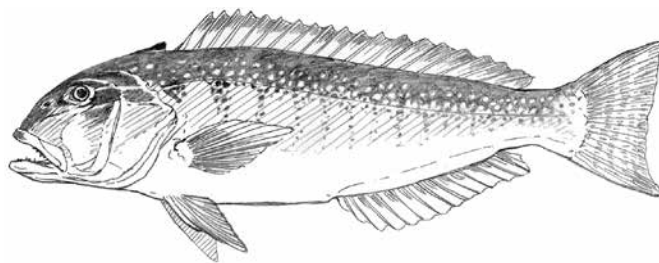
The family Serranidae includes more than 470 species of marine predatory fishes common in tropical and temperate areas of the world.

FAMILY MALACANTHIDAE GÜNTHER, 1861

Genus *Lopholatilus* Goode & Bean, 1880

Lopholatilus ereborensis Carnevale & Godfrey, 2014

FIGURE 3.7



Tilefish – *Lopholatilus ereborensis*

1984 *Lopholatilus* sp. – Kimmel and Purdy, p. 208, fig. 20, pl. 2, figs. 1–2.

HOLOTYPE. USNM 467782, nearly complete well-preserved head skeleton and partial axial skeleton (Figure 3.7).

PARATYPES. CMM-V-4635, partially complete head skeleton; CMM-V-4636, partially complete head skeleton; CMM-V-4638, partially complete head skeleton; CMM-V-4821, partially complete head skeleton plus six articulated abdominal vertebrae; USNM 467776, partially complete head skeleton.

REFERRED MATERIAL. CMM-V-4639, partially complete head skeleton; USNM 467777, partially complete head skeleton; USNM 467779, partially complete head skeleton; USNM 467781, partially complete head skeleton.

HORIZON. Calvert Formation.

REMARKS. All the available material consists of relatively well preserved articulated cranial remains from beds 11 to 14 of the Calvert Formation. USNM 467782 also includes 10 abdominal centra, two caudal centra, some scattered dorsal-fin elements, and large parts of the appendicular girdles.

The head is massive, rather wide, and moderately deep, with its maximum depth contained slightly less than two times in head length. The snout is very short (contained more than four times in head length) and the orbit is moderately large (Figure 3.7). Because of the reduced length of the snout, the anterior profile of the head appears very steep.

The neurocranium is very high and bears a robust, moderately high supraoccipital crest that apparently reaches the anterior margin of the orbit and a less developed temporal crest; two prominent thick anteroventrally directed processes with a nearly ovoid anterior profile arise from the anterodorsal margin of the mesethmoid. The occipital region gently slopes in an oblique direction. The high lachrymal is thickened and extensively ornamented along its lateral surface.

The upper jaw is protrusible and slightly oblique, approximately reaching the posterior margin of the orbit. The premaxilla bears a very short and distally pointed ascending process (length of the ascending process 34–36.5% of the length of the alveolar process) and a laminar articular process with rounded dorsal profile. The alveolar process bears a single outer row of strong conical teeth and an inner dense band of villiform teeth. The dentary bears a single outer row of strong conical teeth similar to those of the premaxilla and villiform teeth restricted to the symphyseal region. A very short, pointed, and vertically directed symphyseal process arises from its anteroventral corner.

The suspensorial bones are relatively well exposed in most of the specimens.

The preopercle has a finely serrated posterior margin; the angle between the vertical and horizontal arms measures about 120°. The vertical arm of the preopercle is considerably shortened, with the horizontal arm measuring between 52.8% and 66.4% of the length of the vertical arm. The opercle is laminar, very thin, and characterized by a strongly thickened anterior margin; a thickened horizontal ridge extends posteriorly from the articular condyle for the hyomandibular process and possibly terminates posteriorly into a spine.

The hyoid bar is very compact, with a medially exposed dorsal hypohyal. There are six saber-like branchiostegal rays.

Except for the atlas and second abdominal vertebra, the vertebral centra are subrectangular, longer than high, with a deep fossa along their lateral sides. Vertebrae 3 through 10 bear relatively large bladelike parapophyses.

The overall morphology of the neurocranium, upper and lower jaws, suspensorial bones, and opercular apparatus is very similar to that of the great northern tilefish *Lopholatilus chamaeleonticeps*. In particular, the specimens examined show some features that are clearly diagnostic of *Lopholatilus*, including the paired prominent curved and anteroventrally directed processes arising from the anterodorsal margin of the mesethmoid, the large thick and extensively sculptured lachrymal, and the oral jaw dentition pattern. Despite their incompleteness, the fossils show a few evident characters that clearly separate them from the extant species of the genus *Lopholatilus* (Carnevale and Godfrey, 2014). Compared to those of extant congeners, the head of *Lopholatilus ereborensis* is moderately developed vertically; its depth is contained slightly less than two times in head length (~52% versus 72%–100% of head length). As a result of the strong shortening of the ethmoid region of the neurocranium, the snout of *Lopholatilus ereborensis* is broadly shortened relative to that characteristic of both extant species (snout length ~22% versus 27%–51% of head length). The ascending process of the premaxilla is notably reduced in size compared to those of extant species, its length being 34%–36.5% of that of the alveolar process (versus 49%–52% in *Lopholatilus chamaeleonticeps*). The vertical arm of the preopercle is remarkably shortened compared with that of extant members of the genus *Lopholatilus* (the length of the horizontal arm of the preopercle measures

between 52.8% and 66.4% of that of the vertical arm versus ~42% in *Lopholatilus chamaeleonticeps*). Finally, the vertical and horizontal arms of the preopercle form an angle (~120°) broader than that of the extant species (105°–110°; see Dooley, 1978). All of these characters appear to be unique to the Miocene fossils, representing a reasonable basis for the creation of a new species. Purdy et al. (2001) described the species *Lopholatilus rayus* on the basis of material from the Pliocene Yorktown Formation, North Carolina. On the basis of their diagnosis, the separate status of that extinct species was supported by a single character, the possession of an inner row of villiform teeth on the dentary that extends backward from the symphyseal region up to the coronoid process. As discussed above, this character is absent in the fossil *Lopholatilus* from the Calvert Formation.

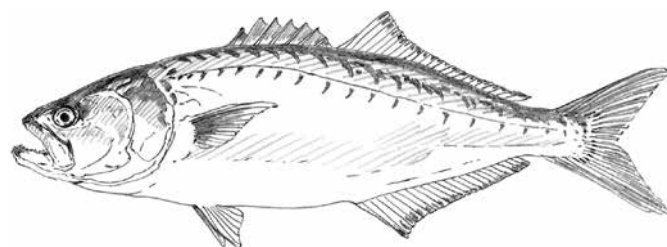
North Atlantic tilefishes of the genus *Lopholatilus* generally occur along the continental slope and the upper reaches of the canyons at depths ranging between 120 and 200 m (Dooley, 1978). *Lopholatilus* has been recorded at depths of more than 500 m. Grimes et al. (1986) recognized two critical habitat requirements for *Lopholatilus*, a temperature range between 9°C and 14°C and shelter; they are known to excavate large vertical and oblique burrows. Carnevale and Godfrey (2014) proposed that certain large (10–25 cm in diameter) cylindrical-shaped trace fossils (dwelling burrows, i.e., domichnia) penetrating the fine-grained sands of the middle part of the Calvert Formation were produced by *Lopholatilus ereborensis*, representing the product of their burrowing activity. Tilefishes of the genus *Lopholatilus* prey on fishes and a variety of invertebrates.

FAMILY POMATOMIDAE GILL, 1865

Genus *Pomatomus* Lacépède, 1802

Pomatomus sp.

FIGURE 3.8A



Bluefish – *Pomatomus* sp.

REFERRED MATERIAL. CMM-V-1933, partially complete right dentary (Figure 3.8A); CMM-V-3237, isolated tooth.

HORIZON. Calvert and St. Marys Formations.



FIGURE 3.8. (Facing page) (A) CMM-V-1933, *Pomatomus* sp., partial right dentary in medial view. Anterior to left. (B, C) CMM-V-3694, *Rachycentron* sp., left preopercle in lateral and medial views, respectively. (D) CMM-V-3694, *Rachycentron* sp., caudal vertebra in lateral view. (E, F) CMM-V-3694, *Rachycentron* sp., premaxilla in ventral view and an enlargement, respectively. Anterior to top. (G) CMM-V-3694, *Rachycentron* sp., left maxilla in medial view. Anterior to right. (H) CMM-V-3694, *Rachycentron* sp., right second pharyngobranchial in ventral view. (I) CMM-V-2023, *Lagodon* sp., isolated tooth. (J, K) CMM-V-3209, *Stenotomus* sp., partial right premaxilla in ventral and dorsal views, respectively. Specimens (except I) are lightly coated with sublimed ammonium chloride. Scale bars equal 10 mm, except for that of (I), the *Lagodon* sp. tooth, which is 1 mm.

REMARKS. The dentary is relatively large, slightly curved, and bears a single row of labiolingually compressed, subtriangular, and deeply socketed teeth along its dorsal margin (Figure 3.8A; Johnson, 1986; Bemis et al., 2005). The symphyseal margin of this bone is strongly thickened and nearly vertical, with a medially curving dorsal portion. A single isolated tooth is also present in the collection of the CMM; it is subtriangular in shape and laterally compressed, identical to those of the extant bluefish *Pomatomus saltatrix*.

The fragmentary nature of the material does not allow for a more detailed taxonomic interpretation, for which much more comparative information would be necessary.

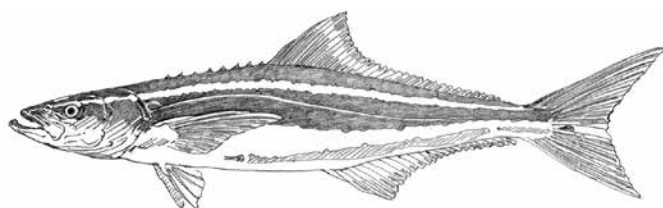
Bluefishes occur in coastal and oceanic tropical and subtropical waters with a circumglobal distribution. Adults often enter estuaries and other brackish-water biotopes. Bluefishes are voracious and aggressive predators that feed on cephalopods, crustaceans, and other fishes.

FAMILY RACHYCENTRIDAE GILL, 1895

Genus *Rachycentron* Kaup, 1826

***Rachycentron* sp.**

FIGURE 3.8B–H



Cobia – *Rachycentron* sp.

REFERRED MATERIAL. CMM-V-3694, several partially articulated bones belonging to a single individual: articulated sclerotic ring, nearly complete right premaxilla (Figure 3.8E,F), nearly complete left maxilla (Figure 3.8G), partially complete left suspensorium, partially complete left preopercle (Figure 3.8B,C), right second pharyngobranchial (Figure 3.8H),

nearly complete right posttemporal, and three caudal vertebrae (Figure 3.8D).

HORIZON. Calvert Formation.

REMARKS. The available material consists of a largely incomplete individual collected from bed 11 of the Calvert Formation.

The premaxilla is long and curved, with massive and articular processes; the dentigerous area is extremely expanded, with a large number of tiny alveoli for the insertion of villiform teeth (Figure 3.8E,F). The maxilla is strongly curved and gradually expands posteriorly; the articular head is massive, separated through a deep sulcus from the lateral process; the latter bears a prominent dorsally thickened apophysis anteroventrally connected with the articular head; the posterior margin of the maxilla is nearly vertical, notably expanded, and characterized by a crenulated margin (Figure 3.8G). The suspensorium consists of several bony fragments, among which the anterior palatine articular head for the maxillary facet can be easily recognized. The preopercle is crescent-shaped, with a thickened anterior ridge preceded by a bony shelf (Figure 3.8B,C). What appears to be the second pharyngobranchial is a thick, rodlike bone with a broad anterior articular head and an elongate dentigerous area along its ventral margin (Figure 3.8H). The posttemporal is laterally flattened, elliptical, and elongate, with two anterior processes for neurocranial articulation. The dorsal process is extremely elongate and terminates anteriorly as a dorsoventrally flattened bony lamina; the ventral process is short and round in cross section; a bony lamina is placed between these two processes. The vertebral centra are subrectangular with well-developed dorsolateral fossa and strong ventral prezygapophyses (Figure 3.8D).

None of the available bony elements can be distinguished from those of the extant cobia *Rachycentron canadum*. However, despite this great similarity, the incompleteness of the specimen does not allow for an unambiguous identification at the species level.

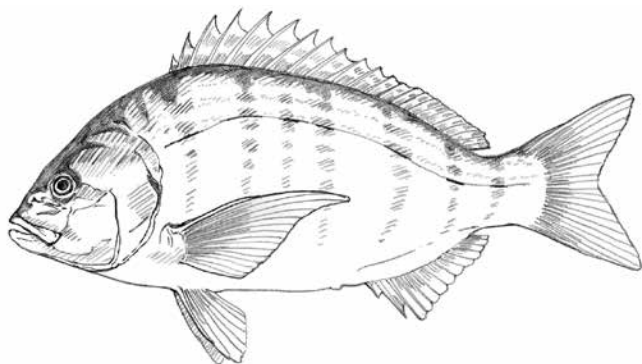
Cobias are marine and occur worldwide in a variety of tropical and subtropical habitats and occasionally enter estuaries and other brackish biotopes, feeding on crustaceans, cephalopods, and other fishes.

FAMILY SPARIDAE BONAPARTE, 1832

Genus *Lagodon* Holbrook, 1855

***Lagodon* sp.**

FIGURE 3.8I

Pinfish – *Lagodon* sp.

REFERRED MATERIAL. CMM-V-2023, isolated tooth (Figure 3.8i); CMM-V-2715, isolated tooth; CMM-V-2778, isolated tooth.

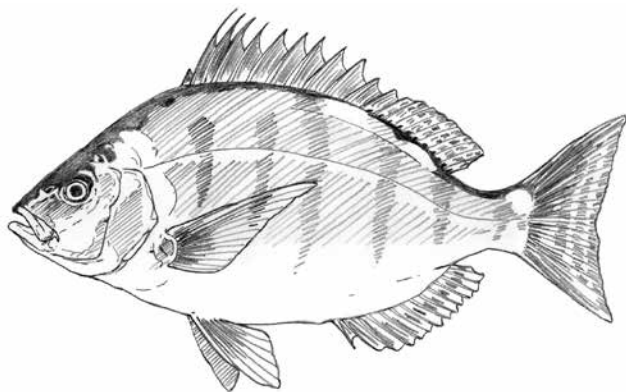
HORIZON. Calvert and St. Marys Formations.

REMARKS. The available material consists solely of isolated incisiform teeth with bilobate tips and a base that is rounded in cross section (Figure 3.8i). These teeth are identical to those characteristic of the extant pinfish *Lagodon rhomboides*. Isolated teeth belonging to the genus *Lagodon* were described from the deposits of the St. Marys Formation by Berry (1932).

The pinfish is a shallow marine sparid commonly found to depths of about 70 m on vegetated or rocky bottoms. It commonly enters brackish and freshwater environments. Pinfishes feed primarily on crustaceans and other invertebrates.

Genus *Stenotomus* Gill, 1865***Stenotomus* sp.**

FIGURE 3.8J,K

Scup – *Stenotomus*

REFERRED MATERIAL. CMM-V-3209, partially complete right premaxilla (Figure 3.8J,K); USNM 559398, partially complete right premaxilla.

HORIZON. St. Marys Formation.

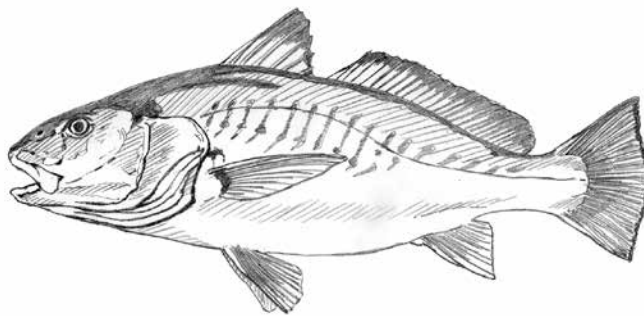
REMARKS. Both available specimens are represented by right premaxillae characterized by largely incomplete ascending processes. The alveolar process is distally spatulate and bears sockets of rounded, possibly molariform teeth that become gradually larger distally.

Despite their incompleteness, the overall morphology of the premaxillae and the gradual distal enlargement of the teeth are very similar to those found exclusively within the extant Atlantic scup *Stenotomus chrysops*.

Scups of the genus *Stenotomus* are shallow marine demersal fishes that often enter brackish waters. They feed on a variety of invertebrates, including worms, crustaceans, cephalopods, and echinoderms.

FAMILY SCIAENIDAE CUVIER, 1829**Genus *Micropogonias* Bonaparte, 1831*****Micropogonias* sp.**

FIGURE 3.9A

Croaker – *Micropogonias* sp.

REFERRED MATERIAL. CMM-V-1688, partially complete left preopercle (Figure 3.9A).

HORIZON. Calvert Formation.

REMARKS. The available material consists of an incomplete left preopercle. The preopercle is crescent shaped, with a strong thickening along its anterior margin. The posterior margin is serrated, with three short spines and a strong robust spine located at the level of the angle formed by the convergence of the horizontal and vertical arms. A broad shallow laterosensory canal is overlaid by narrow struts that run longitudinally behind the anterior thickening of the bone.

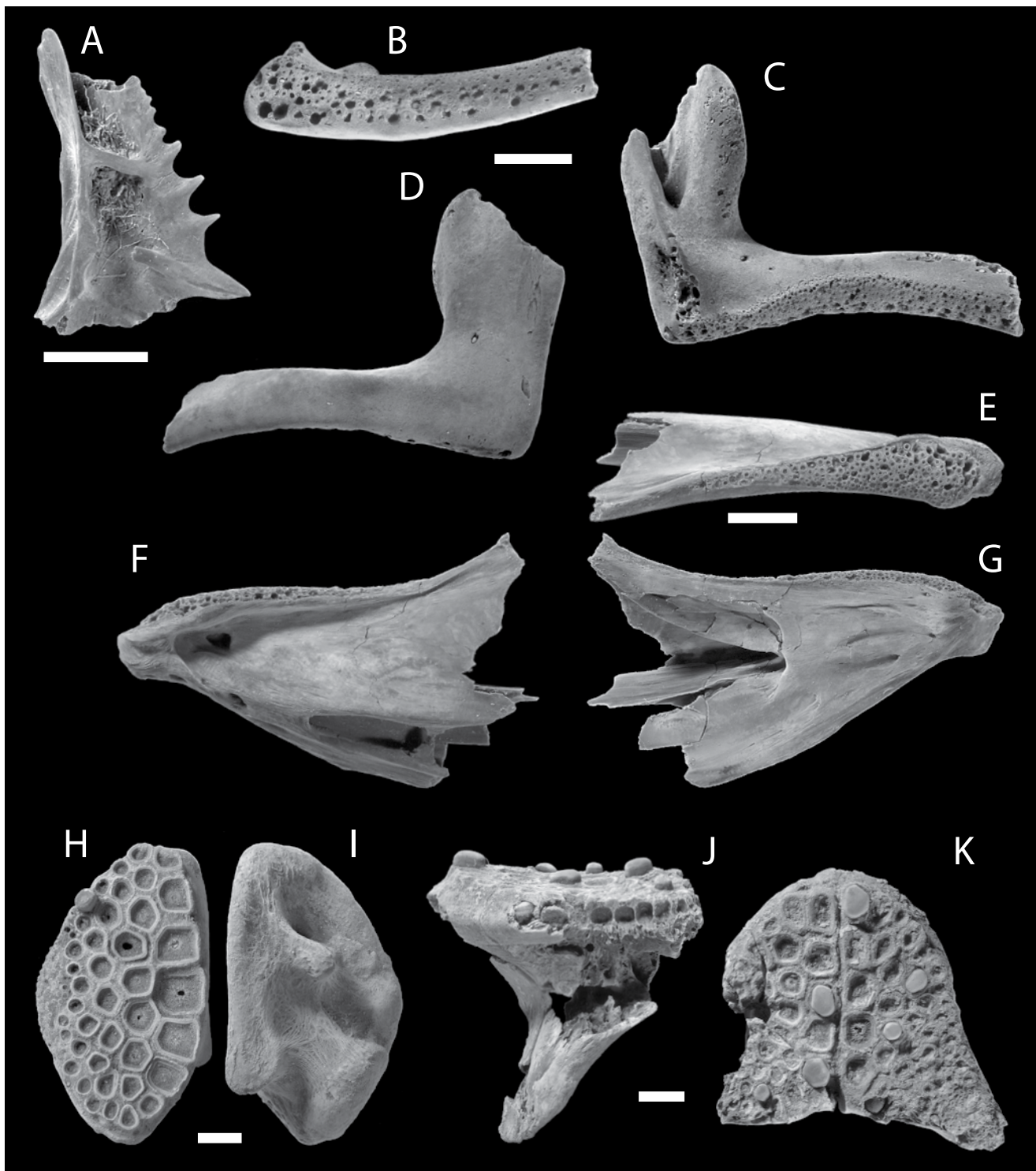


FIGURE 3.9. (A) CMM-V-1688, *Micropogonias* sp., partial left preopercle in lateral view. (B–D) CMM-V-3982, *Pogonias* sp., premaxilla in occlusal, medial, and lateral views, respectively. (E–G) CMM-V-4627, *Pogonias* sp., left dentary in occlusal, lateral, and medial views, respectively. (H, I) CMM-V-2341, *Pogonias* sp., third pharyngobranchial in occlusal and dorsal views, respectively. (J, K) USNM 336494, *Pogonias* sp., partial fifth ceratobranchial in right lateral and occlusal views, respectively. Specimens lightly coated with sublimed ammonium chloride. Scale bars equal 10 mm.

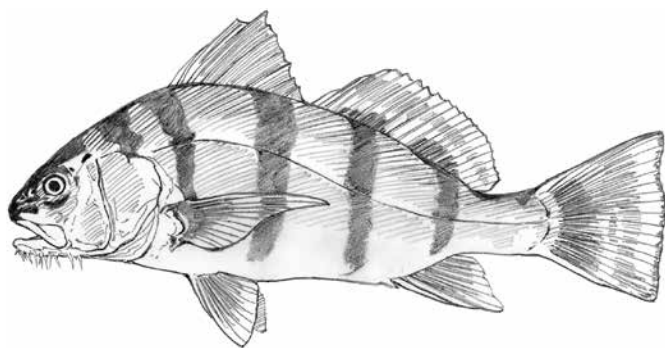
The general morphology of the bone and, in particular, the relative development and position of the spines along its posterior margin are extremely similar to those of the preopercle of the extant species of the genus *Micropogonias*, more specifically to those of the preopercle of the Atlantic croaker *Micropogonias undulatus*.

Croakers of the genus *Micropogonias* are demersal and usually occur in coastal marine or brackish waters over soft bottoms, where they feed on worms, crustaceans, and fishes.

Genus *Pogonias* Lacépède, 1801

Pogonias sp.

FIGURES 3.9B–K, 10



Black Drum – *Pogonias* sp.

REFERRED MATERIAL. CMM-V-173, isolated pharyngeal tooth; CMM-V-201, isolated pharyngeal tooth; CMM-V-272, 23 isolated pharyngeal teeth and partial maxilla; CMM-V-280, nearly complete dentary; CMM-V-328, two isolated pharyngeal teeth; CMM-V-951, partial third pharyngobranchial; CMM-V-1045, isolated pharyngeal tooth; CMM-V-1067, two isolated pharyngeal teeth; CMM-V-1093, isolated pharyngeal tooth; CMM-V-1168, isolated pharyngeal tooth; CMM-V-1375, isolated pharyngeal tooth; CMM-V-1394, isolated pharyngeal tooth; CMM-V-1778, isolated pharyngeal tooth; CMM-V-2142, isolated pharyngeal teeth; CMM-V-2258, isolated pharyngeal tooth; CMM-V-2341, four partial third pharyngobranchials (Figure 3.9H,I) and a single partial fifth ceratobranchial; CMM-V-2372, isolated pharyngeal tooth; CMM-V-2377, six isolated pharyngeal teeth; CMM-V-2584, two isolated pharyngeal teeth; CMM-V-2655, isolated pharyngeal teeth; CMM-V-2779, nine isolated pharyngeal teeth; CMM-V-2793, two isolated pharyngeal teeth; CMM-V-3071, partial third pharyngobranchial; CMM-V-3382, partial third pharyngobranchial; CMM-V-3392, third pharyngobranchial; CMM-V-3566, two complete premaxillae; CMM-V-3794, two third pharyngobranchials; CMM-V-3962, partially complete third pharyngobranchial; CMM-V-3982, premaxilla (Figure

3.9B–D); CMM-V-3999, premaxilla; CMM-V-4100, partially complete third pharyngobranchial; CMM-V-4203, four isolated pharyngeal teeth; CMM-V-4226, partially complete third pharyngobranchial; CMM-V-4254, two isolated pharyngeal teeth; CMM-V-4314, two third pharyngobranchials; CMM-V-4532, two partially complete third pharyngobranchials; CMM-V-4627, dentary (Figure 3.9E–G); USNM 13904, third pharyngobranchial; USNM 16362, partially complete fifth ceratobranchial; USNM 336494, partially complete fifth ceratobranchial (Figure 3.9J,K); USNM 542408, poorly preserved posterior portion of the neurocranium (Figure 3.10A,B); USNM 542409, poorly preserved posterior portion of the neurocranium; USNM uncataloged, extensively fragmented neurocranial remains and a single premaxilla and nine partial third pharyngobranchials.

HORIZON. Calvert, Choptank, St. Marys, and Eastover Formations.

REMARKS. The available material consists primarily of cranial and branchial bones, dominated by the massive and robust pharyngeal plates (third pharyngobranchials and fifth ceratobranchials), which, presumably because they are so robust, seem predisposed to becoming fossilized. The neurocranial remains, even if scarcely preserved, exhibit the characteristic parasphenoid with a flat semicircular facet encircled by a thin crest-like rim (Figure 3.10A,B), which is functionally associated with the upper pharyngeal jaws (e.g., Stiassny and Jensen, 1987; Sasaki, 1989).

The premaxilla bears an anteroposteriorly flattened elongate ascending process that gradually tapers dorsally and an oblong, well-developed articular process (Figure 3.9B–D). The alveolar process is relatively short, with numerous sockets of varying sizes, of which the anterior ones and those of the labial row are more developed. The dentary is relatively short and subtriangular in outline and tapers conspicuously anteriorly; the symphyseal surface is flattened and obliquely oriented; in dorsal view, the alveolar surface has an elongate teardrop shape, with many small circular alveoli (Figure 3.9E–G). A wide furrow through which the mandibular laterosensory canal passes is clearly exposed along the lateral surface of this bone (Figure 3.9F).

The upper pharyngeal jaw (third pharyngobranchial) is massive, elongate, and roughly ovoid in outline (Figure 3.9H,I); its dorsal surface is characterized by a thick ridge along the medial margin. At about the midpoint in the length of this ridge, a strong rounded process for the articulation of the second epibranchial originates and passes posterolaterally toward the center of the bone. Most of the occlusal surface is occupied by 28 to 45 thick, rounded to polygonal molariform crushing teeth of varying sizes. The lateral portion of the occlusal surface exhibits several alveoli for small conical teeth. The lower pharyngeal jaw is very large and massive and consists of the fully coalesced fifth ceratobranchials forming a single unit characterized by an interdigitating suture between the elements (Figure 3.9J,K; see Chao, 1978; Sasaki, 1989; Grubich, 2003), a unique condition of the genus *Pogonias*. The occlusal surface of the lower pharyngeal jaw bears a varying number of rounded to polygonal molariform crushing teeth.

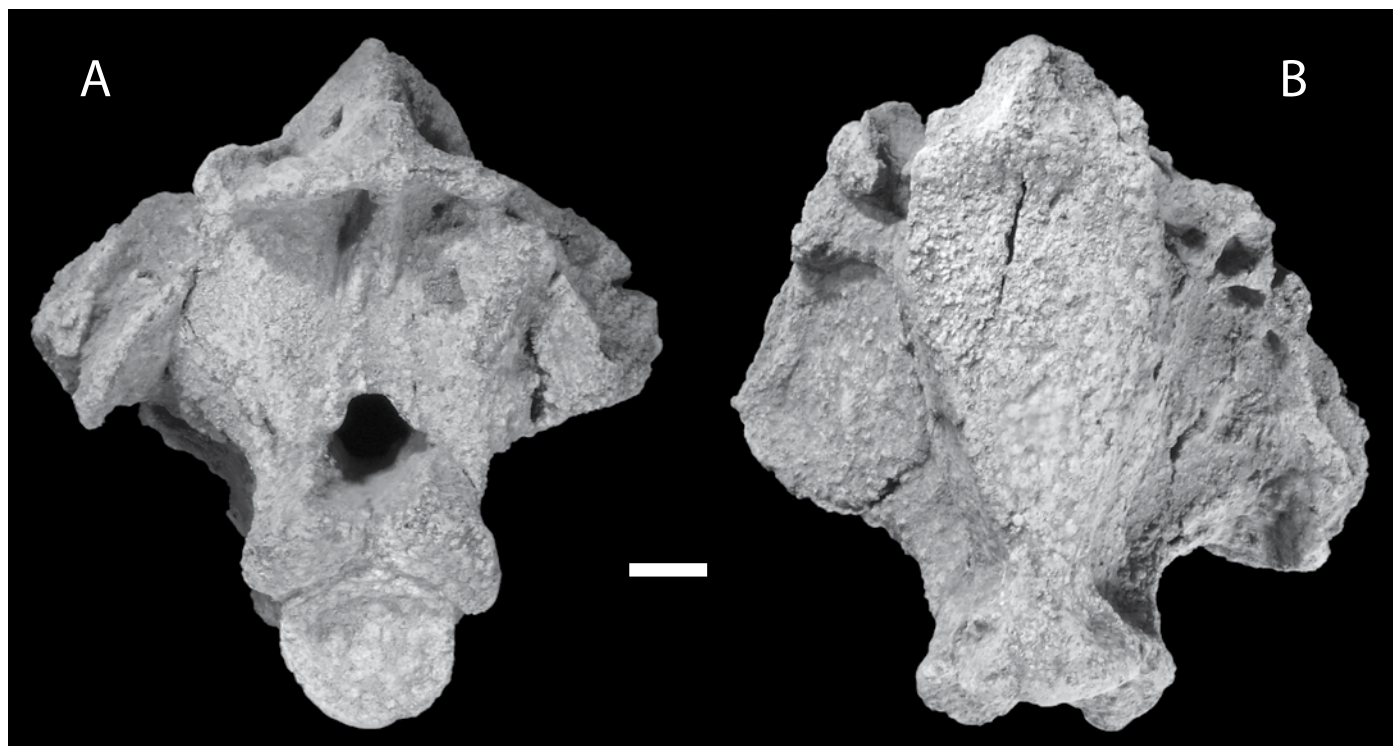


FIGURE 3.10. (A, B) USNM 542408, *Pogonias* sp., poorly preserved posterior portion of the neurocranium in posterior and ventral views, respectively. Specimen is lightly coated with sublimed ammonium chloride. Scale bar equals 10 mm.

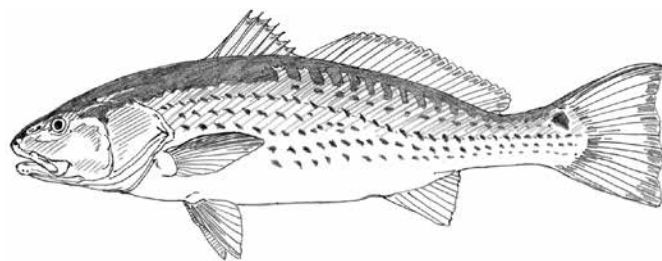
The overall morphology of the upper pharyngeal jaws is extremely similar to that of the extant black drum *Pogonias cromis*; moreover, the number of crushing teeth of each upper pharyngeal element is also within the range of this species. Cope (1869) described the fossil species *Pogonias multidentatus* on the basis of a single upper pharyngeal bone from the Calvert Formation of Westmoreland County, Virginia, characterizing it as having a higher number of molariform teeth on its occlusal surface compared to the extant black drum. Just like the specimen reported by Cope (1869; but see also Smith, 1909; Purdy et al., 2001), some of the upper pharyngeal jaws available to us have 45 molariform teeth, which is more than in the extant species. A cursory comparative analysis of the extant *Pogonias* pharyngeal apparatus reveals broad variability in the number of molariform teeth (22–43) in the occlusal surface of the upper pharyngeal jaws of the black drum, thereby suggesting that the number of molariform teeth in the upper pharyngeal jaw does not represent a valid diagnostic character for the discrimination of the species within the genus *Pogonias*. As a consequence, *Pogonias multidentatus* should be regarded as a nomen dubium.

Black drums occur in brackish and shallow water and are very common over muddy and sandy bottoms, especially in areas with large river runoffs. They feed mostly on mollusks, crustaceans, and fishes.

Genus *Sciaenops* Gill, 1863

Sciaenops sp.

FIGURES 3.11–13



Red Drum – *Sciaenops* sp.

REFERRED MATERIAL. CMM-V-132, opercle (Figure 3.12G); CMM-V-139, opercle and a single vertebral centrum and several pleural ribs; CMM-V-144, opercle; CMM-V-157, premaxilla; CMM-V-166, premaxilla (Figure 3.11A–C); CMM-V-162, two dentaries; CMM-V-167, premaxilla; CMM-V-271, first abdominal vertebra; CMM-V-276, premaxilla; CMM-V-319, 13 vertebrae belonging to a single individual (Figure

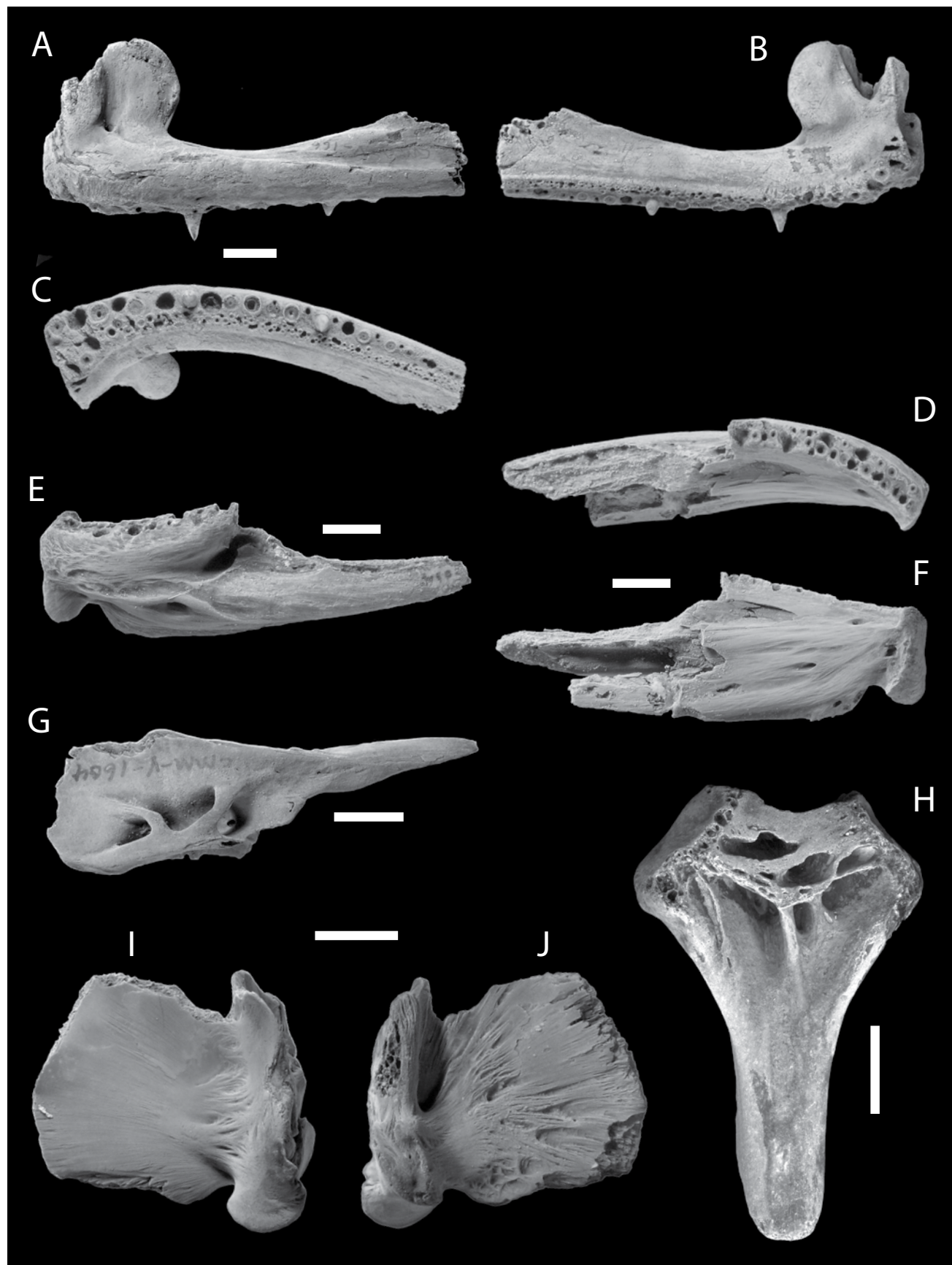


FIGURE 3.11. (Facing page) (A–C) CMM-V-166, *Sciaenops* sp., left premaxilla in lateral, medial, and occlusal views, respectively. (D–F) CMM-V-977, *Sciaenops* sp., left dentary in occlusal, lateral, and medial views, respectively. (G) CMM-V-1604, *Sciaenops* sp., posttemporal in lateral view. (H) CMM-V-3234, *Sciaenops* sp., vomer in ventral view. (I, J) CMM-V-3205, *Sciaenops* sp., right quadrate in lateral and medial views, respectively. Specimens lightly coated with sublimed ammonium chloride. Scale bars equal 10 mm.

3.13A–F); CMM-V-836, premaxilla; CMM-V-896, maxilla; CMM-V-954, lachrymal and opercle; CMM-V-977, dentary (Figure 3.11D–F); CMM-V-1259, premaxilla; CMM-V-1436, articular (Figure 3.12A,B); CMM-V-1600, premaxilla; CMM-V-1604, posttemporal (Figure 3.11G); CMM-V-1721, isolated scale; CMM-V-1781, isolated scale; CMM-V-1868, vomer; CMM-V-1912, premaxilla; CMM-V-2134, premaxilla; CMM-V-2185, premaxilla; CMM-V-2340, premaxilla; CMM-V-2341, three third pharyngobranchials; CMM-V-2356, partial anguloarticular with associated retroarticular (Figure 3.12C,D); CMM-V-2357, dentary; CMM-V-2423, premaxilla; CMM-V-2457, premaxilla; CMM-V-2503, third pharyngobranchial; CMM-V-2786, premaxilla; CMM-V-2954, four premaxillae and two dentaries; CMM-V-2964, first abdominal vertebra; CMM-V-3026, maxilla; CMM-V-3038, opercle; CMM-V-3074, isolated scale; CMM-V-3116, preopercle (Figure 3.12F); CMM-V-3205, quadrate (Figure 3.11 I,J); CMM-V-3234, vomer (Figure 3.11H); CMM-V-3242, palatine; CMM-V-3243, isolated scales; CMM-V-3254, dentary; CMM-V-3395, maxilla; CMM-V-3398, single scale; CMM-V-3460, premaxilla; CMM-V-3462, several scales; CMM-V-3476, palatine; CMM-V-3517, vertebral centrum; CMM-V-3566, three premaxillae and six maxillae, five dentaries, and a single hyomandibula (Figure 3.12E); CMM-V-3567, several vertebral centra; CMM-V-3719, isolated scales and lepidotrichia (Figure 3.13G); CMM-V-3725, two maxillae and four dorsal spines; CMM-V-3735, premaxilla; CMM-V-3798, eight premaxillae and a single dentary; CMM-V-3928, premaxilla; CMM-V-3954, premaxilla; CMM-V-3969, two premaxillae; CMM-V-3974, vomer; CMM-V-4039, opercle; CMM-V-4098, partially complete preopercle; CMM-V-4119, nine opercles and several dorsal-fin spines; CMM-V-4135, opercle; CMM-V-4169, third pharyngobranchial; CMM-V-4249, four opercles; CMM-V-4280, opercle; CMM-V-4294, third pharyngobranchial; CMM-V-4311, 10 premaxillae and two maxillae, a single quadrate, and several isolated vertebrae and dorsal-fin spines; CMM-V-4313, third pharyngobranchial; CMM-V-4493, nearly complete hyoid bar (Figure 3.12I); CMM-V-4529, two maxillae; CMM-V-4554, three opercles and three hypobranchials; CMM-V-4626, third pharyngobranchial (Figure 3.12H); CMM-V-4628, two partial opercles and a single hyoid bar; USNM 387748, premaxilla; USNM uncataloged, four premaxillae, four dentaries, a single anguloarticular with an articulated retroarticular, and a single opercle.

HORIZON. Calvert, Choptank, St. Marys, and Eastover Formations.

REMARKS. The material referred to the genus *Sciaenops* consists mostly of isolated cranial bones collected throughout the Chesapeake Group.

The vomer is diamond shaped and toothless, with a cavernous ventral surface characterized by thick irregular struts (Figure 3.11H); the vomerine lateral process has broad and flat to slightly convex facets.

The posttemporal is laminar and approximately triangular in outline (Figure 3.11G). It possesses an elongate and dorsoventrally flattened dorsal arm that tapers anteriorly into a blunt spine; the posterior portion of the bone consists of a laterally compressed and flat bony lamina marked by a trough for the laterosensory canal. The infraorbital branch of the laterosensory canal occupies most of the ventral portion of this bone, with two external large fenestrae separated from each other by a large laminar strut.

The premaxilla has a large and anteroposteriorly flattened ascending process nearly perpendicular to the alveolar process and an articular process with a thickened and gently rounded posterior margin and relatively low postmaxillary process (Figure 3.11A–C). The alveolar process is elongate, with an outer row of large conical teeth that increase in size toward the symphysis and a dense inner band of villiform teeth that also increase in size anteriorly, reaching remarkable size in the lingual row (Figure 3.11C). The proximal portion of the maxilla is characterized by a large articular head with slightly concave anterior facets of irregular shapes; the articular head is continuous posteriorly with a laterally compressed shank from which it is separated through a marked notch for the articulation of the palatine. All available dentaries are incomplete; the alveolar surface is occupied by a dense series of closely spaced sockets for strongly pointed teeth (Figure 3.11D–F). The thick symphyseal margin is nearly vertical, and there is a deep notch along the anteroventral margin. A relatively deep furrow that held the mandibular laterosensory canal is clearly visible along the lateral surface of the dentary. The anguloarticular is massive, with a large articular condyle for the quadrate (Figure 3.12C,D); along the lateral surface of the anguloarticular there is a deep trough for the mandibular laterosensory canal, which is partially arched by a relatively narrow, flat laminar strut. The thick retroarticular caps the posteroventral corner of the mandible.

The quadrate is flat and rectangularly shaped, with a nearly vertical anterior edge, an extremely large and thickened transverse articular head, and a large medial recess to accommodate the symplectic (Figure 3.11 I,J). The transverse development of

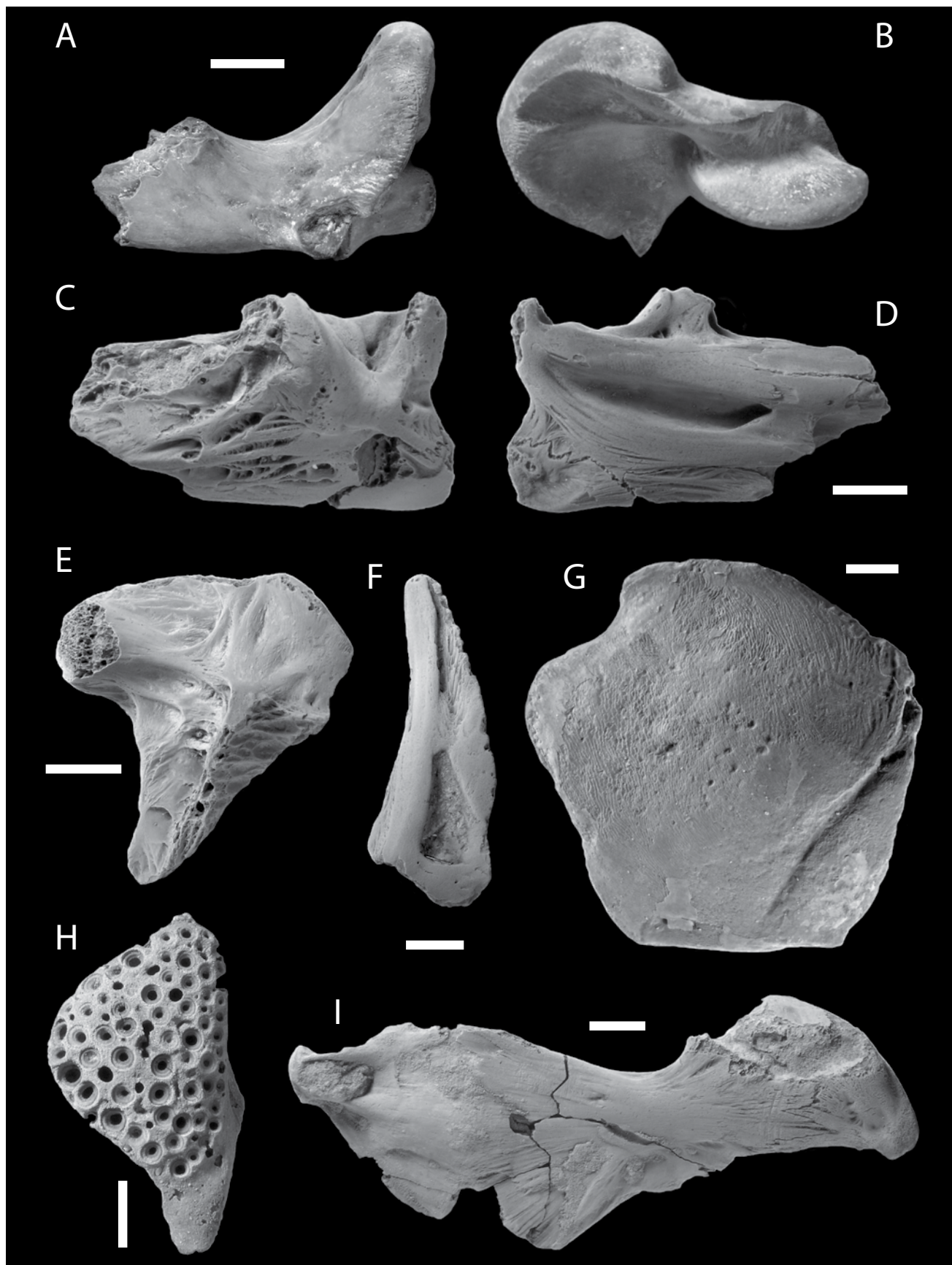


FIGURE 3.12. (Facing page) (A, B) CMM-V-1436, *Sciaenops* sp., anguloarticular. (C, D) CMM-V-2356, *Sciaenops* sp., left partial anguloarticular with associated retroarticular in medial and lateral views, respectively. (E) CMM-V-3566, *Sciaenops* sp., hyomandibula in lateral view. (F) CMM-V-3116, *Sciaenops* sp., preopercle in lateral view. (G) CMM-V-132, *Sciaenops* sp., opercle in lateral view. (H) CMM-V-4626, *Sciaenops* sp., third pharyngobranchial in occlusal view. (I) CMM-V-4493, *Sciaenops* sp., nearly complete hyoid bar. Specimens lightly coated with sublimed ammonium chloride. Scale bars equal 10 mm.

the articular head extends to the whole posterior of the bone. The palatine is a toothless bone with a robust thickened anterior ethmoid process. Both the rostopalatine (anterior) and ethmopalatine (posterior) facets for the connection with the lateral ethmoid are well developed. Only a partial left hyomandibula is available for comparative analysis (Figure 3.12E); it bears an anterior articular head and an anterodorsal lens-shaped condyle for articulation with the prootic and sphenotic. A well-developed lateral crest can be observed along the main shaft of the bone; both lateral and medial surfaces are ornamented by a complex cavernous system of irregular ridges, furrows, and pits.

The preopercle is crescent-shaped (Figure 3.12F), with a strongly thickened anterior margin and a finely serrated posterior margin; the configuration of the canal for the laterosensory system is clarified by five external fenestrae separated from each other by relatively large laminar horizontal struts that overlie the canal itself. The opercle is large, massive, and apparently quadrangular in shape (Figure 3.12G), with a convex dorsal margin and a finely sculptured outer surface characterized by delicate and irregular elongate ridges. Its anterior margin is conspicuously thickened, but it terminates at the anterodorsal corner of the bone with a rounded articular facet for the opercular process of the hyomandibula. A shallow furrow that passes vertically parallel to the anterior thickening of the bone represents the trough for the opercular branch of the facial nerve. Additionally, a strong ridge originates from the anterodorsal corner and terminates posteriorly as a blunt spine with a rounded profile; another spine is located ventral to the major one, separated from it by a shallow concavity.

The hyoid bar is relatively large and robust (Figure 3.12I). The dorsal hypohyal is extremely thick and irregular in shape, with a slightly concave recess for the basibranchial articulation along its medial surface. The ventral hypohyal is conical, with a robust anteroventral process. The anterior ceratohyal is the largest bone of the hyoid bar; it is laterally compressed and hourglass shaped, with a low laminar median process emerging along its ventral margin. The posterior ceratohyal is triangular and laterally compressed.

The upper pharyngeal plate (third pharyngobranchial) appears to be approximately quadrangular in outline. The occlusal surface is flattened to gently convex and completely covered with large and thick conical teeth, in many cases represented by their sockets. The third hypobranchial is short and clavate, with a flattened dorsal surface.

The atlas (first abdominal vertebra) has a very short disk-shaped centrum with an autogenous neural spine, two large anterodorsal condylar surfaces, and posteriorly directed lateral apophyses (Figure 3.13A,B). The second abdominal vertebra is short and disk-shaped, with well-developed dorsal prezygapophyses, posteriorly directed lateral apophyses, and a deep fossa for epineural insertion on the laterodorsal surface of the centrum at the base of the neural arch (Figure 3.13C,D). The third vertebra has a short centrum with well-developed dorsal prezygapophyses, reduced lateral apophyses, and dorsolaterally large fossa for the insertion of pleural ribs (Figure 3.13E). The other abdominal vertebrae are subrectangular (longer than high), with short postzygapophyses, parapophyses, and deep and large lateral fossae (Figure 3.13F; mesonephros pits sensu Topp and Cole, 1968). Some abdominal centra possess a thin osseous bridge across the contralateral parapophyses. The caudal vertebrae are rectangular, longer than high, and morphologically uniform, with two deeply ornamented lateral fossae separated from each other by a strengthening ridge.

The scales are large, feebly ctenoid, and subrectangular to ovoid, with a gently rounded posterior margin (Figure 3.13G).

The classification of the taxa of the family Sciaenidae is based primarily on characters that are not observable (otolith, swim bladder, etc.) in the preserved fossils (e.g., Chao, 1978). However, a comparative osteological analysis of the fossils documented herein has revealed a close similarity to the extant red drum *Sciaenops ocellata*. In particular, the dentition pattern and the morphology of the premaxilla, articular head of the maxilla, opercle, and third pharyngobranchial are clearly diagnostic of the genus *Sciaenops* (Sasaki, 1989; Grubich, 2003). The fossil material cannot be confidently accommodated within the variability of *Sciaenops ocellata* because there are some remarkable differences that might support a separate specific status, including the extremely variable size of the dentary teeth of the inner band, most notably the enlarged ones in the symphyseal area, the presence of an osseous bridge across the parapophyses of the posterior abdominal vertebrae, and the disk-shaped morphology and reduced size of the two anteriormost vertebral centra.

The red drum is demersal and typically is found in coastal marine and brackish waters from Massachusetts to northern Mexico. It feeds primarily on mollusks, crustaceans, and fishes.

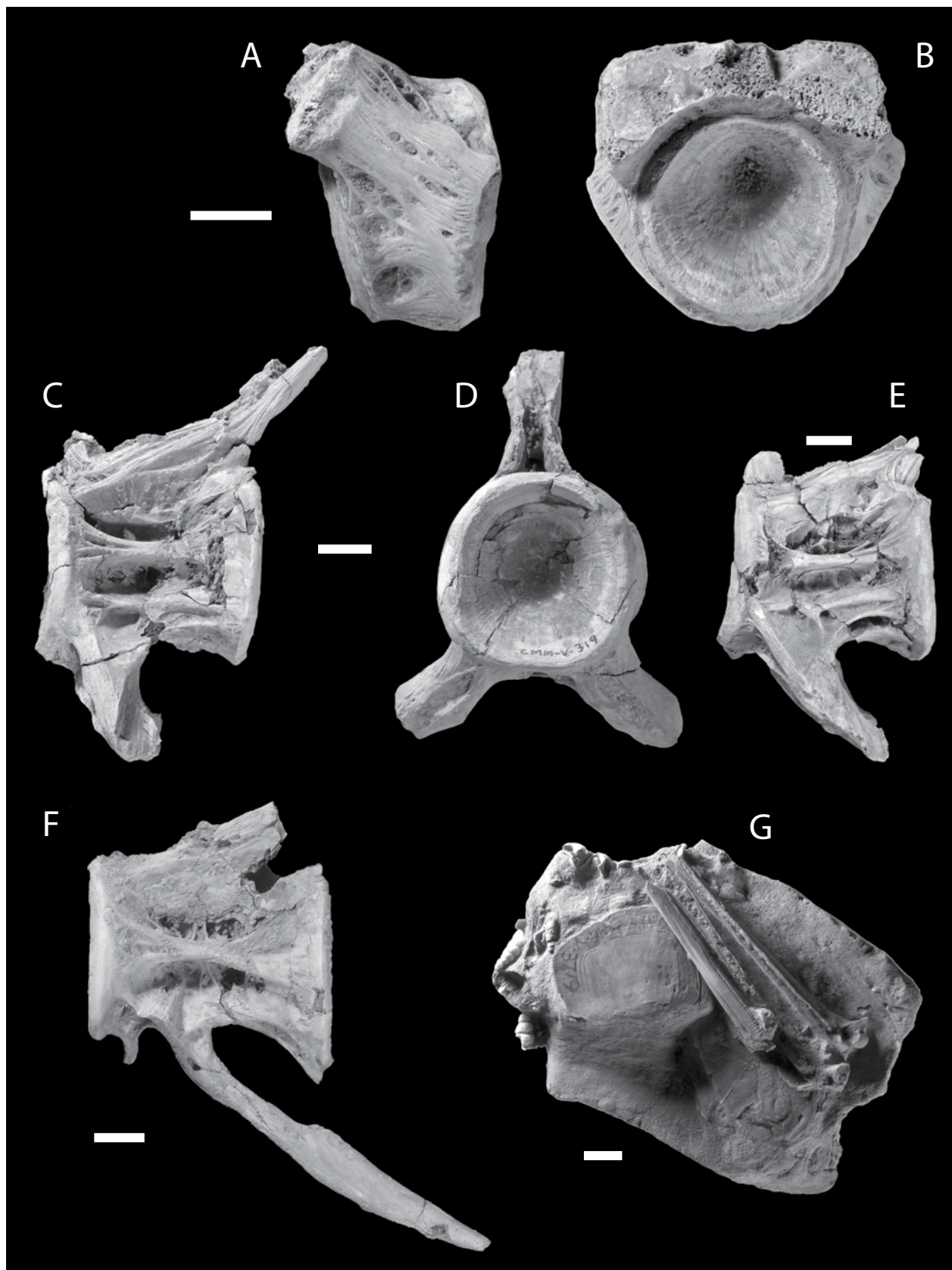


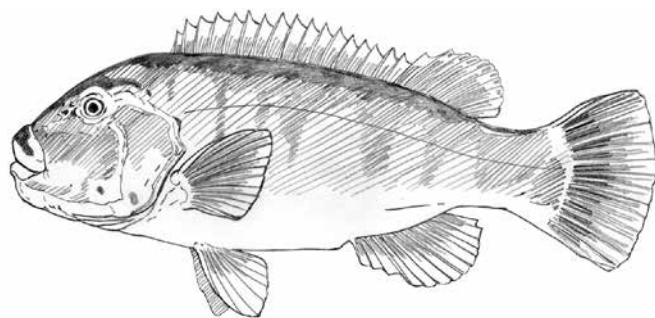
FIGURE 3.13. (Facing page) (A, B) CMM-V-319, *Sciaenops* sp., atlas vertebra in left lateral and anterior views, respectively. (C, D) CMM-V-319, *Sciaenops* sp., second abdominal vertebra in left lateral and anterior views, respectively. (E) CMM-V-319, *Sciaenops* sp., third vertebra in left lateral view. (F) CMM-V-319, *Sciaenops* sp., posterior abdominal vertebra in left lateral view. (G) CMM-V-3719, *Sciaenops* sp., isolated scales and lepidotrichia. Specimens lightly coated with sublimed ammonium chloride. Scale bars equal 10 mm.

FAMILY LABRIDAE CUVIER, 1817

Genus *Tautoga* Mitchill, 1814

Tautoga sp.

FIGURE 3.14A



Tautog – *Tautoga* sp.

1873 *Protautoga conidens* Leidy – (Leidy, 1873c)

1902 *Tautoga conidens* (Leidy, 1873c) – Hay, p. 401.

REFERRED MATERIAL. CMM-V-327, partially complete right premaxilla; CMM-V-4138, left upper third pharyngobranchial; CMM-V-4160, premaxillary tooth; CMM-V-4395, partially complete right premaxilla and three isolated teeth; CMM-V-4632, partially complete left premaxilla (Figure 3.14A); USNM uncataloged, fragmentary pharyngeal jaw.

HORIZON. Calvert, St. Marys, and Eastover Formations.

REMARKS. The available premaxillae are incomplete, lacking the ascending (and fused articular) process (Figure 3.14A). The anteriormost tooth of each premaxilla is the largest and is characterized by an elongate pedicel that sustains a massive thick crown of variable morphology, from blunt and rounded to incisiform and paddle shaped to approximately pointed. The teeth are arranged in two rows, the outer characterized by widely separated large elements, whereas the inner consists of small incompletely erupted elements. The upper pharyngeal jaws (third pharyngobranchials) are subtriangular in shape, with teeth characterized by blunt rounded crowns of varying sizes.

The morphology of the premaxillae, pharyngeal jaws, and teeth are very similar to those of the extant tautog *Tautoga onitis*. The fossils are therefore referred to the genus *Tautoga*; however, because of the fragmentary nature of the available material, it is not possible to extend the taxonomic identification to the species level. According to Purdy et al. (2001), the fossil species *Protautoga conidens* established by Leidy (1873a) on the basis of an incomplete premaxilla from the Miocene of Virginia (see also Leriche, 1942) must be considered a junior synonym of *Tautoga onitis*.

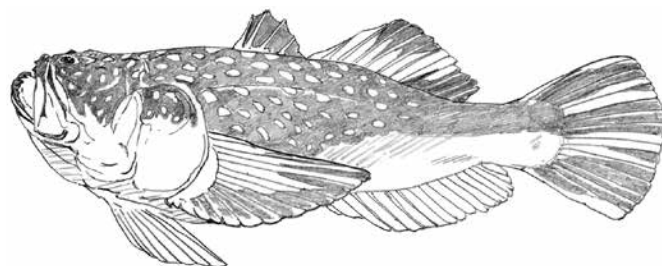
The tautog is a western north Atlantic demersal species typical of hard-bottom habitats at depths up to 75 m. It occasionally enters brackish waters. The tautog diet consists primarily of worms, mollusks, and crustaceans.

FAMILY URANOSCOPIDAE BLEEKER, 1859

Genus *Astroscopus* Brevoort in Gill, 1860

Astroscopus countermani Carnevale, Godfrey, & Pietsch, 2011

FIGURE 3.14B–E



Stargazer – *Astroscopus countermani*

TYPE MATERIAL. CMM-V-4231 (Figure 3.14B–E), holotype, nearly complete neurocranium and a nearly complete right hyomandibula; CMM-V-2022, paratype, partially complete neurocranium.

HORIZON. St. Marys Formation.

REMARKS. The available material was described in detail and illustrated by Carnevale et al. (2011). According to these

authors, the fossils exhibit a number of features that strongly support their placement as a new species of the stargazer genus *Astroscopus*. The neurocranium is short, broad, and dorsoventrally depressed, with a rugose or strongly sculptured outer surface (Figure 3.14B–E). The postorbital portion of the neurocranium is longer than the orbital portion and is laterally expanded, with the distance between the lateral tips of the lateral ethmoids representing less than 60% of the measurement taken between the outermost margins of the sphenotics. The neurocranial length represents more than 90% of its width. The interorbital anterolateral processes of the frontals are broad, not constricted at their bases, with the width of the interorbital region representing 27% of the neurocranial width. The posterior region of the frontal has a large anterolateral expansion that results in the nearly complete exclusion of the sphenotic from the cranial roof. The large parietals are rectangular. The anterolateral corner of the sphenotic is prominent and forms a short posterolateral border of the orbit. The hyomandibula is characterized by having a prominent tuberosity arising from its dorsolateral surface, large and elongate articular heads, and a well-developed anteriorly directed spur.

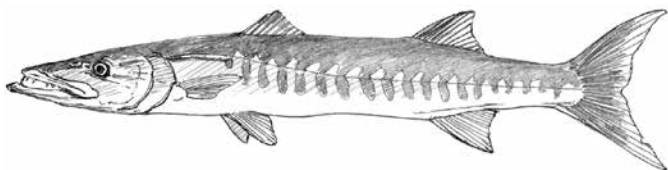
Carnevale et al. (2011) hypothesized that *Astroscopus countermani* was a predatory fish that inhabited the subtropical and warm temperate Atlantic coasts of North America during the Miocene, living in shallow marine and paralic waters nearly totally buried in muddy or sandy substrates.

FAMILY SPHYRAENIDAE RAFINESQUE, 1815

Genus *Sphyraena* Klein, 1778

Sphyraena sp.

FIGURE 3.14F



Barracuda – *Sphyraena* sp.

REFERRED MATERIAL. CMM-V-1063, CMM-V-1098, CMM-V-2376, CMM-V-2776, CMM-V-3198, CMM-V-3335, CMM-V-3580, isolated tooth (Figure 3.14F); USNM uncataloged, 21 isolated teeth.

HORIZON. Calvert, St. Marys, and Eastover Formations.

REMARKS. The presence of barracudas in the Miocene deposits of the Chesapeake Group is evidenced exclusively by isolated teeth (Figure 3.14F). The teeth are lanceolate,

labiolingually compressed, in some cases with a slightly sigmoid cutting edge, and ornamented with short and discontinuous vertical striae. Premaxillary teeth appear to be characterized by a postapical barb (Nishimoto and Ohe, 1982), as seen in Figure 3.14F.

Sphyraenid teeth do not show diagnostic characters to differentiate one species from another. Leidy (1873a) described a sphyraenid, *Sphyraena speciosa* on the basis of isolated teeth from the Calvert Formation, Virginia; this species was also reported from the Miocene of Maryland by Cope (1867). On the basis of his description, it is not possible to detect any diagnostic feature to distinguish such a species from other sphyraenids, thereby suggesting that *S. speciosa* should be considered a nomen dubium.

Barracudas occupy a wide range of marine and brackish habitats, where they live predominantly near the surface. They are voracious predators that feed primarily on fishes and cephalopods and occasionally on crustaceans.

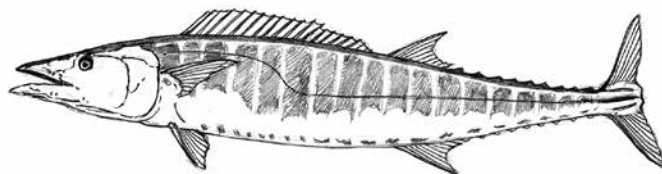
FAMILY SCOMBRIDAE RAFINESQUE, 1815

REMARKS. Kimmel and Purdy (1984) illustrated some scombrid bones that they referred to an indeterminate species of the genus *Katsuwonus*. A morphological analysis of that material has not revealed any diagnostic character of *Katsuwonus*, and it is therefore interpreted as belonging to an indeterminate scombrid taxon. Indeterminate scombrid remains from the Calvert Formation were previously reported by Leriche (1942).

Genus *Acanthocybium* Gill, 1862

Acanthocybium cf. *solandri* (Cuvier, 1832 in Cuvier & Valenciennes, 1831)

FIGURE 3.15



Wahoo – *Acanthocybium* cf. *solandri*

REFERRED MATERIAL. CMM-V-137, hypural complex; CMM-V-158, dentary fragment; CMM-V-159, partial right dentary; CMM-V-160, left premaxilla (Figure 3.15A,B); CMM-V-284, partially complete left dentary; CMM-V-322, dentary fragment; CMM-V-357, premaxillary fragment; CMM-V-1598, partially complete right dentary; CMM-V-1812, partially complete right dentary (Figure 3.15C,D); CMM-V-2010, dentary fragment; CMM-V-2332, partially complete left dentary

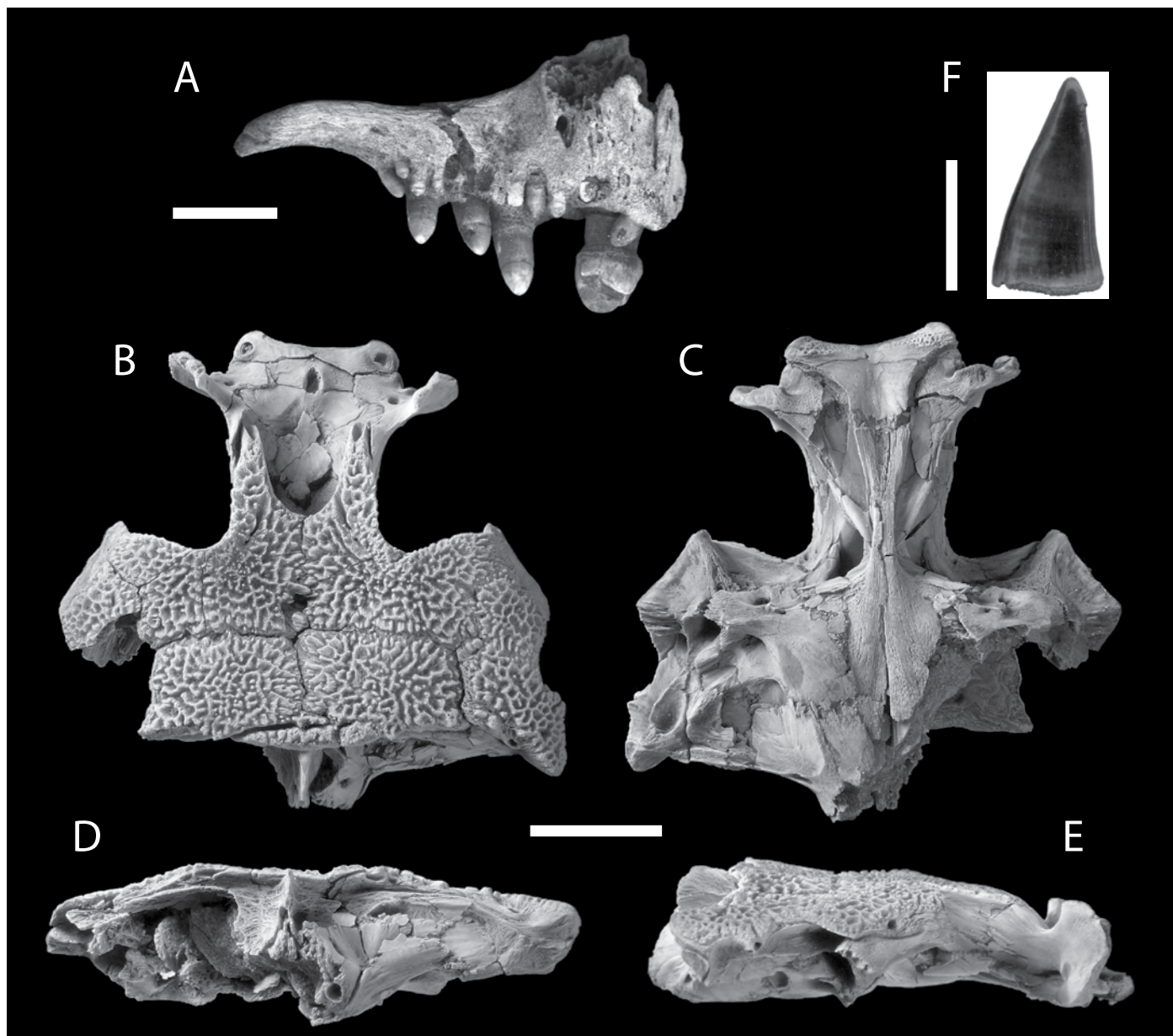


FIGURE 3.14. (A) CMM-V-4632, *Tautoga* sp., partial left premaxilla in medial view. (B–E) CMM-V-4231, *Astroscopus countermani*, holotype, nearly complete neurocranium in dorsal, ventral, posterior, and right lateral views, respectively. (F) CMM-V-3580, *Sphyraena* sp., isolated tooth. Specimens lightly coated with sublimed ammonium chloride. Scale bars equal 10 mm.

(Figure 3.15E,F); CMM-V-2629, partially complete right dentary; CMM-V-3710, dentary fragment; CMM-V-4426, dentary fragment; CMM-V-4432, complete hypural complex (Figure 3.15G); USNM 559394, dentary fragment; USNM 20108, complete right premaxilla; USNM 20109, partially complete left dentary; USNM 135183, premaxillary fragment; USNM 135184, dentary fragment; USNM 135186, dentary fragment; USNM

204217, partially complete left dentary; USNM 214428, partially complete right dentary; USNM 265236, dentary fragment; USNM uncataloged, partially complete left premaxilla, right premaxilla, left dentary, and dentary fragment.

HORIZON. Calvert and Choptank Formations.

REMARKS. The premaxilla is long, curved, and anteriorly pointed (Figure 3.15A,B). The ascending process is long and very

robust. The anterior and ventral margins form an angle of about 37°. The alveolar process bears a single row of large, tightly packed, and labiolingually compressed subtriangular teeth. The dentary is thick, massive, and laterally compressed, with a nearly straight anteroventral margin, a prominent notch along the anterior margin (see Collette and Russo, 1984), and a dense series of large, closely spaced, and labiolingually compressed subtriangular teeth (Figure 3.15C,F).

The hypural complex is rhomboid in outline, with a median notch along its posterior margin (Figure 3.15G). The complex is characterized by the complete fusion of the parhypural and bears a well-developed laterally emerging parhypurapophysis. A deep fossa is usually developed just behind the fused hemicentrum.

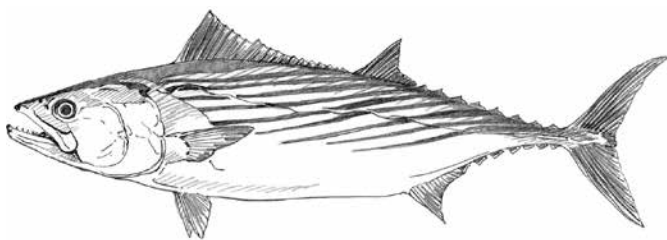
The fossils from the Calvert and Choptank Formations are tentatively referred (see Conrad, 1938; Collette and Russo, 1984) to *Acanthocybium solandri* because of the following characteristics unique to the wahoo. The premaxilla has an arrow-shaped outline, with a relatively low angle between its anterior and ventral margins. The morphology of the dentary is characterized by a prominent notch along its anterior margin. Finally, the structure of the hypural complex has a median posterior indentation, the complete fusion of the parhypural, and the presence of a deep fossa behind the fused hemicentrum.

The wahoo is an oceanic epipelagic piscivorous species distributed worldwide in tropical to warm temperate waters.

Genus *Sarda* Cuvier, 1829

Sarda sp.

FIGURE 3.16A,B



Bonito – *Sarda* sp.

REFERRED MATERIAL. USNM 559305, nearly complete left premaxilla (Figure 3.16A,B).

HORIZON. Calvert Formation.

REMARKS. The premaxilla is moderately curved, with a stout arrow-shaped anterior portion and a single row of well-developed conical teeth. The angle between the anterior and ventral margins measures 50°. The ascending process has a sharp anterodorsal end. The general outline of the bone, more specifically the anterodorsal end of the ascending process, is clearly diagnostic of the genus *Sarda* (see Collette and Chao, 1975).

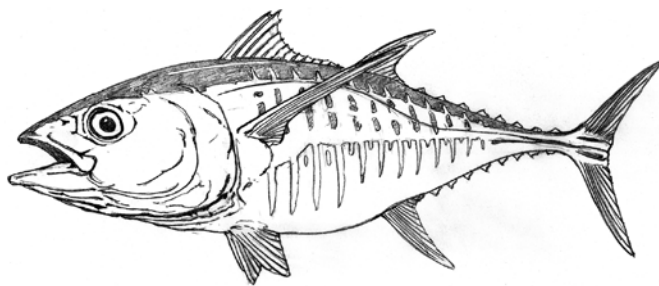
This premaxilla does not present sufficient anatomical information to differentiate or ally it with any extant species within the genus *Sarda*.

Bonitos of the genus *Sarda* are coastal epipelagic fishes that often enter estuaries. They prey on cephalopods and a variety of other fishes.

Genus *Thunnus* South, 1845

Thunnus sp.

FIGURE 3.16C–H



Tuna – *Thunnus* sp.

REFERRED MATERIAL. CMM-V-137, hypural (Figure 3.16F); CMM-V-161, partially complete right dentary (Figure 3.16C,D); CMM-V-932, nearly complete abdominal vertebra; CMM-V-947, partially complete caudal peduncle vertebra; CMM-V-950, partially complete caudal peduncle vertebra; CMM-V-964, three associated nearly complete caudal peduncle vertebrae (Figure 3.16G,H); CMM-V-1363, partially complete articulated vertebral column associated with jaw bones of *Lophius* sp.; CMM-V-1640, partially complete right dentary; CMM-V-2052, numerous partially complete caudal and caudal peduncle vertebrae; CMM-V-4178, nearly complete caudal peduncle vertebra; CMM-V-4388, four partially complete caudal vertebrae and a single nearly complete caudal peduncle vertebra (Figure 3.16E); USNM 24899, extensively fragmented skull bones (premaxillae, dentaries, fragments of opercular bones) and partially complete articulated vertebral column (31 vertebrae); USNM 387790, partially complete abdominal vertebra; USNM, uncataloged specimen consisting of four partially complete isolated caudal vertebrae.

HORIZON. Calvert and Choptank Formations.

REMARKS. The premaxilla is stout and curved, with a single row of small, widely spaced conical teeth. The dentary is rather thick and characterized medially by a strong crest with a rounded profile that originates from the symphyseal region

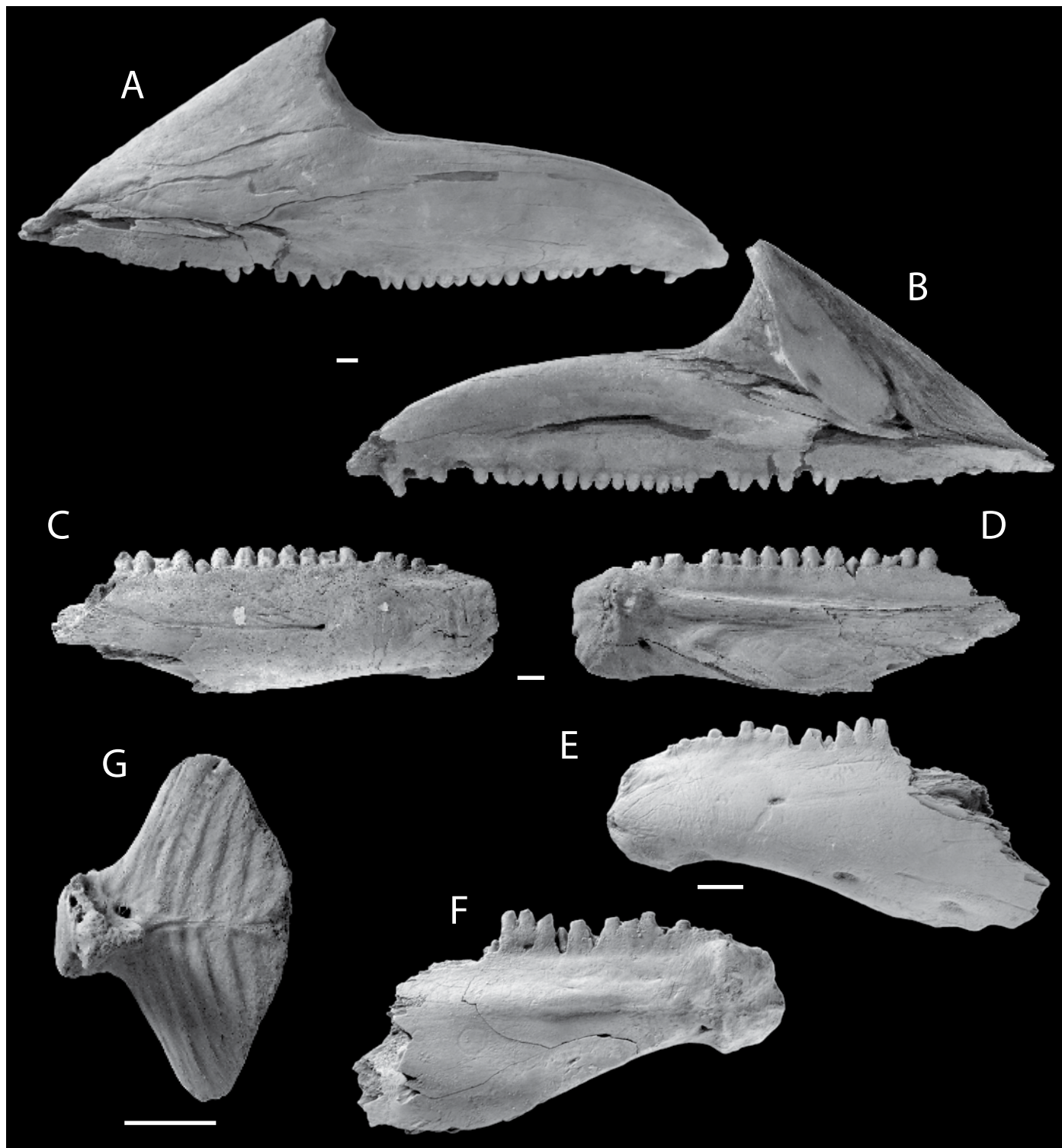


FIGURE 3.15. (A, B) CMM-V-160, *Acanthocybium* cf. *solandri*, left premaxilla in lateral and medial views, respectively. (C, D) CMM-V-1812, *Acanthocybium* cf. *solandri*, partial right dentary in lateral and medial views, respectively. (E, F) CMM-V-2332, *Acanthocybium* cf. *solandri*, partial left dentary in lateral and medial views, respectively. (G) CMM-V-4432, *Acanthocybium* cf. *solandri*, hypural in left lateral view. Specimens lightly coated with sublimed ammonium chloride. Scale bars equal 10 mm.

(Figure 3.16C,D). The anterior margin of this bone is subvertical, with a shallow concave notch developed labially in the middle of its length. Another well-developed notch is located anteroventrally just behind the symphysis. Small and widely spaced conical teeth arranged in a single row occupy the dorsal margin of the dentary. The opercle and subopercle are approximately polygonal in outline.

The abdominal centra are approximately square (Figure 3.16E), whereas the caudal centra are subrectangular and longer than high (Figure 3.16G,H). The centra are characterized by two deep fossae separated by a strong median ridge along the lateral sides, and an approximately triangular articular surface for ligament attachment is located anteriorly on the median strengthening ridge. The vertebrae of the caudal peduncle are remarkably compressed dorsoventrally and possess a thin, broad keel arising laterally from the median ridge on both sides and flattened, stout neural and haemal spines.

The hypural is rhomboid in outline, with a deep fossa developed just behind the fused hemicentrum and immediately above the small hypurapophyses (Figure 3.16F).

The premaxillae, dentaries, and vertebrae have several morphological features that are clearly diagnostic of the genus *Thunnus* (De Sylva, 1955; Gibbs and Collette, 1967; Collette and Chao, 1975). In particular, the outline of the dentaries, the tooth size and arrangement, and the vertebrae with deep fossae separated by a median horizontal strengthening ridge with an anterior articular surface for the insertion of the epineurals, strongly support this generic attribution. Unfortunately, classification at the specific level is not possible because of the fragmentary nature of the available material. Moreover, as reported by Gibbs and Collette (1967), morphological variability is so great in some skeletal elements of the genus *Thunnus* that it is not possible to distinguish between extant species on the basis of these highly variable bones. Some skeletal characters are useful for the positive identification of species, but these are not preserved in the material available to us.

Tunas are oceanic and migrate seasonally close to shore, often entering brackish-water habitats. Usual prey includes schooling fishes, but they also feed on crustaceans and cephalopods.

FAMILY ISTIOPHORIDAE LÜTKEN, 1875

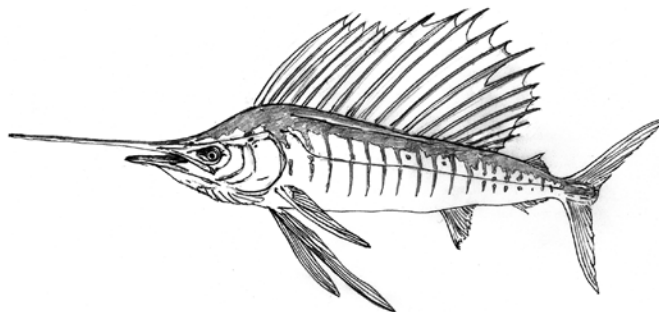
REMARKS. Billfish remains are usually found in the Miocene deposits of the Chesapeake Group as isolated fragmented bones (Berry, 1917; Kimmel and Purdy, 1984). The identification of billfish remains to genus or species is extremely problematic, the results of which are usually broadly subjective. In an attempt to reduce ambiguity in the taxonomic analysis of isolated billfish remains, Fierstine and Voigt (1996) and Fierstine (1998, 2001) examined the range of variation in extant skeletal elements and developed a morphometric technique of identification that could be applied to disarticulated bones, whether fossil or extant. This method has been used to analyze billfish remains from the

Miocene deposits of the Chesapeake Group of Maryland and Virginia, leading to the recognition of at least two taxa, *Istiophorus* cf. *platypterus* and *Makaira* cf. *nigricans*. According to the method elaborated by Fierstine (1998, 2001), an identification can be made by converting measurements of individual fossil bones into ratios and comparing them to those obtained for extant billfishes (see Carnevale et al., 2002). Some of the fossil ratios are outside the ranges observed for extant material; for this reason, specimens identified at the species level are only tentatively assigned to an extant taxon. In many cases the preservation of the material is inadequate to allow for the morphometric survey and, as a consequence, for a reasonable taxonomic interpretation.

Genus *Istiophorus* Lacépède, 1801

Istiophorus cf. *platypterus* (Shaw & Nodder, 1792)

FIGURE 3.17A–D



Sailfish – *Istiophorus* cf. *platypterus*

- 1917 *Istiophorus calvertensis* Berry, pp. 461–463, figs. 1–2.
- 1984 *Istiophorus calvertensis* (Berry) – Kimmel and Purdy, p. 208, pl. 1, fig. 7.
- 1987 *Pseudobistiophorus calvertensis* (Berry) – Schultz, p. 171.
- 1998 *Istiophorus* cf. *platypterus* (Shaw & Nodder, 1792) – Fierstine, pp. 40–41, figs. 8B, 9.
- 2001 *Istiophorus* cf. *platypterus* (Shaw & Nodder, 1792) – Fierstine, pp. 36–37.

REFERRED MATERIAL. CMM-V-270, complete atlas (first abdominal vertebra), (Figure 3.17B,C); CMM-V-1766, articulated partially complete dentaries; USNM 9344, partially complete rostrum (Figure 3.17A); USNM 186813, partially complete rostrum; USNM 542404, hypural complex (Figure 3.17D).

HORIZON. Calvert, Choptank, and Eastover Formations.

REMARKS. The material consists of two partially preserved rostra (Figure 3.17A), a single isolated first abdominal vertebra (Figure 3.17B,C), and a complete hypural complex (Figure 3.17D). One of the rostra, USNM 9344, constitutes the holotype specimen of *Istiophorus calvertensis* described by Berry (1917) from the deposits of the Eastover Formation cropping

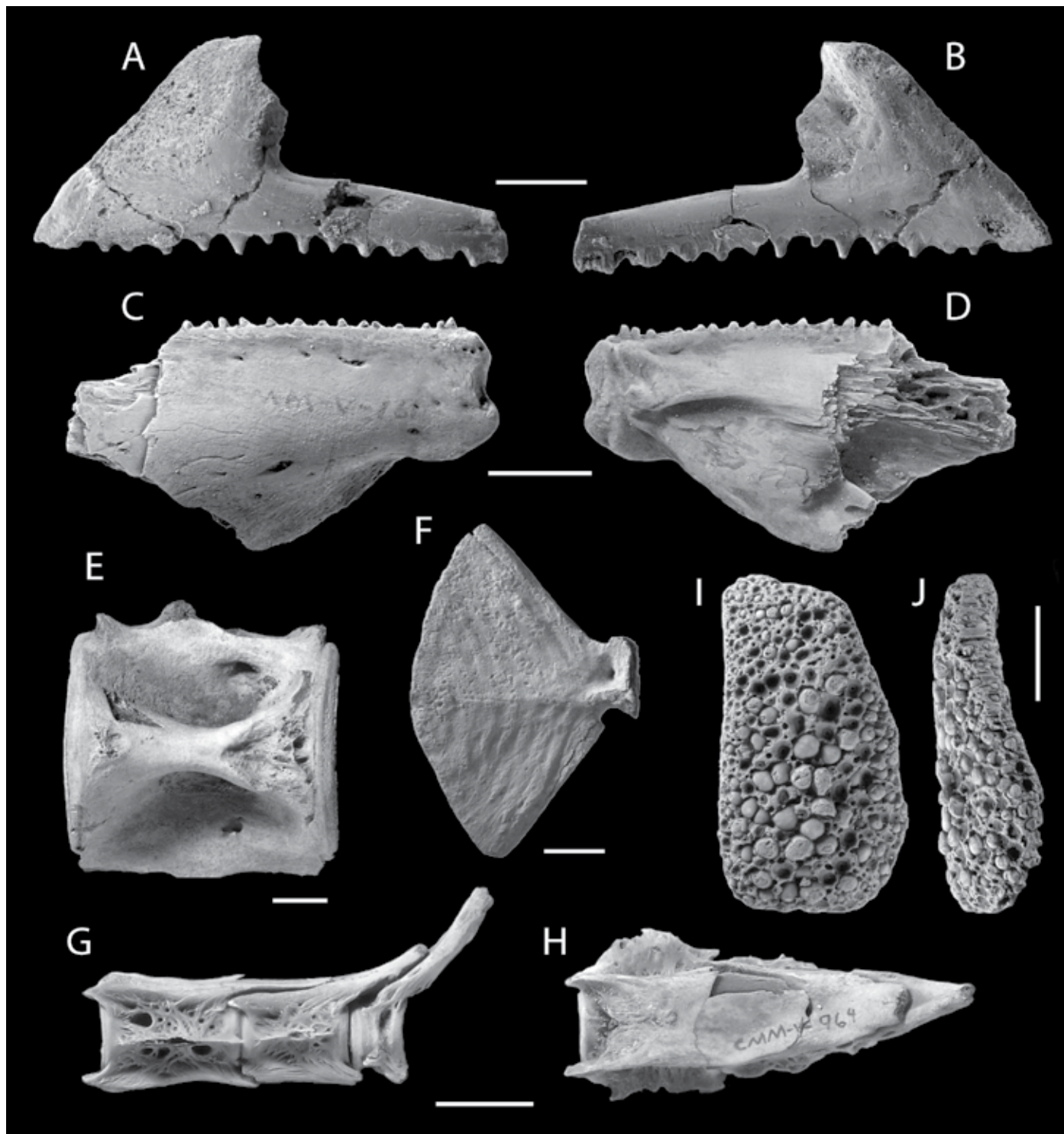


FIGURE 3.16. (A, B) USNM 559305, *Sarda* sp., nearly complete left premaxilla in lateral and medial views, respectively. (C, D) CMM-V-161, *Thunnus* sp., partial right dentary in lateral and medial views, respectively. (E) CMM-V-4388, *Thunnus* sp., abdominal vertebra. (F) CMM-V-137, *Thunnus* sp., hypural in right lateral view. (G, H) CMM-V-964, *Thunnus* sp., three associated caudal peduncle vertebrae. (I, J) CMM-V-2490, “*Paralbula*” *dorisiae*, tooth plate in occlusal and lateral views, respectively. Specimens lightly coated with sublimed ammonium chloride. Scale bars equal 10 mm.

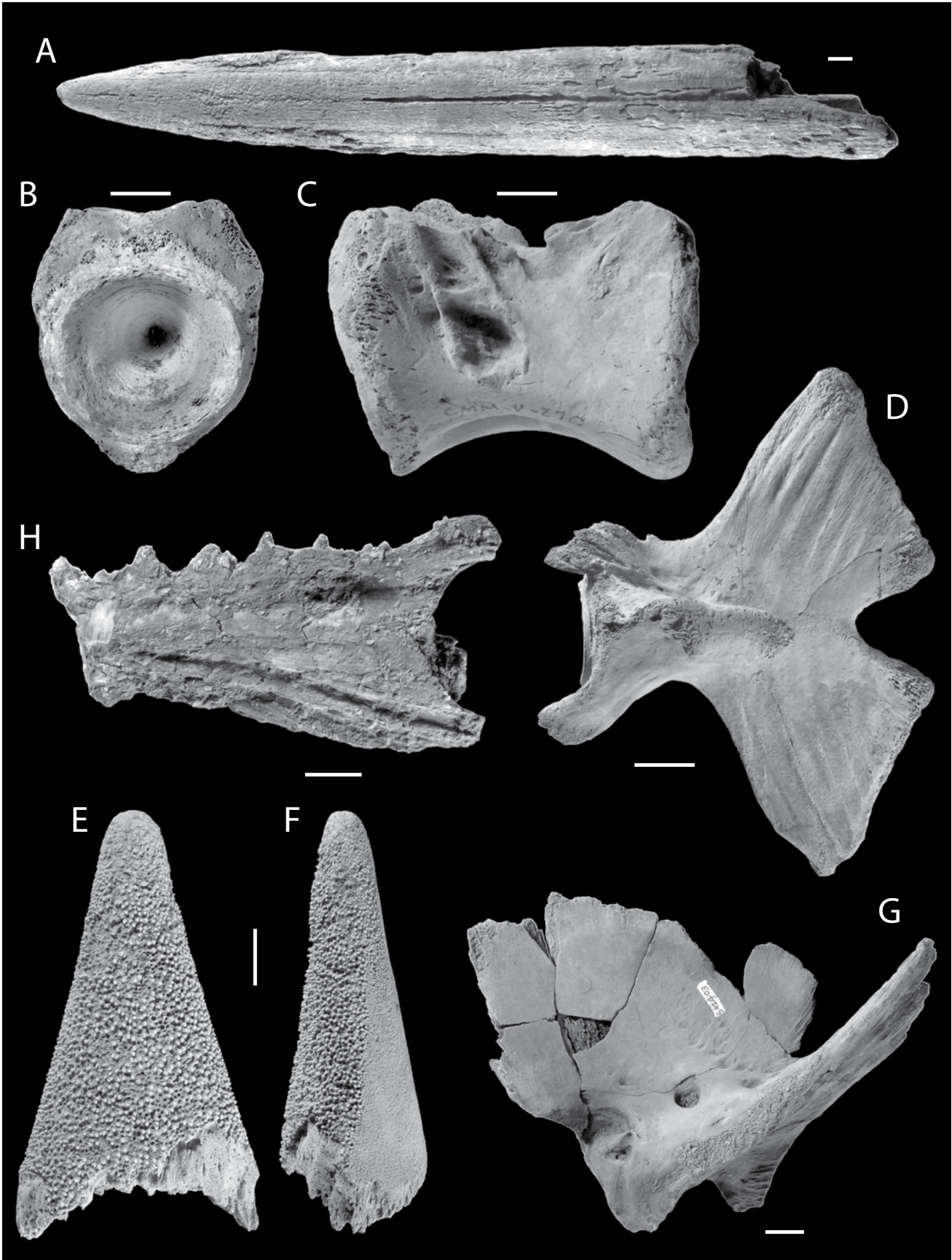


FIGURE 3.17. (Facing page) (A) USNM 9344, *Istiophorus* cf. *platypterus* (holotype of *I. calvertensis*), partial rostrum. (B, C) CMM-V-270, *Istiophorus* cf. *platypterus*, complete atlas in anterior and left lateral views, respectively. (D) USNM 542404, *Istiophorus* cf. *platypterus*, hypural complex in left lateral view. (E, F) USNM 542403, *Makaira* cf. *nigricans*, predentary in occlusal and right lateral views, respectively. (G) USNM 542403, *Makaira* cf. *nigricans*, left quadrate in lateral view. (H) USNM 542407, *Paralichthys* sp., left dentary in lateral view. Specimens lightly coated with sublimed ammonium chloride. Scale bars equal 10 mm.

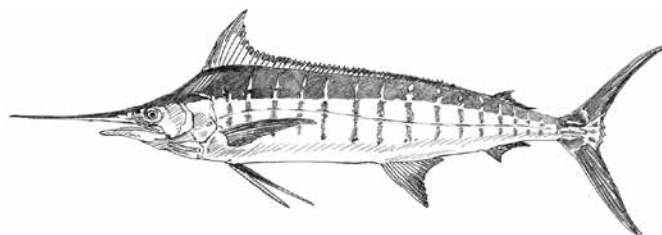
out at Tar Bay, James River, Virginia. Fierstine (1998, 2001) redescribed the specimen in detail and provided morphometric evidence of its affinities with the extant sailfish *I. platypterus*. The ratios of the rostrum formerly referred to *I. calvertensis*, as well as the other material referred herein to *I. cf. platypterus*, are presented in Table 3.1.

The sailfish is an oceanic, epipelagic species usually inhabiting the waters above the thermocline. Sailfishes are distributed close to the coasts, where they feed on fishes, cephalopods, and crustaceans.

Genus *Makaira* Lacépède, 1802

Makaira cf. *nigricans* Lacépède, 1802

FIGURE 3.17E-G



Blue Marlin – *Makaira* cf. *nigricans*

1998 *Makaira* cf. *nigricans* Lacépède – Fierstine, pp. 30–40, figs. 4–8A.

2001 *Makaira* cf. *nigricans* Lacépède – Fierstine, p. 37.

REFERRED MATERIAL. CMM-V-128 and CMM-V-129, partially complete rostra; USNM 375733, partially complete neurocranium, basisphenoid, vomer, rostrum, right lateral ethmoid, right ectopterygoid, right metapterygoid, right angulo-articular, right maxilla, right palatine, left prenasal, left dentary, predentary, and right lachrymal; USNM 542403, predentary and left quadrate (Figure 3.17E–G); USNM uncataloged, complete hypural complex.

HORIZON. Calvert and Eastover Formations.

REMARKS. Fierstine (1998) presented a detailed description of a partially articulated neurocranium, a rostrum, a jaw, and suspensorial bones. The ratios of selected bones described by

Fierstine (1998), as well as the other material referred herein to *Makaira* cf. *nigricans*, are presented in Table 3.2.

The blue marlin is an oceanic species that primarily inhabits blue waters down to 200 m, where it feeds mostly on fishes but also on cephalopods.

Family Istiophoridae, gen. et sp. indet.

REFERRED MATERIAL. CMM-V-183, partially complete rostrum; CMM-V-184, partially complete rostrum; CMM-V-220, complete abdominal vertebra; CMM-V-321, partially complete rostrum; CMM-V-337, complete abdominal vertebra; CMM-V-1839, partially complete predentary; CMM-V-1908, partially complete predentary; CMM-V-1915, two partially complete hypural complexes; CMM-V-1998, complete caudal vertebra; CMM-V-1999, partially complete right scapula; CMM-V-2239, partially complete rostrum; CMM-V-2511, partially complete abdominal vertebra; CMM-V-2684, partially complete rostrum; CMM-V-2983, partially complete rostrum; CMM-V-3835, partially complete rostrum; CMM-V-3956, partially complete rostrum; CMM-V-4148, two complete caudal vertebrae; CMM-V-4576, partially complete rostrum; CMM-V-4827, partially complete neurocranium; USNM 186808, partially complete rostrum; USNM 186809, two vertebrae (one abdominal and one caudal); USNM 186810, five abdominal vertebrae and right cleithrum, right coracoid, right postcleithrum, and caudal-fin rays; USNM 186812, partially complete caudal vertebra; USNM 241559, hypural complex and five isolated dorsal-fin spines; USNM 639712, predentary and partial abdominal vertebra; USNM 415609, partially complete rostrum; USNM 559395, partially complete rostrum; USNM 559393, partially complete rostrum; USNM uncataloged, partially complete rostrum and two partially complete caudal vertebrae, a single abdominal vertebra, and a single hypural complex.

HORIZON. Calvert, Choptank, St. Marys, and Eastover Formations.

ORDER PLEURONECTIFORMES BLEEKER, 1859

FAMILY PARALICHTHYIDAE REGAN, 1910

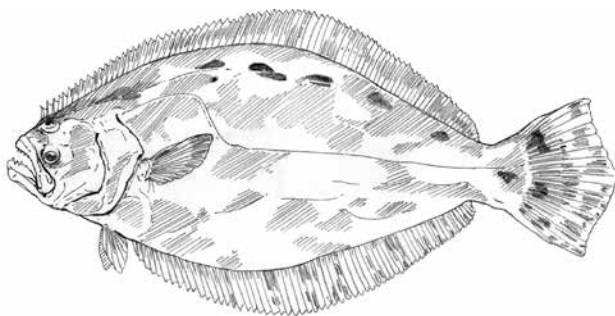
Genus *Paralichthys* Girard, 1858

TABLE 3.1. The ratios of the rostrum formerly referred to *I. calvertensis*, as well of the other material referred herein to *I. cf. platyp-terus*. Abbreviations follow Fierstine and Voigt (1996) and Fierstine (1998, 2001); a dash (–) indicates data are unavailable.

Ratios	USNM 9344	USNM 186813	USNM 542404	CMM-V-270	CMM-V-1766
Rostrum					
D1/W1	0.72	–	–	–	–
H1/D1	0.27	–	–	–	–
DD1/D1	0.43	–	–	–	–
D2/W2	0.69	0.57	–	–	–
H2/D2	0.27	0.27	–	–	–
DZ/P	0.34	–	–	–	–
Dentary					
DAD/DJL	–	–	–	–	0.43
22nd vertebra					
ASW/VAD	–	–	–	0.70	–
VAD/CL	–	–	–	0.83	–
VPD/CL	–	–	–	0.83	–
LAD/LPD	–	–	–	0.86	–
NW/CL	–	–	–	0.57	–
NW/LPD	–	–	–	0.70	–
ASW/CL	–	–	–	0.74	–
VAD/LAD	–	–	–	1.17	–
VPD/LPD	–	–	–	1.01	–
VAD/VPD	–	–	–	1.00	–
LAD/CL	–	–	–	0.70	–
LPD/CL	–	–	–	0.81	–
Hypural					
HDD/HL	–	–	0.56	–	–
HDD/HH	–	–	0.29	–	–
HDD/HW	–	–	0.50	–	–
HL/HH	–	–	0.52	–	–
HW/HL	–	–	0.98	–	–
HW/HH	–	–	0.51	–	–
HNL/HL	–	–	0.30	–	–

***Paralichthys* sp.**

FIGURE 3.17H



Lefteye Flounder – *Paralichthys* sp.

REFERRED MATERIAL. USNM 542407, left and right dentaries belonging to a single individual (Figure 3.17H).

HORIZON. Eastover Formation.

REMARKS. The dentaries are high and very thick, with a single row of strong caniniform teeth (Figure 3.17H). The anterior margin is nearly straight and obliquely oriented. There is a shallow notch along the anteroventral margin. Two parallel and relatively deep grooves run ventrally from the symphyseal region along the lateral surface. A flat bony flange with a linear dorsal profile is located along the dorsal margin behind the tooth row.

The dentaries from the Eastover Formation documented herein cannot be distinguished from those of the extant flounder *Paralichthys dentatus*.

Lefteye flounders of the genus *Paralichthys* are benthic species that occur primarily on sandy or muddy substrates from the

shore to a depth of 200 m. They often enter brackish waters and feed primarily on fishes and crustaceans.

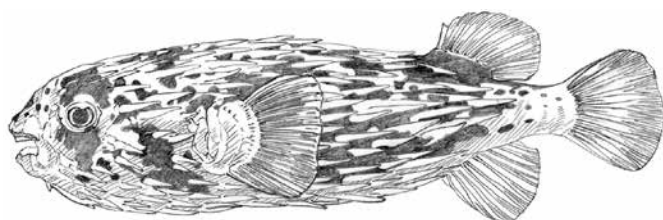
ORDER TETRAODONTIFORMES REGAN, 1929

FAMILY DIODONTIDAE BIBRON, 1855

Genus *Chilomycterus* Bibron, 1846

Chilomycterus sp.

FIGURE 3.18K,L



Burrfish – *Chilomycterus* sp.

REFERRED MATERIAL. CMM-V-172, fused dentaries; CMM-V-361, fused premaxillae; CMM-V-890, fused premaxillae; CMM-V-891, fused premaxillae; CMM-V-3338, fused dentaries (Figure 3.18K); CMM-V-3770, fused dentaries; CMM-V-4624, isolated dermal spine (Figure 3.18L).

HORIZON. Calvert and Eastover Formations.

REMARKS. Mouth plates are represented by both upper and lower jaws, which in origin consisted of the teeth of the biting edge fused with the dentaries and premaxillae into a solid crushing beak. The trituration teeth internal to the biting edge of both upper and lower jaws form a large plate divided into right and left halves, each formed by a series of large, flattened trituration tooth plates (Tyler, 1980; Figure 3.18K). The number of individual plates in the single series to each side of the midline usually increases with increasing specimen size. Unfortunately, all the jaw specimens are strongly eroded, represented only by fused contralateral tooth plates. Lower jaws can be distinguished from the upper jaws because of their rounded rather than pointed profile when observed in occlusal view (Figure 3.18K). Mouth plates, however, are not taxonomically useful because they are nearly indistinguishable in the genera *Diodon* and *Chilomycterus*. However, these two genera can be easily separated on the morphology of their dermal spines (see Tyler, 1980). CMM-V-4624 (Figure 3.18L) consists of a non-erectile, short, thick, and pointed spine arising from a large triradiate basal plate clearly belonging to the genus *Chilomycterus* (see Tyler, 1980; Leis, 2006). Because spines of *Diodon* have not yet been found, we tentatively suggest that all the diodontid skeletal remains found in the Miocene deposits of the Chesapeake Group should be assigned to *Chilomycterus*. The fragmentary nature of

the material does not allow for species-level attribution.

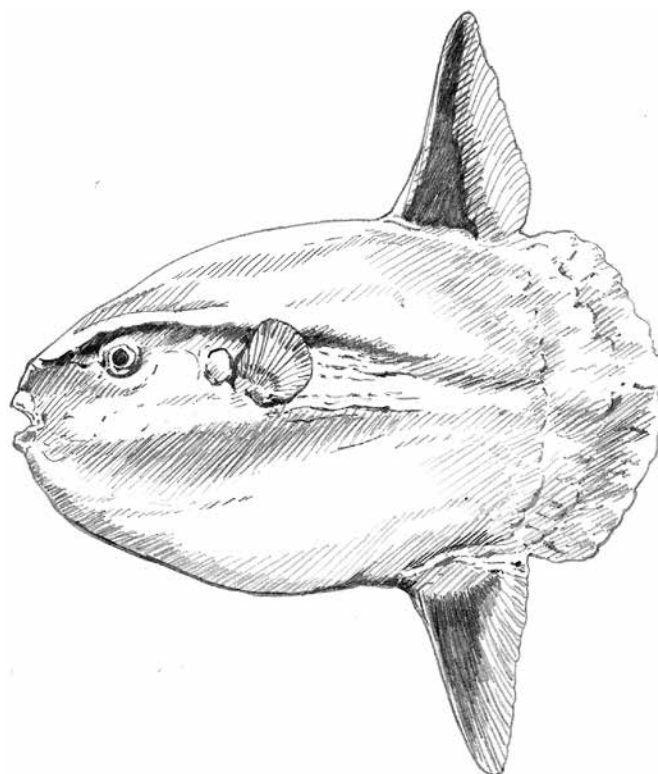
Burrfishes occur primarily in seagrass beds in bays and coastal lagoons, where they feed on crustaceans.

FAMILY MOLIDAE RANZANI, 1837

Genus *Mola* Koelreuter, 1770

Mola pileata (Van Beneden, 1881)

FIGURE 3.18A–C



Ocean sunfish – *Mola pileata*

HOLOTYPE. USNM 186983, premaxillary beak (Figure 3.18A–C).

HORIZON. Choptank Formation.

REMARKS. Weems (1985) referred a toothless premaxillary beak lacking a palatal tooth brace from bed 19 of the Choptank Formation to the molid species *Mola chelonopsis* (Figure 3.18A–C). However, Gregorova et al. (2009) concluded that this same specimen likely belongs to *Mola pileata* or perhaps to a new undescribed species of *Mola*.

Ocean sunfishes of the genus *Mola* are pelagic, with a worldwide distribution in tropical to temperate waters; they feed mainly on jellyfishes and other pelagic soft-bodied invertebrates and fish larvae.

TABLE 3.2. The ratios of selected bones described by Fierstine (1998), as well as of the other material referred herein to *Makaira* cf. *nigricans*. Abbreviations follow Fierstine and Voigt (1996) and Fierstine (1998, 2001); a dash (–) indicates data are unavailable.

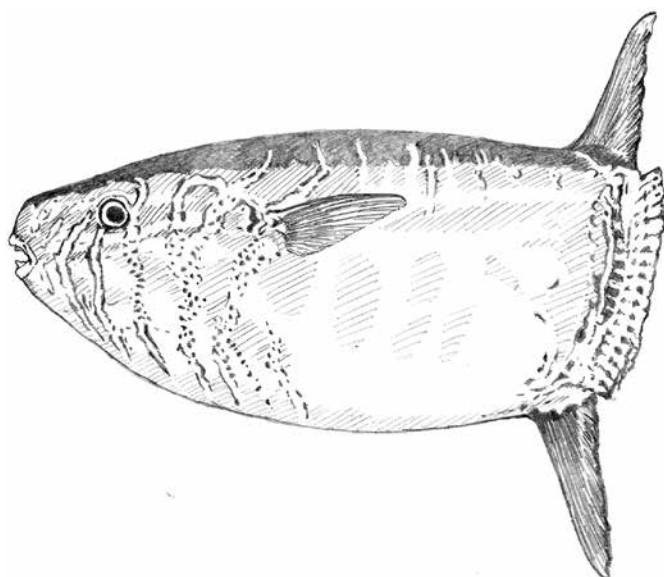
Ratios	USNM 375733	USNM 542403	USNM uncataloged	CMM-V-128+129
Neurocranium				
TD/MBO	0.50	–	–	–
NWB/TD	0.70	–	–	–
PAD/PAFW	0.53	–	–	–
PAW/PAFW	0.70	–	–	–
PAD/PAW	0.76	–	–	–
Prementary				
PW/PL	0.74	0.65	–	–
PD/PL	0.52	0.41	–	–
PD/PW	0.70	0.63	–	–
Rostrum				
D2/W2	0.70	–	–	0.54
H2/D2	0.18	–	–	0.30
DD2/D2	0.47	–	–	0.27
Maxilla				
ML/MOL	0.17	–	–	–
MW/MOL	0.14	–	–	–
MW/ML	0.79	–	–	–
MH/ML	0.64	–	–	–
MVW/MVH	1.3	–	–	–
MVW/ML	0.37	–	–	–
MVW/MW	0.46	–	–	–
MVW/MH	0.57	–	–	–
Articular				
AL/ASM	0.79	–	–	–
AW/AL	0.77	–	–	–
AAL/AL	0.59	–	–	–
ATW/AL	1.2	–	–	–
AW/ATW	0.66	–	–	–
Quadrate				
QAW/QH	–	0.23	–	–
QMW/QAW	–	1.10	–	–
QAW/QHS	–	0.30	–	–
QMW/QHS	–	0.34	–	–
QMW/QHL	–	0.96	–	–
Hypural				
HDD/HL	–	–	0.41	–
HDD/HH	–	–	0.15	–
HL/HH	–	–	0.37	–
HNL/HL	–	–	0.17	–

Genus *Ranzania* Nardo, 1840

REMARKS. The genus *Ranzania* includes a single extant species, *Ranzania laevis*, and at least four fossil species (see Carnevale and Santini, 2007), two of which are known exclusively from the Miocene and Pliocene deposits of the Middle Atlantic Coastal Plain (see Weems, 1985). *Ranzania laevis* is an oceanic pelagic species that occurs worldwide in warm and temperate waters, where it feeds primarily on planktonic crustaceans. On the basis of functional considerations, however, Weems (1985) suggested that the fossil species *Ranzania grahami* was characterized by feeding habits similar to those of *Mola*.

Ranzania grahami Weems, 1985

FIGURE 3.18D-I



Ocean sunfish – *Ranzania grahami*

HOLOTYPE. USNM 186986, premaxillary and dentary beaks (Figure 3.18D,E) and jugular and nasal dermal plates (not illustrated) and a partially complete articulated dorsal dermal shield (Figure 3.18H,I).

PARATYPES. USNM 16364, premaxillary beak; USNM 16668, premaxillary beak; USNM 16743, premaxillary beak; USNM 186982, premaxillary beak; USNM 265391, partial premaxillary beak; USNM 265394, premaxillary beak; USNM 265395, premaxillary beak; USNM 265651, nasal dermal plate; USNM 265653, jugular dermal plate (Figure 3.18F,G).

REFERRED MATERIAL. CMM-V-140, nasal dermal plate; CMM-V-150, dentary beak; CMM-V-186, premaxillary beak; CMM-V-187, premaxillary beak; CMM-V-191, nasal dermal plate; CMM-V-217, premaxillary beak; CMM-V-232, jugular dermal plate; CMM-V-230, nasal dermal plate; CMM-V-233, nasal dermal plate; CMM-V-285, premaxillary beak;

CMM-V-286, premaxillary beak; CMM-V-315, dentary beak; CMM-V-888, premaxillary beak; CMM-V-892, a single nasal and two jugular dermal plates; CMM-V-1004, dentary beak; CMM-V-1005, dermal plate; CMM-V-1641, two premaxillary beaks; CMM-V-1719, nasal dermal plate; CMM-V-1854, premaxillary beak; CMM-V-1883, dentary beak; CMM-V-1891, three premaxillary beaks and five jugular and five nasal dermal plates; CMM-V-1984, jugular dermal plate; CMM-V-2044, premaxillary beak; CMM-V-2064, a single dentary and four premaxillary beaks and one jugular and one nasal dermal plates; CMM-V-2137, three premaxillary beaks; CMM-V-2138, three nasal dermal plates; CMM-V-2139, two dermal plates; CMM-V-2143, two jugular plates; CMM-V-2246, jugular dermal plate; CMM-V-2434, premaxillary beak; CMM-V-2501, dentary beak; CMM-V-2508, jugular dermal plate; CMM-V-2510, nasal dermal plate; CMM-V-2553, jugular dermal plate; CMM-V-2561, a single jugular and two nasal dermal plates; CMM-V-2579, jugular dermal plate; CMM-V-2685, premaxillary beak and nasal dermal plate; CMM-V-2788, dermal plates; CMM-V-3029, three nasal plates; CMM-V-3076, jugular dermal plate; CMM-V-3078, jugular dermal plate; CMM-V-3328, premaxillary beak; CMM-V-3800, two premaxillary beaks and six jugular and two nasal dermal plates; CMM-V-4004, premaxillary beak; CMM-V-4092, premaxillary beak; CMM-V-4211, premaxillary beak; CMM-V-4227, jugular dermal plate; CMM-V-4255, premaxillary beak and three nasal dermal plates; CMM-V-4277, nasal dermal plate; CMM-V-4292, nasal dermal plate; CMM-V-4308, jugular dermal plate; CMM-V-4340, nasal dermal plate; CMM-V-4413, two premaxillary beaks; CMM-V-4420, premaxillary beak and nasal dermal plate; CMM-V-4424, dermal plate; CMM-V-4547, jugular dermal plate; CMM-V-4558, jugular dermal plate; CMM-V-4565, nasal dermal plate; CMM-V-4577, nasal dermal plate; CMM-V-4596, jugular dermal plate; USNM 135737, jugular dermal plate; USNM 265649, premaxillary beak; USNM 265652, partial jugular dermal plate; USNM 391878, premaxillary beak; USNM 410274, jugular dermal plate; USNM 639711, premaxillary beak; USNM 2015682, dentary beak.

HORIZON. Calvert Formation.

REMARKS. Abundant jaw and dermal skeleton remains are referred herein to the species *Ranzania grahami* on the basis of the diagnostic features described by Weems (1985).

The premaxillary beak is massive and does not have a bony shelf on the palatal bracing; it is usually toothless and only rarely has small and irregularly disposed teeth (Figure 3.18D). The dentary beak, with a robust biting edge, is similar to that of the extant *Ranzania laevis*; the teeth appear to be absent or, at least, remarkably reduced (Figure 3.18E).

The massive carapace consists of irregular and extremely thickened plates (Figure 3.18H,I). Of the whole dermal covering, the nasal and jugular plates can be distinguished from the other elements. The nasal plate is approximately ovoid in outline, whereas the jugular plate is greatly elongate, with a rounded external surface and a flat to slightly concave median surface characterized by a thick median ridge (Figure 3.18F,G).

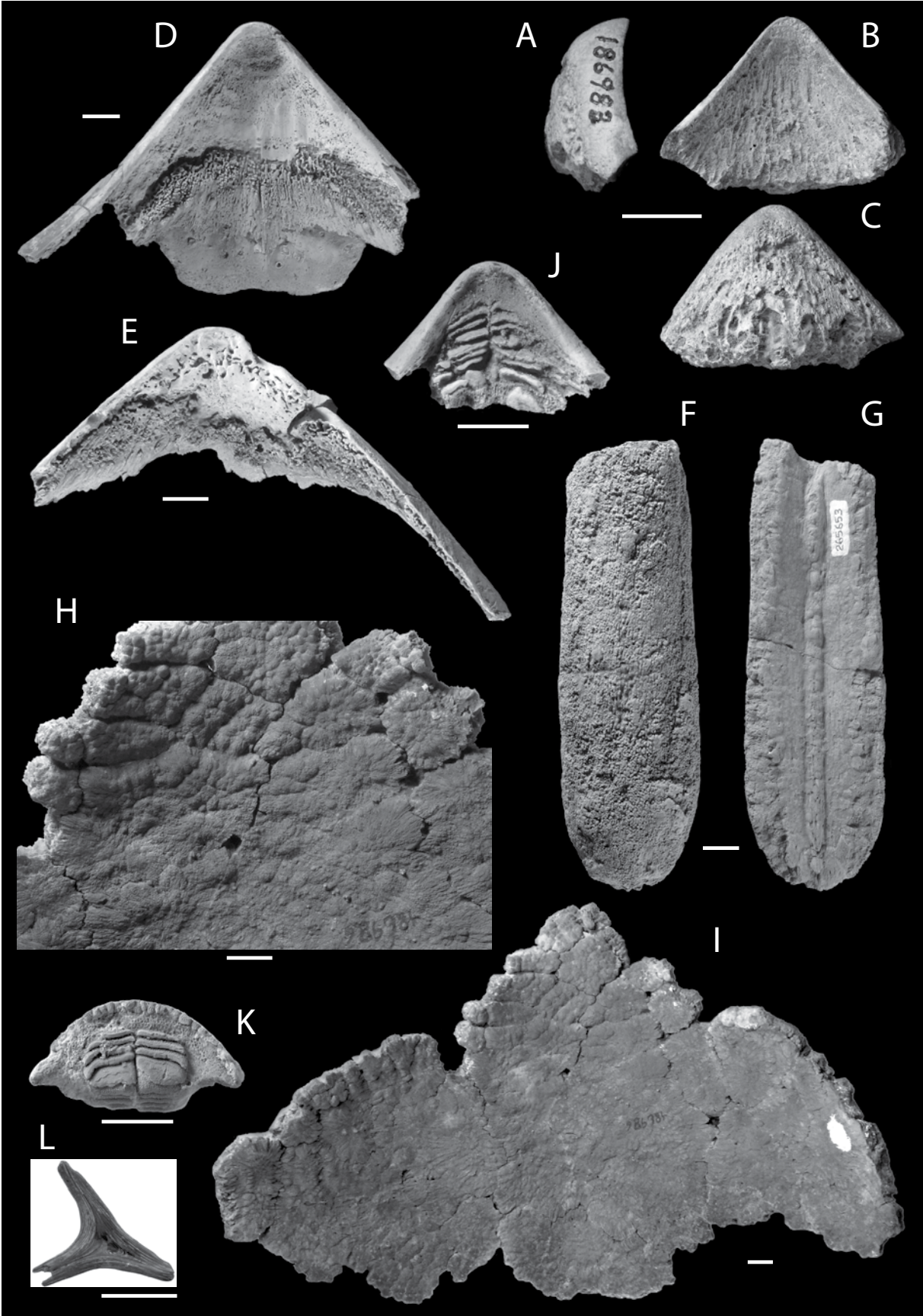
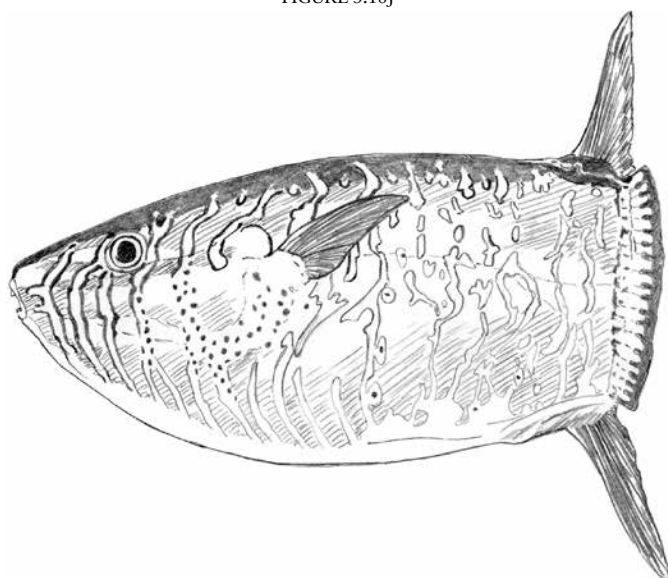


FIGURE 3.18. (Facing page) (A–C) USNM 186983, *Mola pileata*, premaxillary beak in right lateral, ventral (occlusal), and dorsal views, respectively. Anterior to top of page. (D) USNM 186986, *Ranzania grahami*, holotype, premaxillary beak in ventral (occlusal view). Anterior to top of page. (E) USNM 186986, *Ranzania grahami*, holotype, dentary beak in dorsal (occlusal view). Anterior to top of page. (F, G) USNM 265653, *Ranzania grahami*, jugular dermal plate in external and internal views, respectively. (H, I) USNM 186986, *Ranzania grahami*, holotype, partial articulated dorsal dermal shield, internal view (H shows an enlarged view of the anterior margin of I). (J) USNM 265392, *Ranzania tenneyorum*, holotype, premaxillary beak in ventral (occlusal view). Anterior to top of page. (K) CMM-V-3338, *Chilomycterus* sp., fused dentaries, occlusal view. Anterior to top of page. (L) CMM-V-4624, *Chilomycterus* sp., isolated dermal spine. Specimens lightly coated with sublimed ammonium chloride. Scale bars equal 10 mm.

***Ranzania tenneyorum* Weems, 1985**

FIGURE 3.18J



Ocean sunfish – *Ranzania tenneyorum*

HOLOTYPE. USNM 265392, premaxillary beak (Figure 3.18J).

REFERRED MATERIAL. Six premaxillary beaks: CMM-V-185, CMM-V-931, CMM-V-2137, CMM-V-2441, CMM-V-4464, USNM 336431.

HORIZON. Calvert Formation.

REMARKS. The available material consists solely of isolated premaxillary beaks. The beaks are characterized by three well-developed pairs of tooth rows located on a bony shelf separated by a vertical sill from the main level of the palatal bracing bone; a notch is clearly exposed behind the tooth rows (Figure 3.18J).

COMMENTS ON “*PARALBULA*” *DORISIAE* BLAKE, 1940

FIGURE 3.16 IJ

A few thick tooth plates with phyllodont teeth (see Estes, 1969) from the Calvert and St. Marys Formations are present

in the collections of the CMM (CMM-V-325, CMM-V-1024, CMM-V-2154, CMM-V-2215, CMM-V-2490; Figure 3.16 I,J) and USNM (USNM 16134, holotype; USNM 559397; USNM uncataloged). The teeth are irregularly arranged, nearly globular or subspherical in outline, and slightly depressed apically (Figure 3.16 I,J). Blake (1940) interpreted these tooth plates as being related to those of the Eocene albuloid *Paralbula marylandica* and created the new species *Paralbula dorisiae* to accommodate them. In a comprehensive study on the evolution and diversity of phyllodont fishes, Estes (1969) excluded the possibility that the Miocene tooth plates from the Chesapeake Group could belong to the genus *Paralbula* and, more generally, to the albuloid family Phyllodontidae. According to Estes (1969), the Miocene phyllodont tooth plates from the Chesapeake Group actually belong to the percomorph *Crommyodus irregularis*, a species created by Cope (1869) on the basis of material from the Miocene of New Jersey. Within percomorphs, phyllodont teeth are known to occur in the Carangidae, Diodontidae, and Labridae (hypsigenines, odacines, scarines) and, possibly, in certain extinct members of the family Sciaenidae (Estes, 1969). However, the fragmentary nature of the available material, as well as the lack of useful characters to interpret its possible affinities within percomorphs, defies taxonomic identification at this time.

REMARKS ON OTOLITH ASSEMBLAGES

FIGURE 3.19

Otoliths, together with isolated teeth, were the first reported actinopterygian remains from the Miocene deposits of the Chesapeake Group (Eastman, 1904; Hay, 1928). In the first synoptic work on the Miocene fishes from Maryland, Eastman (1904) briefly discussed the otolith record of the Chesapeake Group and illustrated gadid and sciaenid sagittas from the St. Marys Formation without any indication of their taxonomic affinities. About half a century later, Dante (1953) described a new species, *Sciaenops eastmani*, on the basis of the material previously illustrated by Eastman (1904) and additional specimens from the Calvert Formation; his diagnosis was based on juvenile features, and for this reason Fitch and Lavenberg (1983) considered it to be a synonym of the extant *Sciaenops ocellata*. Nevertheless, Schwarzhans (1993) included *Sciaenops eastmani*

within the fossil genus *Trewasciaena* together with material from the Miocene of Germany. A comprehensive study of the Miocene otoliths of Maryland was being prepared by John E. Fitch (n.d.), but unfortunately, his untimely death precluded full revision of the material. More recently, Müller (1999) made an extensive study of Tertiary ichthyofaunas of the Atlantic Coastal Plain, including the Calvert, Choptank, St. Marys, and Eastover Formations. About 64 taxa were described and illustrated from the Miocene of the Chesapeake Group, and several new otolith-based taxa were created. Many of his generic identifications, however, are not consistent with the analysis of skeletal remains presented herein. Since a complete review of the Miocene otolith assemblages of the Chesapeake Group is beyond the scope of our study, we investigated the relatively large otolith collection housed in the CMM in light of the results of the study of skeletal remains. Therefore, our taxonomic interpretations may appear rather conservative and with a broad use of open nomenclature. The most commonly found taxa are compiled in Figure 3.19. Throughout the Miocene, members of the families Gadidae (*Gadiculus* cf. *argenteus*, *Micromesistius cognatus*, *Trisopterus sculptus*) and Sciaenidae (*Cynoscion* sp., *Genyonemus* sp., *Leiostomus* sp., *Menticirrhus* sp., *Pachyurus* sp., *Pogonias* sp., *Sciaenops* sp.) are by far the dominant components of the assemblages, which also include a subordinate contingent of taxa of the families Ophidiidae (*Lepophidium* aff. *cervinum*, *Otophidium* sp.), Merlucciidae (*Merluccius* sp.), Ammodytidae (*Ammodytes* sp.), Triglidae (*Prionotus* sp.), Uranoscopidae (*Astroschelus* sp.), and Paralichthyidae (*Citharichthys* sp.). Representatives of other families are relatively rare (see Müller, 1999, for a detailed account). In some cases, the otolith and skeletal records are strongly consistent, including relative abundances as, for example, in the case of the red drum *Sciaenops*, which is extremely abundant in both records.

DISCUSSION

The analysis of the bony fish remains from the marine and paralic siliciclastic deposits of the Chesapeake Group presented herein provides a substantial improvement of our knowledge about the evolution of the structure and composition of the Miocene fish communities of the Salisbury Embayment and, more generally, of the middle sector of the eastern Atlantic coast of the North American continent. The investigation carried out on the paleoichthyological material housed in the collections of the CMM and the Department of Paleobiology of the USNM resulted in the identification of at least 38 taxa on the basis of fossil bones collected over more than a century from the Calvert, Choptank, St. Marys, and Eastover Formations. This represents a remarkable increase in the number of recognized taxa with respect to the previous reviews of the paleoichthyological record (e.g., Leriche, 1942; Kimmel and Purdy, 1984), which recognized less than a dozen taxa. An evaluation of the Miocene bony fish diversity from the deposits of the Chesapeake Group, however,

should also include the diverse otolith assemblages described by Fitch (n.d.) and more recently by Müller (1999), who recognized at least 55 taxa in the Chesapeake Group. Therefore, a combined census of both the skeletal remains and otoliths of the Chesapeake Group results in the identification of at least 87 fish taxa, of which only a few (e.g., *Ariopsis stauroforus*, *Brotula* sp., *Merluccius* sp., *Pogonias* sp., *Prionotus* sp., *Sciaenops* sp.) are common to both records (Tables 3.3, 3.4).

As previously mentioned, this paleoichthyofaunal survey is based on the study of museum material fortuitously collected over more than a century from the deposits of the Chesapeake Group cropping out in Maryland and Virginia. The complete absence of a quantitative approach in the collection of these fossils makes it very difficult to provide a detailed paleoecological analysis of the fish assemblages. Nevertheless, some general paleoecological considerations can be provided on the basis of the biological and environmental affinities of the recognized taxa.

Within the sedimentary successions of the Chesapeake Group, skeletal remains are much more abundant and diverse in the Calvert and St. Marys Formations, with 26 and 20 taxa respectively, possibly reflecting depositional contexts wherein fossilization was favored. The otolith record shows a similar trend, with highly diverse assemblages in the Calvert and St. Marys Formations and only a few taxa recognized from both the Choptank and Eastover Formations (see Müller, 1999).

The fish assemblages of the Calvert, Choptank, St. Marys, and Eastover Formations exhibit a modern aspect. Although the ichthyofaunal compositions of the various formations are characterized by broad differences, it is interesting to note a persistent abundance of sturgeons (Acipenseridae gen. et sp. indet.), drums (*Pogonias* sp., *Sciaenops* sp.), and billfishes (Istiophoridae gen. et sp. indet.) throughout the sedimentary successions of the Chesapeake Group. The faunistic differences existing between the four formations clearly reflect the physiographic and environmental evolution of the Salisbury Embayment during the Miocene (e.g., Ward and Andrews, 2008; Petuch and Drolshagen, 2010).

The reduced size of many of the otoliths (ammodytids, cynoglossids, gadids, merlucciids, ophidiids, paralichthyids, and sciaenids) from the deposits of the Chesapeake Group is probably related to their juvenile nature. Such an abundance of juveniles suggests that the Salisbury Embayment represented a nursery ground for most of the Miocene.

The Calvert ichthyofauna is dominated by sturgeons (Acipenseridae gen. et sp. indet.), tilefishes (*Lopholatilus ereborensis*), drums (*Pogonias* sp., *Sciaenops* sp.), scombrids (*Acanthocybium* cf. *solandri*, *Thunnus* sp.), billfishes (*Istiophorus* cf. *platypterus*, *Makaira* cf. *nigricans*, Istiophoridae gen. et sp. indet.), burrfishes (*Chilomycterus* sp.), and ocean sunfishes (*Ranzania grahami*). The presence of tunas, billfishes, and other schooling predatory fishes, together with the abundance of large sharks and marine tetrapods, suggests that the Salisbury Embayment was a highly productive feeding ground during the deposition of the Calvert Formation. Overall, the Calvert ichthyofauna consists of a mixture of tropical, subtropical, and

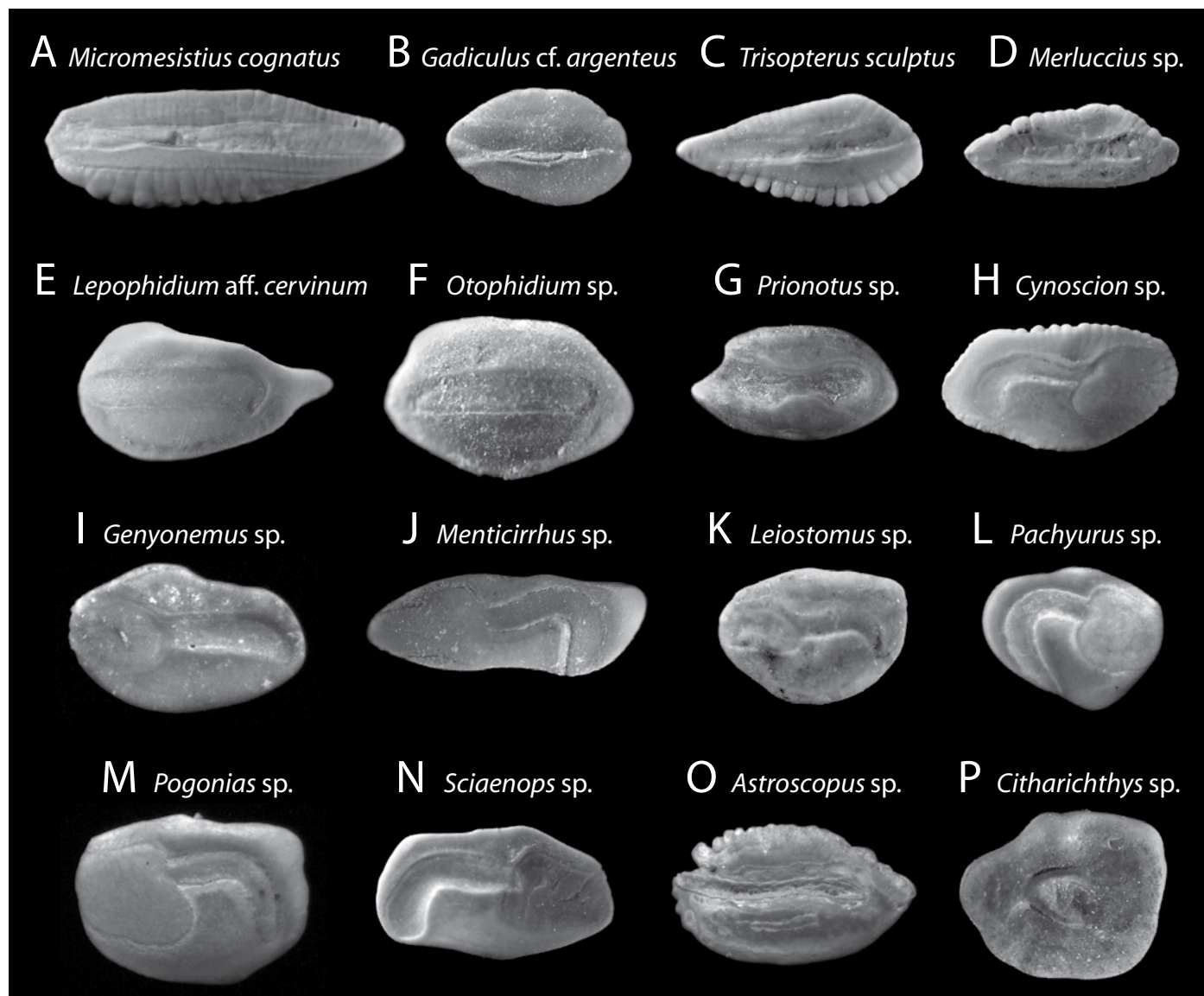


FIGURE 3.19. Otoliths from the Chesapeake Group. (A) *Micromesistius cognatus*. (B) *Gadiculus* cf. *argenteus*. (C) *Trisopterus sculptus*. (D) *Merluccius* sp. (E) *Lepophidium* aff. *cervinum*. (F) *Otophidium* sp. (G) *Prionotus* sp. (H) *Cynoscion* sp. (I) *Genyonemus* sp. (J) *Menticirrhus* sp. (K) *Leiostomus* sp. (L) *Pachyurus* sp. (M) *Pogonias* sp. (N) *Sciaenops* sp. (O) *Astroscopus* sp. (P) *Citharichthys* sp. Not to scale.

warm temperate taxa, with a few taxa of cold temperate affinity (*Lopholatilus ereborensis*). The tropical-subtropical contingent includes the sea catfish *Ariopsis stauroforus*, the wahoo *Acanthocybium* cf. *solandri*, the billfishes *Istiophorus* cf. *platypterus* and *Makaira* cf. *nigricans*, and the barracuda *Sphyræna* sp., which are indicative of temperatures of 27°C or higher (see Purdy et al., 2001). According to Müller (1999), the abundance of gadid otoliths in the deposits of the Calvert Formation is indicative of the presence of cool waters; however, the recognized gadid taxa

belong to the thermophilous genera *Gadiculus*, *Micromesistius*, *Phycis*, and *Trisopterus*, which commonly occur in warm temperate waters (see Carnevale et al., 2012).

The Calvert ichthyofauna shares some taxa (*Bagre*, *Chilomycterus*, *Lagodon*, *Pogonias*, *Sarda*, *Sphyræna*, and *Thunnus*) with the partially coeval Burdigalian assemblage of the Pungo River Formation, North Carolina (see Purdy et al., 2001). However, the Pungo River ichthyofauna is characterized by a lower number of taxa, some of which (*Aluterus* sp., *Auxis* sp.,

Hemirhabdorbhynchus sp., *Megalops* cf. *atlanticus*) have not been recorded in the Calvert Formation or, more generally, in the whole Chesapeake Group.

Fish remains are relatively uncommon in the Choptank Formation. The Choptank ichthyofauna, however, is similar to that of the Calvert Formation, being dominated by sturgeons (*Acipenseridae* gen. et sp. indet.), drums (*Pogonias* sp., *Sciaenops* sp.), scombrids (*Acanthocybium* cf. *solandri*, *Thunnus* sp.), and billfishes (*Istiophorus* cf. *platypterus*, *Istiophoridae* gen. et sp. indet.).

The fish assemblage of the St. Marys Formation seems to document a general cooling, as evidenced by the absence of thermophilous sea catfishes and wahoos and, more specifically, by the presence of *Merluccius* sp. and a member of the family Agonidae, a clade currently exclusive to cold temperate and polar waters of the North Pacific, Arctic Sea, northern North Atlantic, and North Sea and off the Patagonian region of the Southern Hemisphere (Kanayama, 1991). The remarkable cooling trend that occurred during deposition of the St. Marys Formation is also well documented in the otolith record. According to Müller (1999), the presence of otoliths belonging to the larger gadines *Gadus* and *Melanogrammus* in the St. Marys Formation resulted from a transatlantic migration of taxa typical of the North Sea Basin facilitated by a general drop in the temperatures in the North Atlantic. However, despite the abundance of cool-water taxa, remains of a certain number of subtropical and tropical fishes, including barracudas (*Sphyræna* sp.) and billfishes (*Istiophoridae* gen. et sp. indet.), are relatively common in the St. Marys Formation.

The Eastover ichthyofauna is scarcely diversified and is characterized by rare remains, among which drums (*Pogonias* sp., *Sciaenops* sp.) and billfishes (*Istiophorus* cf. *platypterus*, *Makaira* cf. *nigricans*, *Istiophoridae* gen. et sp. indet.) are dominant.

In summary, the mixture of thermophilous fishes with taxa of cold temperate and northern affinities characteristic of the assemblages of the Calvert, Choptank, St. Marys, and Eastover Formations could be indicative of the persistent presence of a well-defined climatic latitudinal zonation but also of wide seasonal temperature changes in a general condition similar to that characterizing the Chesapeake Bay area today (see Murdy et al., 1997).

The fish taxa recognized in the deposits of the Chesapeake Group show a clear general affinity for well-oxygenated muddy and sandy substrates. The assemblages are dominated primarily by shallow-water fishes characteristic of the inner shelf and secondarily by epipelagic taxa. Benthopelagic fishes characteristic of the outer shelf and upper slope are nearly absent in the Calvert Formation (exceptions are *Brotula* sp., *Lopholatilus ereborensis*). The common occurrence of open-ocean taxa (billfishes, tunas, wahoos) in the Calvert, Choptank, and Eastover Formations suggests that the deposition took place in the distal portions of the inner shelf. Overall, the ichthyofaunal composition is consistent with the sedimentary and paleontological record, which evidences a general regressive trend from the Calvert

to the St. Marys Formation, representing a gradual shallowing within the Salisbury Embayment (e.g., Gernant et al., 1971; Kidwell, 1984, 1988, 1989, 1997; Ward, 1992; Shideler, 1994; Ward and Andrews, 2008).

The depth of deposition of the Calvert Formation is highly variable, with bed 11 having originated in the basinward parts of the shelf, recording the maximum depositional depth of the formation (Kidwell, 1989). Fish remains were collected in large part from beds 11, 12, and 14 of the Plum Point Member. These beds include tilefish remains belonging to the genus *Lopholatilus*, which can provide some indication of the minimum depth of the Calvert depositional environment. Extant species of the genus *Lopholatilus* range in depth between 80 and 540 m but usually occur at depths between 100 and 300 m near the 15°C isotherm (Dooley, 1978; Grimes et al., 1980, 1986); this range suggests that it is unlikely that the depositional depths of beds 11, 12, and 14 were shallower than 80 m, as suggested by micro-paleontological studies (Gibson, 1983).

There are no fish taxa that would suggest a precise estimate of the minimum depositional depth for the Choptank Formation. However, toadfishes of the genus *Opsanus* usually occur at depths less than 50 m (Manooch, 1984). Gernant (1970) suggested that depositional environments were less than 60 m deep for the formation as a whole and that the ocean was less than 25 m deep for some beds. On the basis of foraminiferal assemblages, Gibson (1983) suggested that deposition of the Choptank Formation took place in open, shallow marine waters up to 30 m deep.

The presence of brackish and freshwater (e.g., *Amia* cf. *calva*, *Lepisosteus* sp., *Ictalurus countermani*) taxa in the St. Marys Formation and the concurrent abundance of marine euryhaline and stenohaline species could be related to wide seasonal oscillations of salinity that possibly occurred within the Salisbury Embayment because of episodic increase of the freshwater supply, as well as to habitat heterogeneity. Because of the variety of the recognized ecological categories, the evaluation of the depositional depth of the St. Marys Formation is rather problematic; in any case, taking into consideration the presence of the benthopelagic genus *Merluccius* and of indeterminate remains belonging to the billfish family *Istiophoridae*, it seems reasonable to conclude that the average depositional depth for the St. Marys Formation would have been a few dozen meters.

As far as the Eastover Formation is concerned, sedimentary features and macrobenthic assemblages (see Ward and Blackwelder, 1980) appear to be consistent with the ichthyofaunal composition and are indicative of marine depositional environments located in the inner shelf.

As discussed above, the fish assemblages of the Chesapeake Group exhibit a modern aspect, with most of the taxa belonging to genera or higher categories that currently occur in the north-western Atlantic, including the coasts of Maryland and Virginia. Two of the taxa recorded in the St. Marys Formation, however, are very interesting from a biogeographic point of view since today they are absent or have been artificially introduced in

TABLE 3.3. Skeletal taxonomy of bony fishes from the Chesapeake Group. An X indicates a taxon is present in a particular formation or habitat; a question mark (?) indicates a taxon may be present; a dash (–) indicates taxon is not present.

Taxonomy		Formation				Habitat			
Family	Taxon	Calvert	Choptank	St. Marys	Eastover	Freshwater	Brackish	Shallow marine	Open marine
Acipenseridae	<i>Acipenseridae</i> gen. et sp. indet.	X	X	X	X	X	X	X	–
Lepisosteidae	<i>Lepisosteus</i> sp.	–	–	X	–	X	X	–	–
Amiidae	<i>Amia</i> cf. <i>A. calva</i>	–	–	X	–	X	–	–	–
Clupeidae	<i>Alosa</i> sp.	–	–	X	–	X	X	X	X
Ictaluridae	<i>Ictalurus</i> sp.	–	–	X	–	X	X	–	–
Ariidae	<i>Ariopsis stauroforus</i>	X	–	–	–	X	X	X	–
	<i>Bagre</i> sp.	X	–	–	–	–	X	X	–
Merlucciidae	<i>Merluccius</i> sp.	–	–	X	–	–	–	X	X
Ophidiidae	<i>Brotula</i> sp.	X	–	–	–	–	–	X	X
Batrachoididae	<i>Opsanus</i> sp.	–	X	–	–	–	–	X	–
Lophiidae	<i>Lophius</i> sp.	X	–	–	–	–	–	X	X
Belonidae	<i>Belone</i> sp.	–	–	X	–	–	X	X	X
Triglidae	<i>Prionotus</i> sp.	X	–	X	–	–	X	X	–
Agonidae	Agonidae gen. et sp. indet.	–	–	X	–	–	X	X	–
Perciformes indet.	<i>“Paralbula” dorisiae</i>	X	–	X	–	?	?	?	?
Moronidae	<i>Morone</i> sp.	X	–	–	–	X	X	X	–
Serranidae	Serranidae gen. et sp. indet.	–	X	–	–	–	X	X	X
Malacanthidae	<i>Lopholatilus ereborensis</i>	X	–	–	–	–	–	X	X
Pomatomidae	<i>Pomatomus</i> sp.	X	–	X	–	–	X	X	X
Rachycentridae	<i>Rachycentron</i> sp.	X	–	–	–	–	X	X	X
Sparidae	<i>Lagodon</i> sp.	X	–	X	–	–	X	X	–
	<i>Stenotomus</i> sp.	–	–	X	–	–	X	X	–
Sciaenidae	<i>Micropogonias</i> sp.	X	–	–	–	–	X	X	–
	<i>Pogonias</i> sp.	X	X	X	X	–	X	X	–
	<i>Sciaenops</i> sp.	X	X	X	X	–	X	X	–
Labridae	<i>Tautoga</i> sp.	X	–	X	X	–	X	X	–
Uranoscopidae	<i>Astroscopus countermani</i>	–	–	X	–	–	X	X	–
Sphyracidae	<i>Sphyracna</i> sp.	X	–	X	X	–	X	X	X
Scombridae	<i>Acanthocybium</i> cf. <i>solandri</i>	X	X	–	–	–	–	X	X
	<i>Sarda</i> sp.	X	–	–	–	–	X	X	X
	<i>Thunnus</i> sp.	X	X	–	–	–	X	X	X
Istiophoridae	<i>Istiophorus</i> cf. <i>platypterus</i>	X	X	–	X	–	–	X	X
	<i>Makaira</i> cf. <i>nigricans</i>	X	–	–	X	–	–	X	X
	Istiophoridae gen. et sp. indet.	X	X	X	X	–	–	X	X
Paralichthyidae	<i>Paralichthys</i> sp.	–	–	–	X	–	X	X	–
Diodontidae	<i>Chilomycterus</i> sp.	X	–	–	X	–	–	X	–
Molidae	<i>Mola pileata</i>	–	X	–	–	–	–	X	X
	<i>Ranzania grahami</i>	X	–	–	–	–	–	X	X
	<i>Ranzania tenneyorum</i>	X	–	–	–	–	–	X	X

TABLE 3.4. Otolith taxonomy of bony fishes from the Chesapeake Group, based primarily on Müller (1999), except for Sciaenops, which is based on Fitch (n.d.). An X indicates a taxon was present in a particular formation; a dash (–) means taxon was not present.

Taxonomy		Formation			
Family	Taxon	Calvert	Choptank	St. Marys	Eastover
Congridae	<i>Conger</i> sp.	X	–	–	–
	<i>Brevoortia</i> aff. <i>B. tyrannus</i> (Latrobe, 1802)	–	–	X	–
Ariidae	<i>Ariopsis</i> aff. <i>A. felis</i> (Linnaeus, 1758)	–	X	–	–
	<i>Ariopsis stauroforus</i> (Lynn & Melland, 1939)	X	–	–	–
Argentinidae	<i>Argentina</i> sp.	–	–	X	–
Myctophidae	<i>Diaphus</i> sp.	X	–	–	–
Gadidae	<i>Phycis</i> spp.	X	–	–	–
	<i>Urophycis</i> aff. <i>U. tenuis</i> (Mitchill, 1815)	–	–	X	–
	“gen. aff. <i>Urophycis</i> ” sp.	–	–	X	–
	<i>Gadiculus argenteus</i> (Guichenot, 1850)	–	–	X	–
	<i>Gadiculus labiatus</i> (Schubert, 1905)	X	–	X	–
	<i>Gadiculus</i> aff. <i>benedeni</i> (Leriche, 1926)	–	–	–	X
	<i>Trisopterus sculptus</i> (Koken, 1884)	X	X	X	–
	<i>Gadus marylandicus</i> Müller, 1999	–	–	X	–
	<i>Melanogrammus antecessus</i> Müller, 1999	–	–	X	–
	<i>Micromesistius cognatus</i> (Koken, 1891)	X	X	X	–
Merlucciidae	<i>Merluccius albidus</i> (Mitchill, 1817)	X	–	X	–
	<i>Merluccius</i> sp.	X	–	–	–
Ophidiidae	<i>Brotula</i> sp.	X	–	–	–
	<i>Lepophidium</i> aff. <i>cervinum</i> (Goode & Bean, 1885)	–	–	–	X
	<i>Lepophidium elongatum</i> Müller, 1999	–	–	X	–
	<i>Chilara</i> aff. <i>C. taylori</i> (Girard, 1858)	–	–	–	X
	<i>Otophidium nolfi</i> Müller, 1999	–	–	X	–
Triglidae	<i>Prionotus</i> spp.	X	X	X	–
	“genus <i>Triglidarum</i> ” sp.	X	–	–	–
Chandidae	“genus <i>Chandidarum</i> ” sp.	–	–	X	–
Serranidae	“genus <i>Serranidarum</i> ” spp.	–	–	X	X
	<i>Epinephelus</i> sp.	–	–	X	–
	“gen. aff. <i>Epinephelus</i> ” sp.	X	–	–	–
Haemulidae	“genus <i>Pomadasydarum</i> ” sp.	–	–	–	X
Carangidae	“genus <i>Carangidarum</i> ” sp.	–	–	X	–
Sparidae	<i>Archosargus</i> sp.	–	–	X	–
	<i>Lagodon</i> aff. <i>L. rhomboides</i> (Linnaeus, 1766)	X	–	X	–
	“genus <i>Sparidarum</i> ” sp.	–	–	X	–
Sciaenidae	<i>Umbrina</i> sp.	–	–	X	–
	<i>Pogonias</i> sp.	–	–	X	–
	<i>Sciaenops</i> sp.	X	–	X	–
	<i>Leiostomus compressus</i> Müller, 1999	X	–	–	–
	<i>Leiostomus crassior</i> Müller, 1999	–	–	X	–

TABLE 3.4. (Continued)

Taxonomy		Formation			
Family	Taxon	Calvert	Choptank	St. Marys	Eastover
	<i>Genyonemus calvertensis</i> Müller, 1999	X	–	–	–
	“gen. aff. <i>Genyonemus</i> ” <i>pertenuis</i> Müller, 1999	X	–	–	–
	<i>Menticirrhus</i> aff. <i>M. litoralis</i> (Holbrook, 1855)	–	–	X	–
	<i>Menticirrhus</i> sp.	–	–	X	–
	“gen. aff. <i>Pachyurus</i> ” <i>atavus</i> Müller, 1999	X	–	–	–
	“gen. aff. <i>Pachyurus</i> ” <i>breviformis</i> Müller, 1999	–	–	X	–
	<i>Cynoscion senior</i> Müller, 1999	X	–	X	X
Uranoscopidae	<i>Astroscopus</i> sp.	–	–	X	X
Ammodytidae	<i>Ammodytes</i> aff. <i>hexapterus</i> Pallas, 1814	–	–	X	X
	<i>Ammodytes</i> sp.	–	–	X	–
	“genus <i>Percoideorum</i> ” <i>subcircularis</i> Müller, 1999	X	–	–	–
	“genus <i>Percoideorum</i> ” sp.	–	–	X	–
Pleuronectidae	“genus <i>Pleuronectidarum</i> ” sp.	–	–	X	–
Paralichthyidae	<i>Citharichthys</i> spp.	X	–	X	X
Cynoglossidae	<i>Symphurus</i> sp.	X	–	–	–
	“genus <i>Pleuronectiformorum</i> ” spp.	–	–	X	–

the northwestern Atlantic waters. One of these is the needlefish *Belone* that is today restricted to the eastern Atlantic and the Mediterranean Sea; the occurrence of *Belone* in the St. Marys Formation might be in some ways related to the same transatlantic migration that resulted in the arrival of the gadine *Gadus* and *Melanogrammus* in the northwestern Atlantic waters.

Lundberg and Luckenbill (2012) discussed the biogeographic significance of the peculiar distribution of the Miocene catfish *Ictalurus countermani*, which is extralimital to the known range of fossil and extant channel catfish species (*I. punctatus* group) and, more generally, the entire genus *Ictalurus*; the current presence of at least two *Ictalurus* species along the Atlantic coasts of the United States is the result of transplantation that started in the last decades of nineteenth century (Lundberg and Luckenbill, 2012).

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