

SMITHSONIAN CONTRIBUTIONS TO PALEOBIOLOGY • NUMBER 100



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

Edited by Stephen J. Godfrey SMITHSONIAN CONTRIBUTIONS TO PALEOBIOLOGY • NUMBER 100

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Smithsonian Institution Scholarly Press WASHINGTON, D.C. 2018

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

Giorgio Carnevale^{1*} *and Stephen J. Godfrey*²

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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Received 1 May 2015; accepted 25 August 2017.

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 posttemporal 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 specieslevel 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 LEPISOSTEIFORMES HAY, 1929

FAMILY LEPISOSTEIDAE 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), wellpreserved 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





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 pharvngobranchial; CMM-V-3392, third pharvngobranchial; 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 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 3.9],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

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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 3.13. (*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

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	_	-

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.

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 triturating 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 nonerectile, 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.

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	-	-	_
Predentary				
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	_

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.