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## A New Early Miocene Species of *Pogonias* (Teleostei: Sciaenidae) Based on Otoliths from California

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**Abstract.**—A new species of early Miocene croaker of the genus *Pogonias* (Perciformes: Sciaenidae) from the marine upper Olcese Sand, southeastern San Joaquin Valley, Kern County, California is described based on saccular (=sagittae) otoliths. This is the first fossil record of the genus *Pogonias* from the eastern Pacific Rim. It is hypothesized that this new species of *Pogonias* or its ancestor emigrated from the Gulf Stream of the western Atlantic into the eastern Pacific via the Panama seaway during or prior to the late early Miocene.

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*Pogonias* Lacepède, 1801 in the genus of the family Sciaenidae (croakers or drums), is represented by a single extant species, *P. cromis* Linnaeus, 1766, which is the largest member of the family in the western North Atlantic Ocean (Jones and Wells 1998), with a maximum size of over 117 cm and may weigh as much as 54 kg (Murphy et al. 1998). A long-lived fish, *P. cromis* can reach almost 60 years of age (Jones and Wells 1998). The species occurs along the Atlantic and Gulf of Mexico coasts of America, from Argentina to southern New England (Bigelow and Schroeder 1953), and as far north as the Bay of Fundy (Bleakney 1963). It is common from the Chesapeake Bay south to Florida and most abundant along the Texas coast (Simmons and Breuer 1962). *Pogonias cromis* is a demersal fish of shallow (to 10 m) brackish and marine, subtropical waters, and is usually found over sand and sandy mud substrates in coastal waters. Reported fossil occurrences of *Pogonias* include fish remains from Miocene age deposits of Delaware, Maryland, North Carolina, and Virginia, and Pliocene age deposits of North Carolina.

Paleontological studies of Tertiary teleostean otoliths from California are few and reported detailed descriptions of fossil otolith assemblages are almost nonexistent. This is especially true for the southeastern San Joaquin Basin along the western flank of the Sierra Nevada, California, despite the presence of richly fossiliferous shallow-marine Tertiary sedimentary deposits. These sediments have yielded, in addition to otoliths, abundant marine invertebrates, locally rich concentrations of marine vertebrates, and very rare land mammal remains (Mitchell 1965; Addicott 1970; Savage and Barnes 1972). The late John E. Fitch and field parties in the 1960's and early 1970's intensely bulk sampled matrix from numerous localities for fossil teleostean otoliths from the Barker's Ranch area in the hills to the northeast of Bakersfield, Kern County, California (Huddleston and Takeuchi 2007; Fig. 1). Nearly 1,800 kg of fossiliferous matrix was removed and processed (Clarke and Fitch 1979). This material has produced approximately 21,000 saccular (= sagitta) otoliths, representing at least 67 species belonging in 26 or more families, several thousand teeth of sharks, skates, and rays, *Cetorhinus* sp. (basking shark) gill rakers, and hundreds of squid statoliths. The teleost

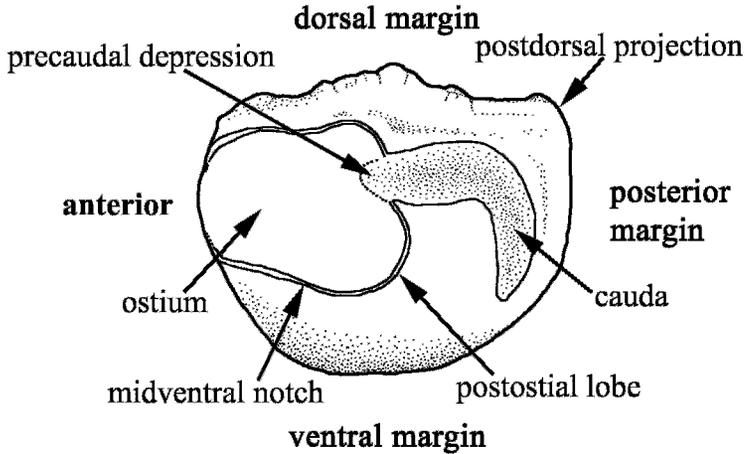


Fig. 1. Diagram of the inner face of a right saccular otolith of *Pogonias* illustrating its various diagnostic features. Modified after Schwarzhans (1993).

assemblage at this site includes pleuronectids and bothids (right- and left-eyed flatfishes), serranids (basses), atherinids (silversides), mugilids (mulletts), gobiids (gobies), clupeids (herrings), and other nearshore forms (Clarke and Fitch 1979), but the vast majority of the otoliths are of sciaenids. The Sciaenidae represent approximately 58% of the total number of otoliths (approximately 12,000 of the approximately 21,000 otoliths) and include at least 7 genera.

The Barker's Ranch ichthyofauna lacks a comprehensive faunal study. Some groups, such as the mollusks and other invertebrates, are well documented from the Barker's Ranch area (Addicott 1956, 1965, 1970, 1972; Clarke and Fitch 1979). However, the Barker's Ranch ichthyofauna has been largely untouched except for a few brief reports. Fitch (1969:13, fig. 2d) reported, but did not describe otoliths of the lanternfish *Lampanyctus* in a review of fossil Myctophidae of North America. Clarke and Fitch (1979:492) in a study of fossil teuthoid (cephalopod) statoliths of North America briefly mentioned some of the associated teleost fauna based on otoliths. Olson and Welton (1986:49) listed the selachian taxa and otoliths of unidentified sciaenids and bothids. More recently, the authors have reported a fin spine of the chimaeroid fish *Edaphodon* (Takeuchi and Huddleston 2006) and described the first fossil occurrence of the sciaenid genus *Totoaba* based on saccular otoliths from the Barker's Ranch area (Huddleston and Takeuchi 2007).

We describe here a new late early Miocene species of sciaenid, in the genus *Pogonias* from California based on three saccular otoliths. This is a significant discovery, not only because it is an undescribed form, but also it is the only representative of the genus from the eastern Pacific Rim.

#### Material and Methods

Otoliths are comprised of three calcium carbonate structures, mainly in the form of aragonite, and organic matter called otoline (Nolf 1985), in the inner ear of teleosts: utricular (lapillus), lagenar (asterisk), and saccular (sagitta). They have been discussed extensively by Nolf (1985) including their anatomy, morphology, variability, ontogenetic changes, and preservation. The saccular otolith is generally the most widely used in comparative morphology because of their large size, degree of interspecific variation, and

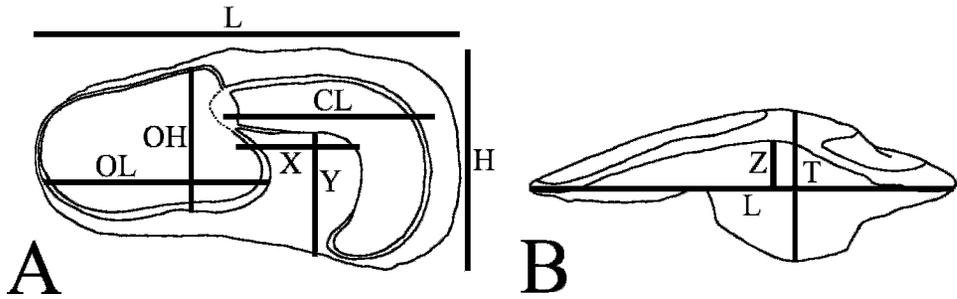


Fig. 2. Generalized sciaenid right saccular otolith illustrating measurements used for proportional ratios. **A**, inner face; **B**, ventral view. **Abbreviations:** *cl*, cauda length; *h*, otolith height; *l*, otolith length; *oh*, ostium height; *ol*, ostium length; *t*, otolith thickness; *lz*, curvature index of the inner face (*cii*); *x*:*y*, caudal curvature index (*cci*). Modified after Schwarzhans (1993).

ease by which the structures can be accessed (Gaemers 1984; Nolf and Steurbaut 1989; Lombarte et al. 1991). Sciaenid saccular otoliths in particular, are characterized by their large size and diverse morphology (Schwarzhans 1993). The taxonomic identification of fossil otoliths is based on comparative studies with sagittae of the nearest Recent relative (see Nolf 1985; Smale et al. 1995). Fossil otolith assemblages have repeatedly been shown to provide a more detailed and accurate account of Tertiary ichthyofaunas than the exclusive use of isolated skeletal elements or articulated remains (Nolf 1995). Fossil otoliths are found in a wide spectrum of sedimentary environments and are common fossils in many marine sediments, in contrast, the preservation of fish skeletons nearly always represents unusual environmental circumstances (Nolf 1985, 1995). Patterson (1993) in a survey of the fossil record of teleostean fishes showed that among the 244 extant families that do have a fossil record, 58 families (24%) are exclusively recorded from otoliths. In addition, the fossil record for many families is extended considerably geographically and temporally by otoliths (Nolf 1995).

Recent comparative materials used in this study are from the collections of the Department of Ichthyology, Natural History Museum of Los Angeles County, Los Angeles, California (LACM), and include 18 uncatalogued saccular otoliths of *P. cromis*. Additional saccular otoliths of *P. cromis* were provided from the private collection of M. A. Roeder.

The specimens studied are deposited in the collections of the Department of Vertebrate Paleontology, LACM. Undescribed and uncatalogued material from the Barker's Ranch locality is stored in the John E. Fitch Otolith Collection housed in the Department of Ichthyology, LACM. Bulk matrix samples were wet-screened in water to remove the fine fraction and the remaining concentrated matrix was manually sorted under a dissecting microscope to remove identifiable otoliths, teeth, and bones. This method is fully described in Clarke and Fitch (1979:480–481). Specimens were photographed with a Nikon D70 digital camera.

Morphological terms (Fig. 1) used in the general description mainly follow those of Nolf (1985) and Schwarzhans (1993). Linear measurements were made on an EPOI Shopscope optical micrometer. Measurements and proportional ratios of the otolith for the Sciaenidae follow the method proposed by Schwarzhans (1993), and are described below. Otolith measurements are shown on Fig. 2. Measurements used for proportional ratios on the inner face include the following: otolith length (*L*) is the greatest anterior to posterior length; otolith height (*H*) is the greatest dorsal to ventral height; ostium length

(ol) is taken from the anterior edge of the ostium to the posterior most extension of the ostium, including the postostial lobe, if present; ostium height (oh) is the greatest dorsal to ventral height of the ostium with the otolith in natural position; cauda length (cl) is measured from the dorsal edge of the cauda at the dorsal caudal joint to the posterior most extension of the dorsal caudal margin; length of horizontal portion of the cauda (x) is measured from the caudal joint of the ventral caudal margin to the posterior most extension of the ventral caudal margin; length of down turned portion of cauda (y) is from the highest point of the ventral caudal margin to the ventral most point of the cauda termination. Measurements used for proportional ratios from lateral view: otolith thickness (T), is the greatest inner face to outer face thickness taken in dorsal view; z, is measured from L to the highest point of the ventral margin; curvature index of the inner face (cii), is the ratio of the otolith length (L) to z in dorsal view.

#### Systematic Paleontology

Class Actinopterygii sensu Nelson, 2006

Division Teleostei sensu Nelson, 2006

Order Perciformes sensu Johnson and Patterson, 1993

Family Sciaenidae Cuvier, 1829

Subfamily Sciaeninae Gill, 1861

Genus *Pogonias* Lacepède, 1801

*Type-species.*—*Pogonias fasciatus* Lacepède, 1801

*Generic Diagnosis (emended from Schwarzhans 1993).*—The saccular otolith is subovate with a strongly convex inner face and an L:H index of 1.2–1.4. The dorsal margin is semi-flat, except for a strong to moderate mediodorsal dome and low mediodorsal angles. The posterior margin is strongly curved and slightly blunted at its upper edge with a moderate to well developed postdorsal projection. The ventral margin is broadly rounded, as is the anterior margin. The ostium is large and subrectangular, tapering or constricted at the anterior end with an ol:oh index greater than 1.0. The cauda is narrow and steeply curving. The length of the anterior part of the cauda is equal to or less than the length of the posterior part. The outer face is slightly concave, and a tuberculate ornamentation is sometimes present in the area of the postcentral umbo.

*Pogonias stringeri*, sp. nov.

(Figs. 3–5; Table 1)

*Holotype.*—LACM 151868, right saccular otolith (Figs. 3, 4A, B).

*Paratypes.*—LACM 151869, right saccular otolith (Fig. 4C, D); LACM 151870, right saccular otolith (Fig. 4E, F).

*Locality and Horizon.*—The type locality is in the early Miocene Olcese Sand, part of the Temblor Group, in the southeastern San Joaquin Basin, California, at the “Ledge Site,” LACM locality 6602, NW  $\frac{1}{4}$  of Sec. 33, T. 28 S., R. 29 E., (Rio Bravo 7.5' quadrangle), approximately 13 km northeast of Bakersfield, Kern County, California (Huddleston and Takeuchi 2007; Fig. 1). The specimens studied have been collected from near the top of the upper Olcese Sand (Clarke and Fitch 1979:492; Huddleston and Takeuchi 2007) in a shell bed directly below a calcareously cemented sandstone that is approximately 14 m stratigraphically below a mottled siltstone of the lower Round

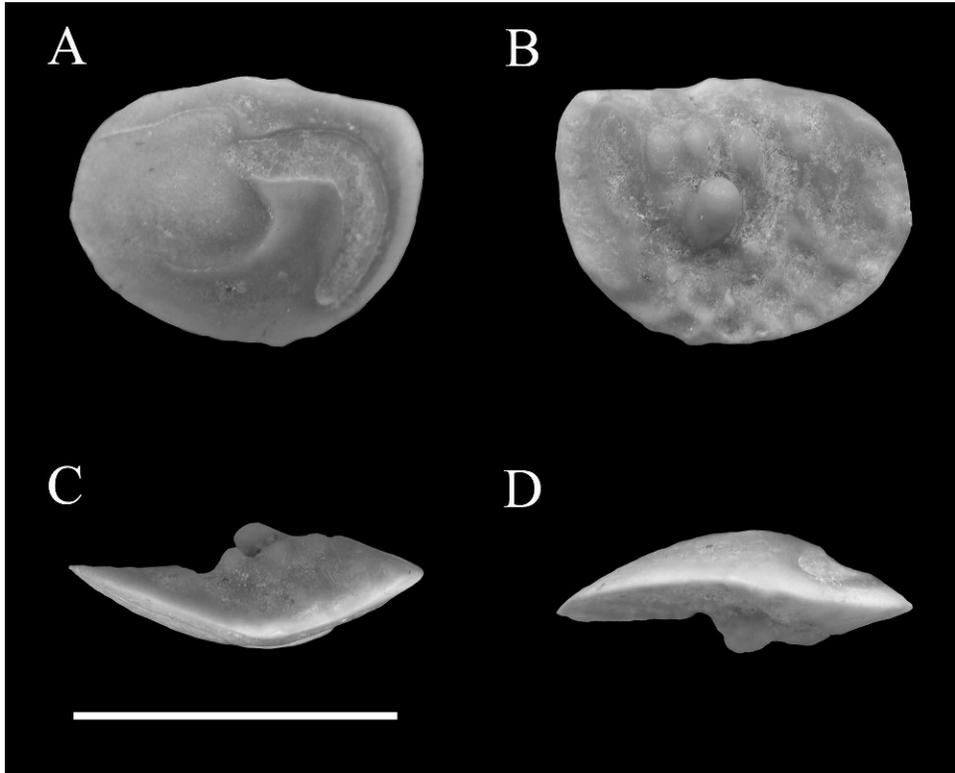


Fig. 3. *Pogonias stringeri* sp. nov. (holotype; LACM 151868), right saccular otolith, late early Miocene, upper Olcese Sand, Kern County, California. **A.** inner face; **B.** outer face; **C.** dorsal view; **D.** ventral view. Scale bar equals 1 cm.

Mountain Silt. The upper Olcese Sand is interpreted to represent shelf deposits that were deposited below normal wave base, signified by the presence of oscillations of storm-induced, wave-formed beds and concentrated shell lags based on abundant mollusks and foraminifera (Addicott 1970; Olson 1990). Recent paleomagnetic studies by Prothero et al. (in press) have correlated the upper member of the Olcese Sand with paleomagnetic Chrons C5Cn2–C5Cn3 (16.1–16.6 Ma), confirming the latest early Miocene age for this unit. The locality is discussed at length in Huddleston and Takeuchi (2007).

**Diagnosis.**—The saccular otolith of *Pogonias stringeri* is distinguished from the extant *Pogonias cromis* in the following combination of characters: 1) a narrower ostium, constricted anteriorly, with a well developed midventral notch (Fig. 5); 2) a lower rounded mediadorsal angle with a reduced posterior dorsal projection (Fig. 5); and 3) a tubuculate ornamentation in the postcentral umbo area (Fig. 5).

**Discussion.**—The saccular otolith of *Pogonias stringeri* shows a number of characters diagnostic of Sciaenidae, including: a strongly homosulcoid sulcus, with both the rostrum and antirostrum absent; a broad, flat, shallow ostium with a distinct postostial lobe; and a narrow and horizontal cauda with a curved posterior cauda. The inclusion of the species in the genus *Pogonias* is justified by the presence of the following features: a compressed otolith with deeply rounded ventral rim and shallow dorsal rim; a moderately convex inner face; a strongly enlarged ostium with a ol:oh index larger than 1.0; a short,

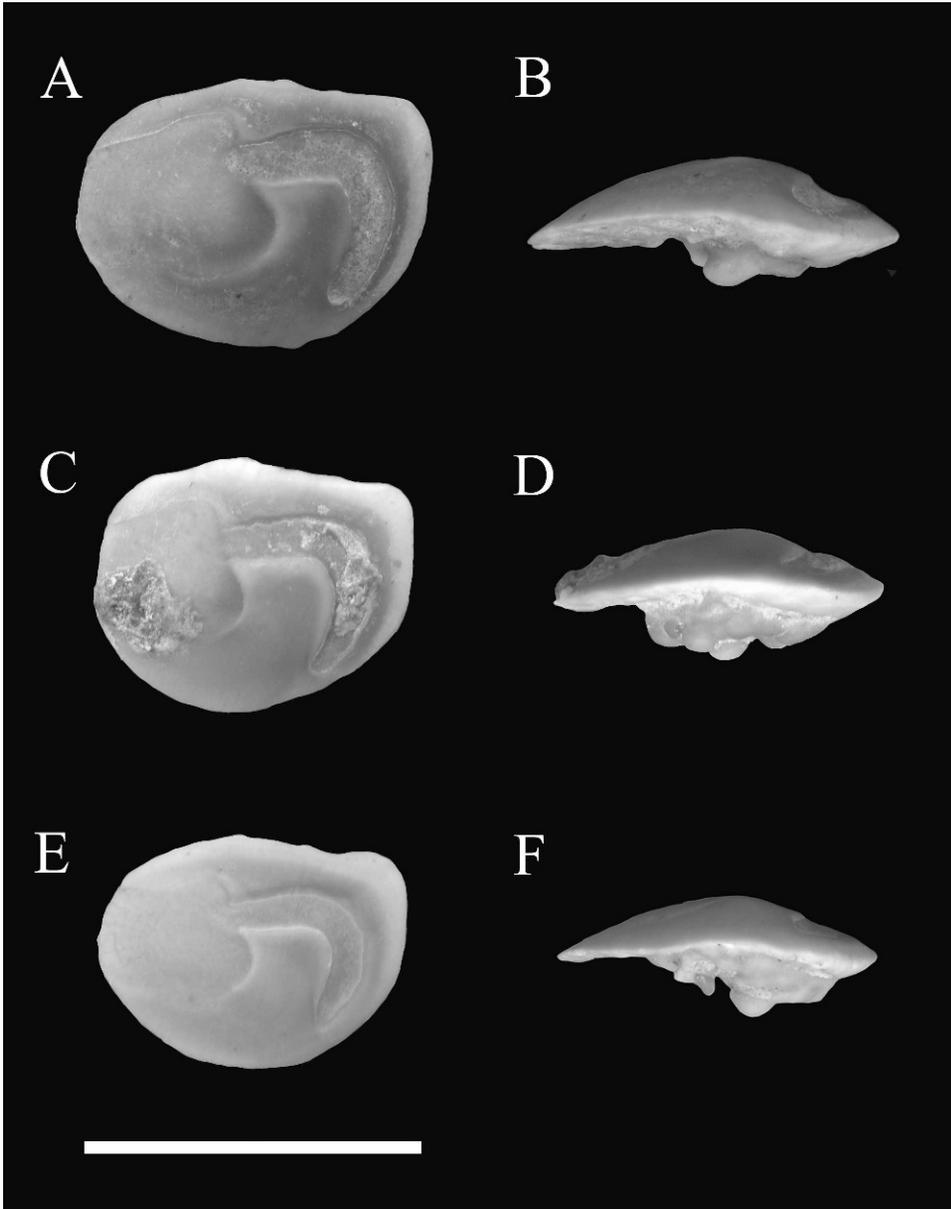


Fig. 4. *Pogonias stringeri* sp. nov. holotype right saccular otolith, LACM 151868, **A**, inner face; **B**, ventral view; paratype right saccular otolith, LACM 151869, **C**, inner face; **D**, ventral view; paratype right saccular otolith, LACM 151870, **E**, inner face; **F**, ventral view. Scale bar equals 1 cm.

narrow, moderately deep and steeply curving cauda; and a sharply pointed, slightly projecting, posterodorsal projection.

*Etymology*.—The species is named in honor of Dr. Gary L. Stringer, Professor of Geology, University of Louisiana at Monroe, Louisiana in recognition of his contribution to the study of fossil fish otoliths, particularly in the Gulf Coast of North America.

*Description*.—The holotype of *P. stringeri* (LACM 151868) is a slightly eroded right saccular otolith with a total length of 10.5 mm and a greatest height of 7.9 mm.

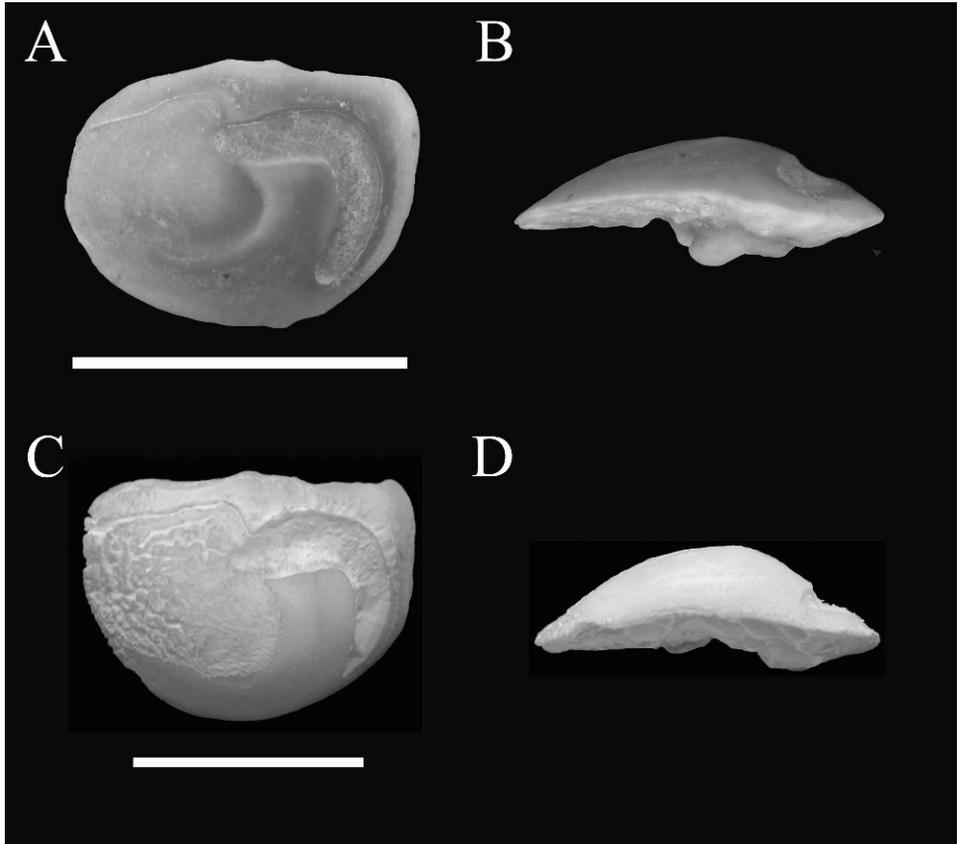


Fig. 5. Saccular otolith of fossil and Recent *Pogonias* species. *Pogonias stringeri* sp. nov. (holotype; LACM 151868), **A**, innerface **B**, ventral view; *Pogonias cromis*, **C**, innerface **D**, ventral view. Scale bars equals 1 cm.

Measurements and proportional ratios for the saccular otolith of *P. stringeri* are summarized in Table 1. The otolith is small, subovate with the inner face strongly convex. The dorsal margin has a low mediodorsal dome and low mediodorsal angles, with a moderate posterodorsal projection. The anterior margin is sharply rounded and posterior margin is strongly curved, with the ventral margin deeply to broadly rounded. The ostium is large, subrectangular, and constricted anteriorly, creating a prominent midventral notch, with a moderate postostial lobe. The precaudal depression is short with a moderately long curved cauda. The anterior cauda is horizontal and shorter than the posterior cauda, which is bent or curved ventrally. The outer face is slightly concave and thick, with a strong tuberculate ornamentation in the postcentral umbo area. The paratypes of *P. stringeri* (LACM 151869 and LACM 151870) vary only slightly from the type in having a slight flattening at the upper edge of the posterior margin (Fig. 4C–F).

#### Discussion and Conclusions

All prior reported fossil occurrences of *Pogonias* are from the east coast of North America, with a fossil record ranging from Miocene to Pliocene. Purdy (1998:139, plate 2, fig. 24) reported pharyngeal plates and isolated teeth referred to *Pogonias* sp. from the lower shell bed of the Cheswold sands of the early Miocene Calvert Formation, Pollack

Table 1. Comparison of measurements and proportional ratios of the saccular otolith between species of *Pogonias*. Abbreviations: l, otolith length; h, otolith height; t, otolith thickness; ol, ostium length; oh, ostium height; cl, caudal length; x, horizontal portion of cauda; y, down turned portion of cauda; x:y, caudal curvature index (cci); lz, curvature index of the inner face (cii). See text and Fig. 3 for definition of abbreviations. Measurements are in mm.

	l	h	t	ol	oh	cl	x	y	z	l:h	h:t	cl:ol	ol:h	cci	cii	
<b><i>P. stringeri</i> (adult)</b>																
LACM 151868 (holotype)	10.5	7.9	3.7	6.0	4.8	4.4	2.8	3.7	2.7	1.33	2.13	0.73	1.25	0.76	3.89	
LACM 151869 (paratype)	9.0	6.9	3.6	4.4	3.8	3.8	2.5	3.4	2.0	1.30	1.91	0.86	1.16	0.74	4.50	
LACM 151870 (paratype)	8.9	6.7	3.3	4.4	3.4	3.7	2.5	3.0	1.9	1.33	2.03	0.84	1.29	0.83	4.68	
Mean	9.46	7.17	3.53	4.93	4.0	3.97	2.60	3.36	2.20	1.32	2.03	0.81	1.23	0.78	4.36	
Standard Deviation	0.90	0.64	0.21	0.92	0.72	0.38	0.17	0.35	0.43	0.01	0.11	0.07	0.07	0.05	0.42	
Coefficient of Variation	9.46	8.97	5.89	18.72	18.02	9.54	6.66	10.43	19.81	1.07	5.39	8.57	5.63	6.65	9.55	
Maximum	10.5	7.9	3.7	6.0	4.8	4.4	2.8	3.7	2.7	1.33	2.13	0.86	1.29	0.83	4.68	
Minimum	8.9	6.7	3.3	4.4	3.4	3.7	2.5	3.0	1.9	1.30	1.91	0.73	1.6	0.74	3.89	
<b><i>P. cromis</i> (adult)</b>																
Mean	14.15	11.04	3.77	7.47	7.05	5.83	3.95	4.80	3.19	1.28	3.02	0.78	1.07	0.83	4.44	
Standard Deviation	2.36	1.65	0.97	1.44	1.54	1.35	0.89	0.95	0.50	0.43	0.44	0.05	0.05	0.10	0.25	
Coefficient of Variation	16.70	14.98	25.66	19.23	21.81	23.12	19.73	25.66	15.72	3.39	14.62	6.09	4.87	12.00	5.71	
Maximum	18.5	14.2	5.5	9.8	9.4	8.7	5.8	6.5	4.0	1.36	3.63	0.89	1.13	1.00	5.00	
Minimum	11.4	9.2	2.7	5.6	5.1	4.2	2.9	3.5	2.6	1.21	2.18	0.72	0.93	0.64	4.14	
Number = 15																
<b><i>P. cromis</i> (juvenile)</b>																
Mean	7.3	5.98	1.86	3.62	3.38	2.96	2.14	2.22	1.6	1.22	3.21	0.82	1.07	0.96	4.58	
Standard Deviation	0.73	0.58	0.09	0.48	0.35	0.43	0.40	0.34	0.21	0.01	0.25	0.07	0.04	0.08	0.29	
Coefficient of Variation	10.07	9.64	4.80	13.30	10.33	14.64	18.87	15.41	13.26	0.79	7.92	8.61	4.15	8.67	6.31	
Maximum	7.9	6.4	2.0	4.1	3.7	3.5	2.6	2.5	1.9	1.23	3.56	0.90	1.14	1.04	4.88	
Minimum	6.4	5.3	1.8	3.1	3.0	2.5	1.7	1.8	1.4	1.21	2.94	0.71	1.03	0.84	4.11	
Number = 5																

Farm Site, Chewold, Delaware. No detailed description of the material was given. Purdy (1998) noted that the fish fauna from the Pollack Farm Site is identical to those of the Calvert and Pungo River formations of Maryland and North Carolina, respectively. Purdy et al. (2001:176, fig. 72 f, g) tentatively assigned upper and lower pharyngeal plates, premaxillae, and isolated pharyngeal teeth to *P. cromis* from the early Miocene Pungo River and the early Pliocene Yorktown formations, Lee Creek Mine, Aurora, North Carolina. Using an upper pharyngeal tooth length/count ratio, they concluded the Lee Creek Mine pharyngeal compared favorably with the extant species. However, they did note some inconsistencies in the shape and articulating surfaces of the fossil specimens. In addition, Fitch and Lavenberg (1983:523) reported a saccular otolith of *Pogonias* cf. *P. cromis*, based on a small (6.1 mm long), badly chipped specimen from the Yorktown Formation. They noted, “the inner face is concave and it has a sharply pointed, slightly projecting posterodorsal corner that is unique to *Pogonias*. In these features and other characters it agrees well with otoliths of *P. cromis*.” The specimen was not illustrated. Müller (1999:171, fig. 35/27a–b) in his extensive monograph of the Tertiary bony fish fauna of the U. S. Atlantic Coastal Plain, referred a single incomplete otolith to *Pogonias* sp. from the late Miocene age Little Cove Point Member of the St. Marys Formation, Maryland. He considered the otolith similar to, but distinct from *P. cromis* based on apparent differences of the sulcus, a wider cauda, and a slightly convex outerface. Unfortunately, there was insufficient material to assign this specimen to a species. He also noted that “jaw bones, characteristic pharyngeal teeth and other pharyngeal items of *Pogonias* have also been found in St. Marys Formation (Little Cove Point Member).” Cope (1869) described a nearly complete right upper pharyngeal plate from Nomini Cliffs, Westmoreland County, Virginia, which he named *P. multidentatus*. This pharyngeal plate contains more teeth in the same relative area than the extant species, *P. cromis*. In the area of Nomini Cliffs the Calvert, Choptank, and St. Marys formations are all well exposed at this site and the precise collecting locality is unclear from Cope’s (1869) description. Smith (1909) speculated that the type was collected from the late Miocene age St. Marys Formation based on a second specimen referred to *P. multidentatus*.

Fossil material removed from *Pogonias* includes the following: Weinfurter (1952:473–475, pl. 1 fig. 6a–d) described and illustrated a right saccular otolith, “*Sciaenidarum*” *stryriacus* from the middle Miocene of Austria that he was unable to place taxonomically, and was left in open nomenclature. Schwarzhans (1993:86) tentatively place this species in *Pogonias* based on Weinfurter’s (1952) drawings of the otolith and did not review the type or any other material representing the species. However, the type is a strongly eroded non-diagnostic otolith and should be considered as a rejected species (D. Nolf pers. comm., 2006).

Based on the limited fossil record of *Pogonias*, as well as its extant distribution, we suggest the genus or its ancestor evolved entirely in Tropical America during the mid-Tertiary. The family Sciaenidae is a strongly provincialized group of fishes, with nearly all of the 70 extant genera confined to a specific bioprovince (Sasaki 1989). Distribution of extant sciaenids reveals the greatest diversity and highest number of species in two primary regions of the world’s oceans, the Indo-West Pacific and Tropical America (on both Pacific and Atlantic sides). Each region may represent a major evolutionary center for sciaenid radiation and dispersal (Chao 1986; Sasaki 1989; Schwarzhans 1993). Sasaki (1989) noted that 14 extant sciaenid genera possess an Amphi-American distribution and the family possibly originated in a restricted area of the New World. The North American

otolith-based fossil record of the Sciaenidae strongly supports the hypothesis that Tropical America was the major evolutionary center for this family. The earliest geologic occurrence of the family is from middle to late Eocene deposits of the Gulf Coast region of North America (Koken 1888; Frizzell and Dante 1965; Breard and Stringer 1999; Nolf 2003; Nolf and Stringer 2003) and the family does not appear in the European fossil record until the Relian (lower Oligocene). Remarkably, sciaenids are totally absent from otolith-rich Eocene deposits in California. They first appear in the early Miocene (ca 23 Ma) Jewett Sand Formation in central California and consist of a small poorly preserved fauna including several undescribed taxa. By the late early Miocene the family is well established in the eastern Pacific and is reflected in the occurrence of at least 7 genera from the Barker's Ranch locality (LACM locality 6602). This has led us to hypothesize that the family initially invaded the eastern Pacific from the Gulf Coast region through the Panamanian Seaway sometime after the Eocene (Huddleston and Takeuchi 2006) and *Pogonias* or its ancestor evolved in the Gulf Coast/Western Atlantic coastal region prior to its dispersal into the Eastern Pacific.

The presence of *Pogonias* in the eastern north Pacific realm during the late early Miocene is particularly significant from a biogeographic point of view. Its presence in the eastern north Pacific could be explained by an expanded area of distribution of this genus today restricted to the Atlantic shores of America. A wider distribution of these fishes was probably related to the Panama seaway, which formed a corridor linking the modern eastern Pacific and Atlantic during much of the Tertiary. Assuming fossil sciaenids had similar ecological preferences to Recent sciaenids, this seaway made it possible for nearshore fishes, such as *Pogonias*, to move along subtropic shorelines, which are now disrupted. The vicariant closure of the seaway with the uplift of the Isthmus of Panama occurred between 3.7 and 3.0 Ma (Duque-Caro 1990; Coates et al. 1992; Coates and Obando 1996; Ibaraki 1997), dividing a former single bioprovince in two; separating the Pacific faunas and the Atlantic faunas. In addition to ecological and evolutionary effects, the emergence of the isthmus caused substantial variations in regional surface water temperature, changes in oceanic circulation (Keigwin 1978, 1982), modifications of sedimentation rates, variations of climatic marine conditions in both the Atlantic and Pacific oceans, and an increase of salinity in the Caribbean Sea and western Atlantic (Coates and Obando 1996; Ibaraki 1997). This was not a single event and had major biological effects on marine organisms that are likely to have spread since the late Miocene (Coates and Obando 1996; Collins 1996).

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