A RARE OCCURRENCE OF MATCHED OTOLITHS AND ASSOCIATED SKELETAL REMAINS OF *APOGON TOWNSENDI* (OSTEICHTHYES) FROM THE CALOOSAHATCHEE FORMATION (LOWER PLEISTOCENE) OF FLORIDA

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ABSTRACT

A matched pair of otoliths (right and left saccular otoliths) and associated skeletal remains (n = 107) of *Apogon townsendi* (belted cardinalfish) were obtained in unconsolidated sediment from inside the valves of an articulated scallop *Carolinapecten eboreus*. The scallop specimen was collected in Hendry County, Florida, from the lower Pleistocene Caloosahatchee Formation, approximately 1.7 to 2.1 Ma. The recovery of this vertebrate material is highly significant because no skeletal remains of bony fish with *in situ* or associated otoliths are known from the Gulf or Atlantic coasts of the United States. Furthermore, the specimen represents the first fossil record of the family Apogonidae and the genus *Apogon* from Florida and the first report of the species *Apogon townsendi* in the fossil record. The length of the fossil *Apogon townsendi* was determined to be 4.7 cm based on the linear relationship between fish length and otolith length and utilizing modern specimens of the species for comparison and analysis. The length of the fossil *Apogon townsendi* indicated that it was an adult fish upon death (> 2.1 cm). Although several taphonomic scenarios are considered, including commensalism, it is believed that the apogonid died in close proximity to the empty scallop shell, which was followed by fairly rapid washing in of sediment with the fish into the valves of the scallop (i.e., sediment trapping). This determination is based on several factors including the biology, distribution, and behavior of extant *Apogon townsendi.* The presence and preservation of the two matched saccular otoliths and the large number of associated, fragile skeletal remains in the scallop shell suggest that the apogonid was not ingested and excreted by a piscivorous predator.

Key words: *Apogon townsendi*; Caloosahatchee Formation; Florida; otolith; Pleistocene; taphonomy.

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INTRODUCTION

Osteological fish remains with otoliths *in situ* or with associated otoliths are rarely found. Nolf (1985) listed 23 fossil taxa of otoliths associated with skeletal material in which the otoliths were adequately preserved to be taxonomically beneficial. Since Nolf (1985), other skeletal remains with *in situ* or associated otoliths have been reported in North America, Europe, and Asia (Fierstine et al., 2012; Nolf, 2013:16–18; Schwarzhans et al., 2016:2–3).

There are at least three previous cases where fish skeletal remains with associated otoliths were found inside mollusk shells. Schwarzhans and Weiler (1971) described otoliths of a *Pristigenys* species (under the name of "*Trigla arambourgi?*"; see comments in Taverne and Nolf, 2010:233) from sediment inside a shell of the gastropod *Natica crassatina* collected in the Reupelian "Meeressand" of the Mainz Basin, Germany. Stinton (1980:209) mentioned otoliths of *Pristigenys dentifer* (a synonym of *Pristigenys rutoti*) collected with associated bones in a shell of the gastropod *Clavilithes macrospira* from the English Bartonian, and Taverne and Nolf (2010) reported *Pristigenys* skeletal material and associated otoliths recovered from the inside of several nautilid shells from the Sands of Lede (middle Eocene) of Belgium at the locality of Meldert, Belgium. Two *Pristigenys* species (*P. rutoti* and *P. hermani*) were recognized from different nautilid shells.

Studies of fish skeletons with otoliths (*in situ* or associated) in North America are even scarcer but have been reported from the western United States by Huddleston and Takeuchi (2002, 2006), Takeuchi and Huddleston (2008), and Fierstine et al. (2012). The importance of skeletal remains with associated otoliths for the purpose of taxonomic identifications and relationships was emphasized by Takeuchi and Huddleston (2008). No reports of skeletal remains with *in situ* or associated otoliths are known from the Gulf or Atlantic coasts of the United States, which increases the significance of the matched otoliths associated with osteological material from the Caloosahatchee Formation.

LOCALITY DATA AND STRATIGRAPHY

The otoliths and associated skeletal remains were collected at UF locality HN017 located in Clewiston in Hendry County, Florida (26.75389, -80.93389 WGS84)(Fig. 1). The collected material is from the lower Pleistocene Caloosahatchee Formation, approximately 1.7 to 2.1 Ma (Kolbe et al., 2011 and references therein). The deposit is predominately marine in origin with minor interbedded freshwater marls. The areal extent of the Caloosahatchee Formation (with a few exceptions) is southern peninsular Florida. Lithologies consist of shelly quartz sands, calcarenites, and limestones. Much of the deposit is unconsolidated except areas converted to limestones or calcarenites by subaerial weathering or action of groundwater (DuBar, 1974). Caloosahatchee Formation index mollusks found at UF locality HN017 include *Siphocypraea problematica* (Heilprin, 1886), *Diodora carolinensis* (Conrad, 1875), and *Cerithioclava caloosaense* (Dall, 1892). DuBar (1974) interpreted the paleoecology of the Caloosahatchee Formation to reflect deposition in a shallow, marginal sea and adjacent low-lying coastal areas.

MATERIAL AND METHODS

The matched pair of otoliths (right and left saccular otoliths) and associated skeletal material were obtained from unconsolidated sediment found inside an articulated set of valves of the scallop *Carolinapecten eboreus* (Conrad, 1833)(UF/IP 256774; Fig. 2). The scallop was 8.6 cm in width and 8.9 cm in length. It was collected by the late George and Wylda Stephens and was part of a collection transferred to the Florida Museum of Natural History from the Virginia Tech Department of Geosciences. The otoliths and associated bones were discovered during the water screening of the unconsolidated sediments in the scallop shell. The skeletal remains were disarticulated prior to processing but may have been fragmented further during the screening. The sediment was water screened using U.S. sieve sizes #14 (1.41 mm openings), #35 (0.50 mm openings), and #70 (0.20 mm openings). The otoliths and associated skeletal remains were recovered in

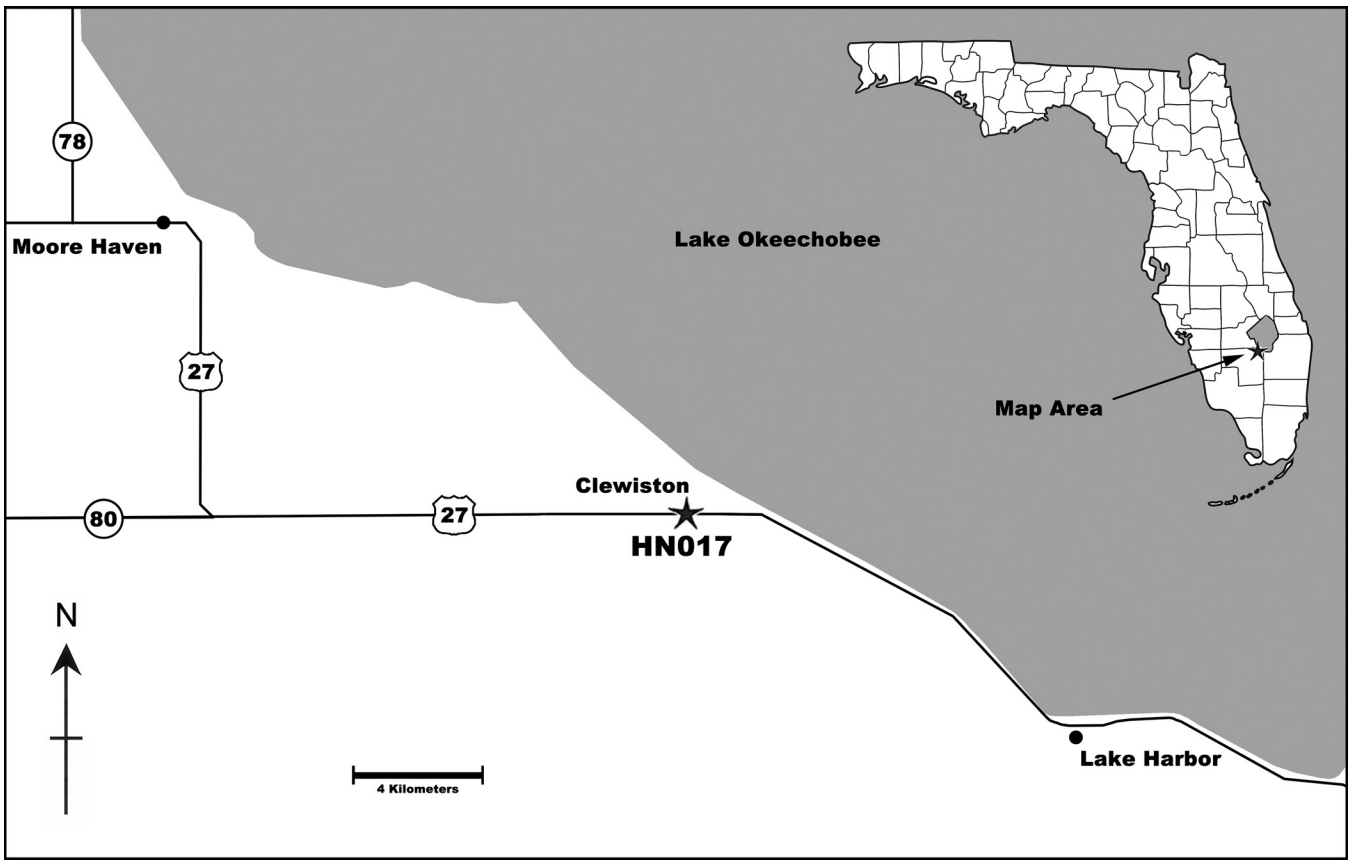

Figure 1. Map showing the location of UF locality HN017 in Hendry County, Florida, which produced the matched pair of fish otoliths and associated skeletal remains

the largest residue (sieve size #14). No other vertebrate remains were found within the scallop.

The vertebrate remains (UF 319000) consisted of well-preserved right and left saccular otoliths and associated skeletal material consisting of 107 disarticulated bones. Although much of the bony material was broken and fragmented, various skeletal elements were recognized including fin spines, vertebrae, premaxilla, maxilla, dentary, quadrate, posttemporal, and numerous fragmented bones of the skull. Institutional abbreviations are as follows: **IRSNB**, Institut royal des Sciences naturelles, Brussels, Belgium; **UF**, Division of Vertebrate Paleontology, FLMNH, Gainesville, Florida, USA; **UF/IP**, Division of Invertebrate Paleontology, FLMNH, Gainesville, Florida, USA; **FLMNH,** Florida Museum of Natural History, Gainesville, Florida, USA; **YPM**, Yale Peabody Museum of Natural History, New Haven, Connecticut, USA.

SYSTEMATIC PALEONTOLOGY

Key morphological features, such as the sulcus consisting of a wide ostium and narrower cauda with a collicular crest near the crista inferior, the prominent depression above the sulcus, the shape of the otolith, and the prominent anterodorsal dome, of the matched pair of saccular otoliths from the Caloosahatchee Formation clearly indicate an apogonid. Böhlke and Chaplin (1968) and McEachran and Fechhelm (2005) indicated the following Recent apogonids as occurring in southern Florida and the northern Caribbean: *Apogon* (12 species), *Astrapogon* (2 species), *Cheilodipterus* (1 species), *Paroncheilus* (1 species), and *Phaeoptyx* (2 species). Apogonid otoliths are often distinguished by subtle differences in the sulcus and the outline of the saccular otoliths and require well-preserved and abundant specimens (Nolf, 2013). Fortunately, the Caloosahatchee Formation otoliths were almost

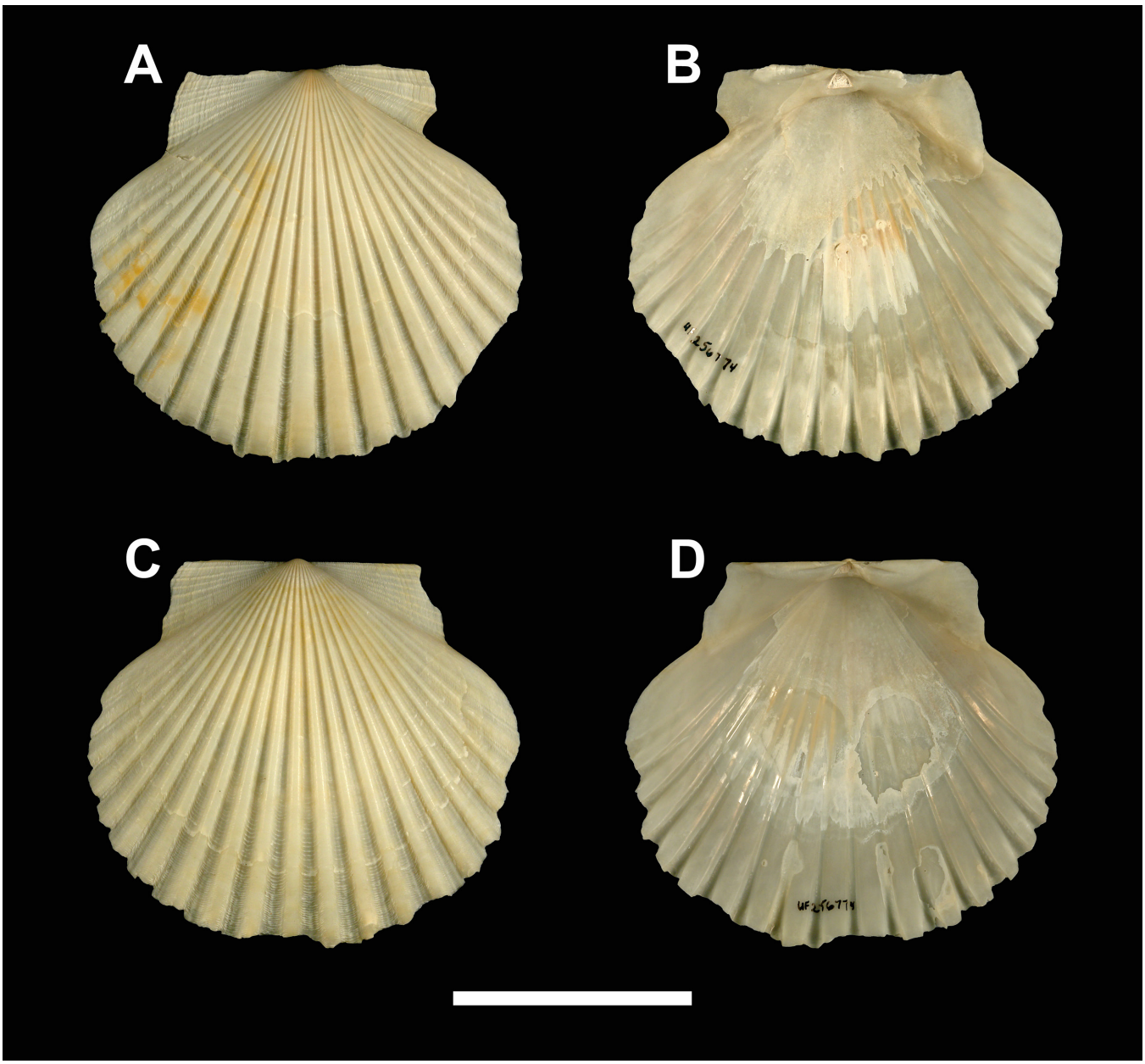

Figure 2. Paired valves (UF/IP 256774) of *Carolinapecten eboreus* (Conrad, 1833) that contained sediments with matched pair of fish otoliths and associated skeletal material. A. Exterior view of right valve. B. Interior view of right valve. C. Exterior view of left valve. D. Interior view of left valve. Scale Bar equals 5 cm.

perfectly preserved and allowed for identification. The Caloosahatchee Formation otoliths were compared with the otoliths of Recent apogonids that occur in southern Florida and the Caribbean from the IRSNB collection. They agree best with those of *Apogon townsendi*, which was illustrated by Nolf and Bajpai (1992)(Fig. 3). Stringer (1992) reported a similar apogonid from a late Pleistocene mudlump island in the Gulf of Mexico. Higher level taxonomy follows Nelson et al. (2016).

Class OSTEICHTHYES
Subclass ACTINOPTERYGII
Order KURTIFORMES
Family APOGONIDAE Günther, 1859
Subfamily APOGONINAE Günther, 1859
Genus *APOGON* Lacepède 1801

APOGON TOWNSENDI (Breder, 1927)

Figures 4–5

Type specimens.—YPM 460, holotype; YPM 463 to 465, paratypes, taken from Saddle Rock, Washerwoman Cut, Bahamas (Eschmeyer et al., 2017).

Saccular otolith description.—Both of the otoliths (from the left and right side; UF 319000) measure 3.5 mm in length and 2.85 mm in height (Fig. 4). The length to height ratio is 1.23. The outline of the otolith is primarily oval with a conspicuous anterodorsal dome. The margins tend be sinuate with the ventral margin more equally broad. The inner face is only very slightly convex and is characterized by a clearly delimited sulcus that is located approximately in the center. The distinct ostium is approximately 25% wider and 20% longer than the cauda. The ostium is slightly slanted toward the dorsal margin, whereas the cauda is essentially horizontal. The crista superior is well developed over part of the ostium and cauda. Colliculum is present in the ostium and cauda. The dorsal area is characterized by a pronounced oval depression located above the junction of the ostium and the cauda. The ventral area is characterized by a shallow ventral groove that is parallel to the ventral margin. The outer face is markedly more convex than the inner face and primarily smooth with some slight undulations.

Skeletal elements description.—Although no skeletal remains of *A. townsendi* were available, lateral and medial views of the maxilla, premaxilla, dentary, angular, and quadrate of the Recent apogonid *Apogon menesemus* in Dye and Longenecker (2004) were compared to the bones found in association with the otoliths. The Caloosahatchee skeletal remains, especially the diagnostic premaxilla, compared very favorably with the Recent apogonid, but the actual species determination was based on the otoliths. However since the matched otoliths were found in the scallop valve, then it is highly probable that the skull of the fish was present. Since the only vertebrate remains in the scallop shell were the otoliths and the apogonid bones, it appears to be a valid assumption that the bones were *A. townsendi*. As noted previously, the majority of the skeletal remains of *A. townsendi* (UF 319000) were broken and highly fragmented. However, some skeletal elements were recognizable and are briefly described.

One of the best-preserved skull elements is the right premaxilla; possible fragments of the left premaxilla are also present. This is fortunate since

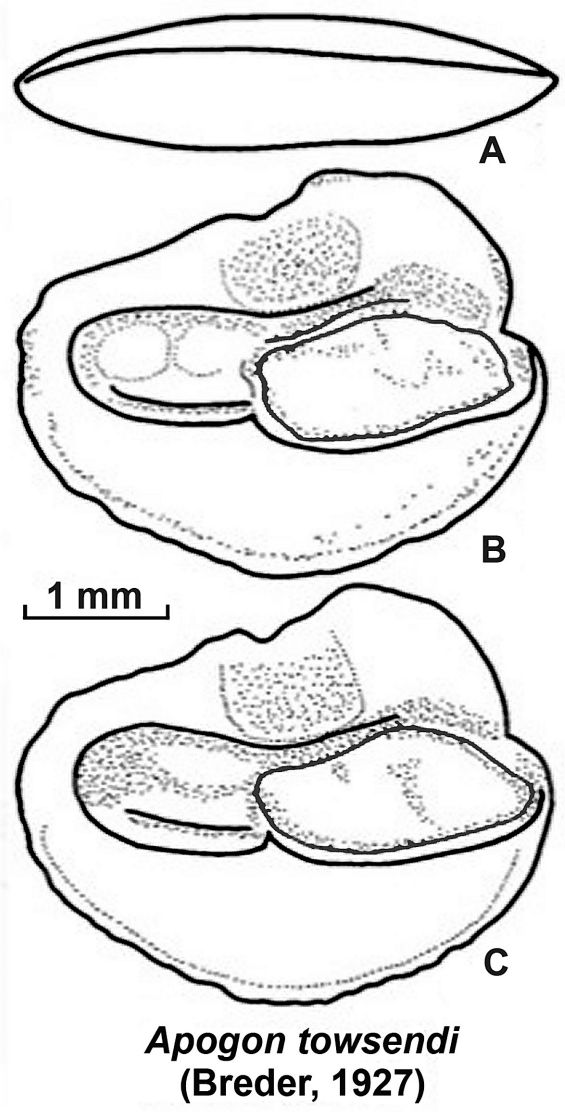

Figure 3. Left saccular otoliths from two Recent specimens of *Apogon townsendi* (Breder, 1927) from off Mona Island, Lesser Antilles (Coll. IRSNB). Dorsal view of first specimen (A). Inner face of first specimen (B). Inner face of second specimen (C). Figure modified from Nolf and Bajpai (1992).

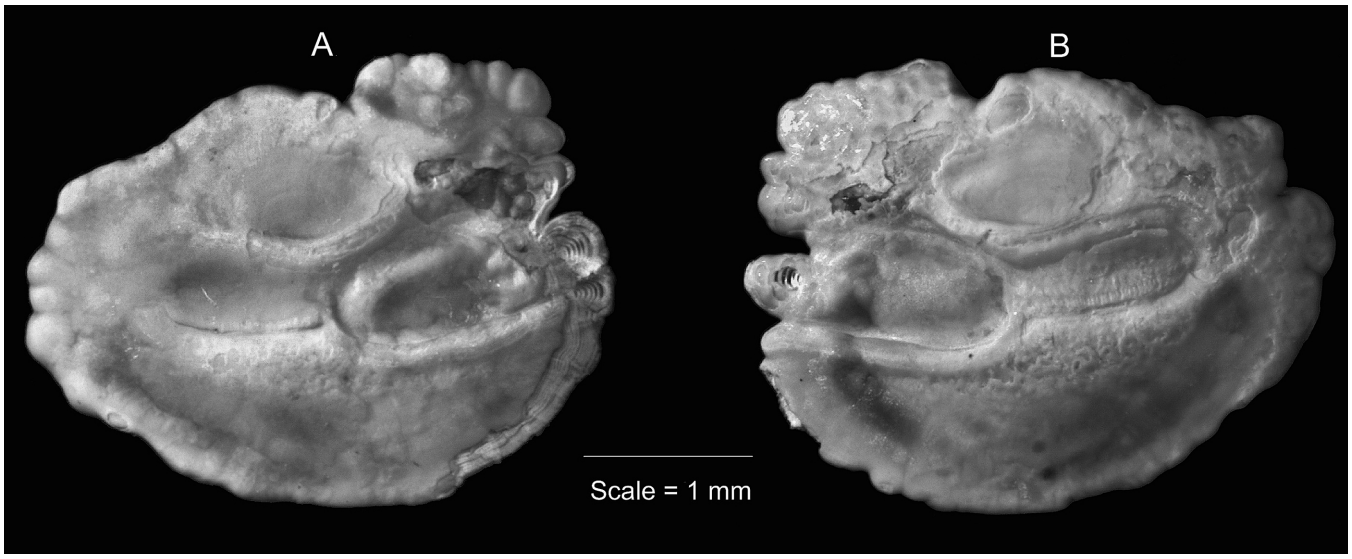

Figure 4. Matched pair of fossil otoliths (UF 319000) from *Apogon townsendi* from the Caloosahatchee Formation (lower Pleistocene), Hendry County, Florida (UF locality HN017). Left saccular otolith (A) and right saccular otolith (B).

premaxillae have been utilized in identification of marine fishes (Watt, 1997), and Dye and Longenecker (2004) refer to it as the second most distinctive bone in the fish skull. The right premaxilla measures 4.72 mm in length and is 2.19 mm in anterior width and 1.75 mm in posterior width (Fig. 5F). In lateral view, the anterior is characterized by the ascending process and the articular process. Numerous highly distinctive features of the Caloosahatchee premaxilla match Recent apogonid premaxillae (Dye and Longenecker, 2004). These include: 1) although incomplete, the ascending process is quite thin and delicate; 2) the interprocess notch between the ascending process and articular process is a very diagnostic, acute v-shape; 3) the shape of the articular process; 4) the outline and shape between the articular process and the postmaxillary; 5) the postmaxillary is quite expanded in length and height, and the height is about the same as the height of the articular process; and 6) the caudal process is broken but appears that it would be quite short. All of these features on the Caloosahatchee premaxilla match those of apogonids (Cannon, 1987; Watt, 1997; Dye and Longenecker, 2004). In medial view, the anterior has a distinct articular surface and obvious fossa, and these features are almost identical in the aforementioned Recent apogonid. In ventral view, the anterior has a pronounced occlusal surface with buccal and lingual socket rows. The socket rows on the anterior tend to be smaller in diameter than at the posterior. The ramus is slightly curved and increases in width towards the posterior as found in the apogonid of Dye and Longenecker (2004). There are fragments of what appear to be parts of the occlusal surface of the left premaxilla. A fragment of an occlusal surface measuring 1.3 mm by 1.4 mm had approximately 120 tooth bases (Fig. 5G). The fragment probably came from the premaxilla or the dentary.

A fairly significant portion of one of the maxilla is preserved and measures 7.49 mm in length (Fig. 5I). The anterior end is broken. The maxilla is rounded at the anterior and becomes broader and flatter towards the posterior. The posterior has some breakage also. A part of the quadrate, measuring 3.18 mm in length, was recovered. Although incomplete, several features were discernible. The anterior end is 1.1 mm in width and is characterized by two condyles (lateral and mesial). The preopercular process runs along the ventral of the quadrate and is fairly complete. The process has a concavity in the middle (preopercular groove). The dorsal (ectopterygoid margin) is broken irregularly but is much thinner than the preopercular process.. Two

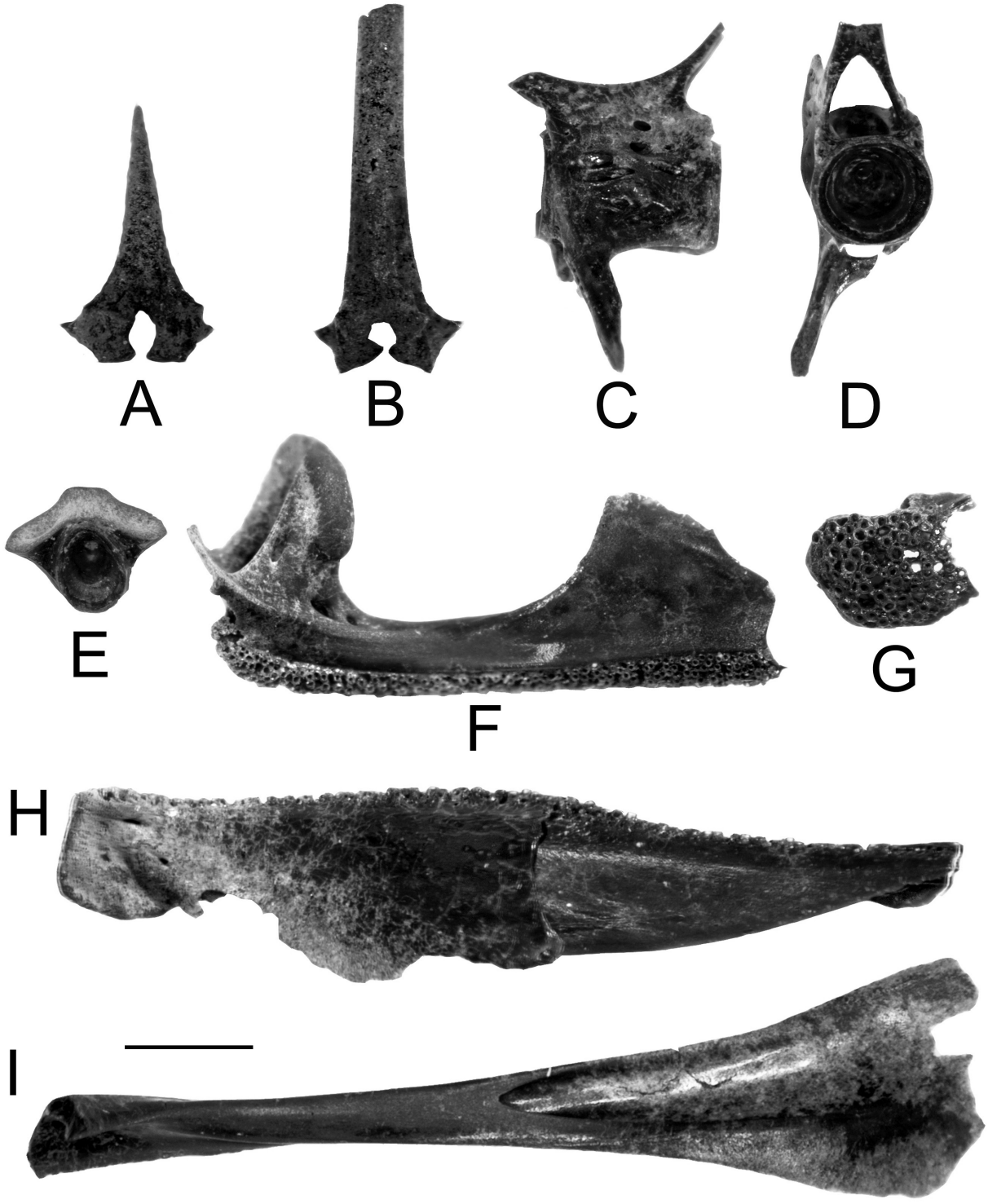

Figure 5. Skeletal remains of fossil *Apogon townsendi* (UF 319000) found in association with a matched pair of saccular otoliths in the Caloosahatchee Formation (lower Pleistocene), Hendry County, Florida (UF locality HN017). Anterior views of two dorsal spines (A, B). Lateral view of caudal vertebra (C). Anterior view of caudal vertebra showing partial neural and hemal arches (D). Anterior view of first anterior abdominal (atlas) vertebra showing articular surfaces for attachment to the basioccipital (E). Lingual lateral view of right premaxilla (F). Oral view of an occlusal surface fragment (G). Lingual lateral view of right dentary (H). Lingual lateral view of right maxilla (I).

incomplete, narrow bones with lengths of 4.58 mm and 4.21 mm and widths of approximately 0.60 mm are believed to be portions of the posttemporals. The proximal ends of the bones are broken, while the distal ends appear to be mainly complete. The bones are more rounded towards the proximal and become wider towards the distal. The distal end is flattened with a concavity (spatula-like).

There are two adjacent portions of the right dentary with a total length of 7.10 mm (Fig. 5H). Unfortunately, the preservation of the dentary is extremely fragile, and part is missing. The dentary is slightly curved, and the internal and external walls are clearly visible. The most distinct feature is the occlusal surface with socket rows for teeth. The socket rows tend to narrower and smaller in diameter at the anterior, near the symphysis. A deep, oval-shaped foramen (mental foramen) is visible on the labial lateral.

Nine spines (primarily dorsal but some possibly anal) were identified and ranged in length from 4.14 to 1.40 mm. Although the extant *A. townsendi* possesses seven dorsal and two anal spines (Snyder and Burgess, 2016), three of the recovered spines are medial sections, and it is not known if they represent a single spine or more. The only complete spine measured 1.90 mm in length and 0.60 mm at the proximal articulation (Fig. 5A). The distal end is slightly curved and quite aciculate. Another spine, which was 2.90 mm in length and 0.62 mm at the proximal articulation, is complete except for the distal end (Fig. 5B). The longest spine, which is 4.14 mm in length, is missing the proximal end (i.e., the articulation).

Fourteen vertebrae were recognized, most consisting of only the centra. All of the centra were distinctly amphicoelous. The best-preserved is a caudal vertebra measuring 1.43 mm in length and 2.80 mm in height, which included the arches (Fig. 5C). Both the neural and haemal spines are preserved with the enclosed arches (Fig. 5D). The neural and haemal spines are missing on three other caudal vertebra (1.35–1.43 mm in length), but the bases of the spines are visible. Two others (1.00–1.10 mm in length) appear to be abdominal vertebrae based on the presence of the remains of neural spines and parapophyses. One of these is the first anterior abdominal vertebra or atlas. It is 1.10 mm in length and 1.00 mm in height, and the neural spine is broken. In addition to being quite compressed, the vertebra has distinct articular surfaces for attachment to the basioccipital at the base of the skull (Fig. 5E).

RESULTS

As noted in the Systematic Paleontology section, the salient morphological features of the Caloosahatchee Formation saccular otoliths agreed best with those of *A. townsendi*, and Nolf and Bajpai (1992) illustrated left otoliths from two Recent *A. townsendi* collected off Mona Island in the Lesser Antilles. The Recent fish were approximately 5.1 cm and 5.3 cm in body length with corresponding saccular otoliths of 3.7 mm and 3.8 mm in length (Coll. IRSNB). An approximate length of the fossil *A. townsendi* from the Caloosahatchee Formation can be determined because the relationship between the length of the fish and the length of the otolith is linear (Harvey et al., 2000; Mendoza, 2006; Rypel, 2008; Jawad et al., 2011). The matched pair of otoliths from the Caloosahatchee Formation are both 3.5 mm in length and would represent a fish of approximately 4.7 cm in length. Of course, the number of Recent specimens available limits this approximation, but it does provide a viable length for the fossil *A. townsendi* from the Caloosahatchee Formation. A determination of the length of the living fish provides important information with regards to the feasibility of certain taphonomic processes. Studies by Baldwin et al. (2011) using molecular data (DNA barcoding) determined that Recent *A. townsendi* 1.1 cm and smaller were larvae, while juveniles were 1.2 to 2.1 cm in length. This would indicate that the Caloosahatchee Formation fossil *A. townsendi* at 4.7 cm in length would be an adult, but still much smaller than the valves of *Carolinapecten eboreus* in which it was found.

The Caloosahatchee skeletal remains, especially the highly diagnostic premaxilla, compared quite well with the Recent apogonid *A. menesemus* and indicate an apogonid. Although the skeletal material indicates an apogonid, no comparative material was available for *A. townsendi*. Therefore, the actual species determination was based on the

otoliths of Recent *A. townsendi* . However, the skull of the fish was most likely present in the valves of the scallop given the matched pair of otoliths. The only vertebrate remains in the scallop shell were the otoliths and the apogonid bones, and it appears quite likely that the bones were also of *A. townsendi* and the same individual.

DISCUSSION

Biology, Habitat, and Behavior of *Apogon townsendi*

Most apogonids are small, carnivorous reef fishes that commonly live in close association with reef invertebrates and are found primarily in tropical and subtropical areas (Nelson et al., 2016). *Apogon townsendi* follows these generalizations (Robins and Ray, 1986). Lieske and Myers (1994) and Gilmore and Fraser (2015) characterized the species as marine and reef-associated with a depth range of 3–55 m. Böhlke and Chaplin (1968) reported that *A. townsendi* was found in waters from 2.4–27.4 m with few shallower than 6.1 m. They also noted that the species was rather abundant on patch reefs in the 12.2–18.3 m depth range in the Nassau area of the Bahamas. Dennis et al. (2005) also reported *A. townsendi* from the reef biotype. Harborne et al. (2012) in a study of cryptobenthic fish in reef environments in the U. S. Virgin Islands found that *A. townsendi* was the most characteristic species in sheltered reef areas with <50% dead coral cover. *A. townsendi* is often found near drop-offs and may be found solitary or in groups in caves or holes (Lieske and Myers, 1994; Snyder and Burgess, 2106). It is often seen hovering in the spines of long-spined sea urchins (Gilmore and Fraser, 2015). Dominici-Arosemena and Wolf (2005) classified *A. townsendi* as a predator that hunts macrofauna and a mobile invertebrate feeder, whereas Halpern and Floeter (2008) and Gilmore and Fraser (2015) classified it as a midwater nocturnal planktivore. Based on the various references, it is probable that the species feeds on invertebrates as well as zooplankton.

Böhlke and Chaplin (1993), Claro (1994), and Randall (1996) listed *A. townsendi* in the Caribbean, Gulf of Mexico, and southeast U.S. Continental Shelf, respectively. The species is indicated as present in the Atlantic, Western-Central major fishing area (#31) according to the Food and Agriculture Organization (FAO) of the United Nations major fishing areas (2017) with an approximate range of 5°–35° N and 40°–90° W. The reported distributions of Recent *A. townsendi* would include the fossil locality in Hendry County, Florida, during the early Pleistocene.

Most Recent apogonids are less than 10 cm in total length, and this would certainly increase the chances of being preserved in a bivalve (Nelson et al., 2016). Rivaton and Bourret (1999) illustrated otoliths from 15 different Recent *Apogon* species representing juveniles and adults. They ranged from 3.7 cm to 9.2 cm in total length with otoliths that ranged from 2.9 mm to 6.75 mm in length. The maximum known size of *A. townsendi* is about 6.5 cm (McEachran and Fechhelm, 2005; Snyder and Burgess, 2016).

Fossil Record of *Apogon*

The oldest specimens referred to the genus *Apogon* in the scientific literature are from the middle Eocene of Pakistan, India, and England and are represented by otoliths (Gingerich et al., 1979; Kemp, 1985; Nolf and Bajpai, 1992). Gingerich et al. (1979) noted otoliths of *Apogon* sp. from the Domanda Formation in Pakistan while Nolf and Bajpai (1992) reported otoliths of *Apogon* sp. 4 from the Harudi Formation in India. Kemp (1985) listed *Apogon boulei* and *Apogon bellovacinus* from the Bracklesham Group in England. A middle Eocene age for *Apogon* seems very reasonable given that comprehensive molecular studies have shown a date of approximately 45 Ma for the Apogonidae (Betancur-R. et al., 2013). Other morphology- and molecular-based systematic revisions of apogonids (e.g., Bergman, 2004; Mabuchi et al., 2014) have indicated that *A. townsendi* is a valid species in the family Apogonidae.

The specimen UF 319000 represents the first fossil record of the family Apogonidae and the genus *Apogon* from Florida. Neither were listed in the two largest fossil bony fish assemblages from the early Pleistocene of Florida, Richardson Road Shell Pit 6A (34 species; Emslie et al., 1996) and Leisey Shell Pit 1A (50 species; Scudder et al., 1995). Otoliths within the size range of UF 319000

were recovered at Richardson Road Shell Pit 6A (Emslie et al., 1996), so that collecting bias was not a factor in their absence. Instead this is likely related to unsuitable habitat for apogonids at these two sites. This is the first fossil record anywhere of the species *A. townsendi*.

Taphonomic considerations

The occurrence of otoliths and associated skeletal remains believed to belong to the same species and individual of *A. townsendi* in the articulated shells of *Carolinapecten eboreus* may be the result of a commensal relationship between the fish and the scallop. However, commensal relationships that are not manifested by abnormalities or distinct structures in the preserved remains of the host are difficult to establish in the fossil record (Zullo and Chivers, 1969). The best-known examples of commensalism of fish with mollusks, specifically bivalves, occur in several species of the Carapidae (Parmentier and Das, 2004). Smith (1955) noted *Carapus margaritiferae* in South African waters as being "taken from inside clams at Durban." Mahadevan (1961) reported the same pearlfish species as being collected in the bivalve *Pteria* from the East Indies and the Gulf of Mannar in India. Trott (1981) described the hosts of several species of carapids as bivalves. Nazar et al. (2011) indicated that the hosts of the pearlfish *Onuxodon margaritiferas* were limited to bivalves (*Pteria penguin* and *Pycnodonta hyotis*). Most adults of *Carapus* use their host for shelter and leave it to hunt, but other pearlfishes are free-living (*Echiodon*) and parasitic (*Encheliohis*) according to Trott (1970), Parmentier et al. (2000), and Parmentier and Das (2004), In addition to the carapids, some of the gobiids display a type of commensal relationship with burrowing invertebrates. For example, the Eastern Pacific *Lepidogobius lepidus* often occupies the burrows of invertebrates on intertidal mud flats (Hieb, 2000).

McEachran and Fechhelm (2005) observed that a number of Gulf of Mexico apogonids live within the body cavities of other organisms such as sponges and mollusks without causing harm to them, while others are closely associated with sea urchins. One of the apogonids, *Astrapogon stellatus* or conchfish, has a commensal relationship with the queen conch shell *Lobatus gigas* and with the bivalve *Atrina rigida* (Cervigón, 1993). The relationship of this species with *L. gigas* was noted by Plate (1908), who reported that *Astrapogon stellatus* emerged from the shell only at night to feed on small crustaceans. Randall (1967) specified that *A. stellatus* was a commensal in the mantle cavity of the queen conch. McEachran and Fechhelm (2005) also reported that another species of *Astrapogon* (*A. puncticulatus*) is often found in empty shells and that *Phaeoptyx conklini* is associated with empty conch shells. So, there are several apogonids commensal or associated with bivalves in the Gulf of Mexico.

As noted earlier, *A. townsendi* is often reported hovering in long-spined sea urchins and is in intimate contact with invertebrates, especially in reef settings. The positioning of the fish within the sharp spines of the sea urchin could provide some protection and perhaps even camouflage from predators. If commensalism is defined as a relationship between two kinds of organisms in which one obtains food or other benefits from the other without damaging or benefiting it, then *A. townsendi* could be considered commensal with the sea urchin on a limited basis (i.e., the amount of time spent in the sea urchin's spines). However, Albins and Lyons (2012), Snyder and Burgess (2016), and other references herein identify *A. townsendi* as a nocturnal, hole-dwelling species found primarily in reefs. Furthermore, there are no known reports of commensalism of *A. townsendi* with bivalves, but its proximity with bivalve species in the reef setting is well established.

Another taphonomic scenario for consideration is *A. townsendi* actually occupying the empty scallop shell with subsequent death and rapid sediment infilling. As noted above, several Gulf of Mexico and Caribbean apogonids consistently occupy empty bivalve shells. While *A. townsendi* has not been reported as occupying empty shells, it is a possibility since the species is hole dwelling and may have sought temporary shelter in the shell. Another alternative is sediment trapping or washing in of the fish into the empty scallop shell. This is a feasible consideration because complete,

delicate carapaces of crabs similar in size to *A. townsendi* have been described within articulated bivalves (Zullo and Chivers, 1969; Gašparič et al. 2015). This type of taphonomic process would most likely require death of the fish in close proximity to the empty scallop shell followed by fairly rapid washing in of sediment with the fish into the valves of the scallop (i.e., sediment trapping). Subsequent burial of the scallop assisted in preserving the unique assemblage. The otoliths do not appear to have been exposed to any type of invertebrate settlement on the sea bottom as described by Stringer (2016) and were washed into the scallop intact in the apogonid's skull. It is possible that the fossil *A. townsendi* was the prey of a piscivorous predator (ingested and excreted) but this is considered unlikely based on several factors. There is no indication of the corrosive action of digestion on the otoliths. Furthermore, it is highly unlikely that the delicate skeletal bones were preserved in a coprolite and subsequently extracted from the calcium fluoride phosphate matrix

CONCLUSIONS

The excellent preservation of the matched pair of otoliths from the Caloosahatchee Formation allowed them to be attributed to an *Apogon townsendi* of about 4.7 cm in length and was an adult fish at death. The skeletal remains, especially the premaxilla, compared extremely well to an apogonid and are believed to be from the same individual as the otoliths. Based on the biology, distribution, and behavior of living *A. townsendi*, the taphonomic process that led to this rare and unusual assemblage is believed to have involved the death of the apogonid near or within the empty scallop shell followed by fairly rapid washing in of sediment into the scallop valves. The preservation of the saccular otoliths and the large number of associated, fragile skeletal remains believed to belong to the same individual fish in the scallop shell suggest that the apogonid was not ingested and excreted by a piscivorous predator.

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