

Evidence and implications of marine invertebrate settlement on Eocene otoliths from the Moodys Branch Formation of Montgomery Landing (Louisiana, U.S.A.)

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Microscopic analysis of 3,256 fish otoliths from the Eocene Moodys Branch Formation at Montgomery Landing, Louisiana, U.S.A., revealed 93 specimens with evidence of marine invertebrate settlements, primarily encrustings and boreholes. Although size, abundance, shape (stability), durability, and surface residence-time influenced the use of otoliths, key factors were size, abundance, and surface time. Invertebrates affecting otoliths were cnidarians (scleractinian solitary corals), bryozoans (cheilostome species), molluscs (mainly gastrochaenid bivalves), and annelids (serpulids), noted by larval form settlement, encrustation, and drilling. The size of the scleractinian corals, the time duration of the serpulids, encrustation by cnidarians and serpulids and paucity of other epifauna such as bryozoans, and the lengths of *Gastrochaena* borings appear to indicate that the otoliths did not remain exposed on the sea floor for an extended period. Surface residence-time may also explain why the abundant, diverse invertebrates present affected only about 3% of the otoliths.

KEY WORDS: fish otoliths, Eocene, invertebrates, surface residence-time.

Introduction

The vast majority of literature on fossil otoliths has concentrated on taxonomy and paleoecology (Nolf, 2013). There is a substantial and notable paucity of research on otoliths after their release from the fish's neocranium until they become fossilised. Courville & Collin (2002) in their discussion of taphonomic sequences referred to the events recorded on the fossils between the time the dead organisms settled on the seafloor and the moment they become permanently incorporated into the sediment.

The objective of the present research was to analyse fossil fish otoliths to determine what evidence, if any, they provided of the taphonomic process from the death of the fish to fossilisation in the marine environment. Samples and surface collections were obtained from the Eocene Moodys Branch Formation at the Montgomery Landing locality in Louisiana (U.S.A.) since abundant otoliths and invertebrates were known from the site. In addition to taxonomic identification, the otoliths were microscopically scrutinised on the inner and outer faces as well as the margins. This analysis indicated that some of the otoliths provided clear evidence of processes occurring after liberation from the skull but before fossilisation. The indications of invertebrate settlement on the otoliths are described and discussed.

Background and previous studies

Otoliths are unique because they are specialised and integral components of the fish's acoustico-lateralis system (Norman, 1931; Lowenstein, 1957; Lagler *et al.*, 1962). Schäfer (1972) noted that otoliths are the last parts of a dead fish to be freed because of the location of the labyrinths in the bony neocranium, which is quite strong and durable. Fitch & Brownell (1968), Gaemers (1977), Gaemers & Langeveld (2015) and Nolf (1985; 2013) noted that fish otoliths can be enriched in marine bottom sediments through the excretion of piscivorous organisms such as sharks, fish, and mammals. Only one study (Gaemers & Langeveld, 2015) is known that addresses the activity of invertebrates on otoliths during taphonomy. Otoliths ($n = 32$) with drill holes, representing four species of gadid fishes from a Miocene-Pliocene site in southeast Netherlands, were reported by these authors. Over 81% of the drill holes, attributed to naticid gastropods, were found in otoliths of one gadid species.

Location of collecting site

Otolith specimens for this study were collected in Grant Parish, Louisiana, U.S.A. (31.7°N, 92.9°W) at a site known as Montgomery Landing (Schiebout, 1986). The site is located approximately 100 m west of Creola Cemetery on

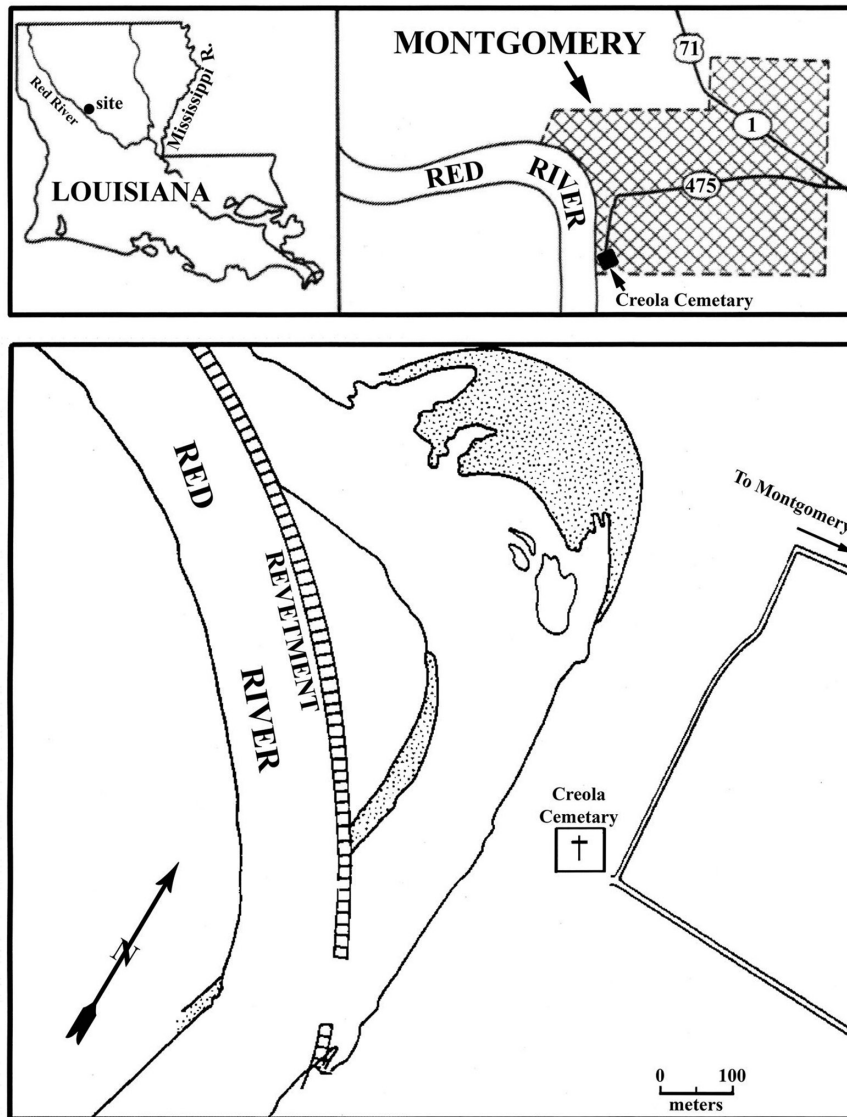


Figure 1. Location of the Montgomery Landing site on the Red River near Montgomery, Grant Parish, Louisiana, U.S.A.

the east side of the Red River (Fig. 1). Prior to channelisation activities on the river by the U.S. Army Corps of Engineers, the location was characterised by a cut-bank that formed a cliff known as Creola Bluff. Creola Bluff was about 500 m in length and reached a maximum height of 14 m. Unfortunately, the channelisation essentially destroyed the site, but bulk and surface samples previously collected were utilised for this study.

Stratigraphy of site

Three Eocene formations were exposed at the Montgomery Landing locality (Fig. 2), but only otoliths from the middle Eocene Moodys Branch Formation were employed in this study, but it cannot be excluded that some were eroded from underlying rocks. The Moodys Branch Formation, which is in the Jackson Group, represents a marine transgression facies (Schiebout, 1986; Breard, 1986). The formation is a massive, greenish-gray marly sand with abundant glauconite, angular quartz, and fecal pellets. One of the most distinguishing characteristics of

the formation is the highly abundant and diverse shelf assemblage, which includes micro- and macroscopic invertebrates and vertebrates (Schiebout, 1986; John, 2010).

Methodology

Several unwashed sediment samples (2 kg and 4 kg) stored at the University of Louisiana at Monroe Museum of Natural History and a surface collection by S. Breard were used in this study. Otolith studies typically employ much larger samples to increase the probability of recovering an as complete as possible assemblage, with samples exceeding 100 kg and even 1000 kg (Nolf & Dockery, 1990; Nolf & Stringer, 2003). The samples were wet screened using plain water with no additives because of their potential adverse effect on the aragonitic otoliths. During the wet screening, all residue that was retained on a U.S. Standard Sieve #30 (mesh size .595 mm) was kept for study. An Olympus binocular microscope (6.7x to 40x) was employed to extract the otoliths from the residue. After identification, the otoliths were carefully

Age	Stage	Group	Formation	Lithology
E O C E N E	P R I A B O N I A N	J A C K S O N G R O U P	Y A Z O O C L A Y	Deep blue-gray clay (weathers tan), minor marl and limy clay beds, distinct ledges, abundant marine microscopic fossils, megascopic fossils less abundant
	B A R T O N I A N		MOODY'S BRANCH FORMATION	Blue-gray sandy clay marl, highly fossiliferous (marine microscopic and megascopic forms)
			CLAIBORNE GROUP	COCKFIELD FORMATION

Figure 2. Stratigraphy of the Montgomery Landing locality on the Red River near Montgomery, Grant Parish, Louisiana, U.S.A.

examined on the inner and outer faces as well as along the margins for evidence related to invertebrate settlement. An extensive comparative invertebrate collection from the site was utilised in identifying the remains on the otoliths. Otolith identification was aided by a comparative collection from the site developed by the late J. Fitch (Natural History Museum of Los Angeles County) as well as a comparative collection from the overlying Yazoo Clay supplied by D. Nolf (Royal Belgian Institute of Natural Science, Brussels, Belgium).

Results

The 4 kg sample produced 2,133 otoliths, the 2 kg sample yielded 762 otoliths, and surface collected specimens added 361 for a total of 3,256 otoliths, which is a significant number for analysis. Microscopic examination of the otoliths resulted in the identification of 93 specimens (2.86% of the total otoliths) that exhibited evidence of invertebrate settlement. Otoliths from the site ranged from approximately 1.5 to 26.5 mm in length. However, 67%

of the specimens that indicated invertebrate settlement were in two size categories (2-3.99 mm and 4-5.99 mm). This indicated that at least some of the otoliths experienced delayed burial during the taphonomic process and were subjected to biological actions on the substrate. Invertebrate activities recognised on the otoliths included settlement by larval forms, encrustation, and drilling. Otoliths from ten fish taxa retained evidence of invertebrate settlement, and the greatest evidence of invertebrates was found on the outer face of the otoliths ($n = 54$) followed by the inner face ($n = 42$). Only two remains of invertebrates were found uniquely on the margins. The total number exceeds 93 because some otoliths had invertebrate traces on both inner and outer faces.

Analysis revealed that representatives of at least four phyla of invertebrates affected the otoliths. Invertebrate phyla included the Cnidaria, Bryozoa, Mollusca, and Annelida. The most commonly occurring traces on the otoliths was by cnidarians, which were recognised by salient characteristics such as septa and radial symmetry. A total of 36 remains of scleractinian corals were found on the otoliths, and all of these remains appear to represent

solitary corals. Although several complete corals were located on the otoliths, most of the scleractinian remains were partial, and some were just faint outlines. Thirty-four of these remains are believed to represent *Discotrochus orbignianus* Milne Edwards & Haime, 1848 (Pl. 1, figs A-C), which was extremely abundant at Montgomery Landing (Breard, 1986). Two other cnidarians do not appear to be *Discotrochus orbignianus* and could not be identified further.

Five bryozoan remains were recognised on otoliths based on the characteristic pattern of the zooids (Cheetham *et al.*, 1969; Taylor, 1999; Grischenko *et al.*, 2000). These remains were classified as cheilostome bryozoans (Pl. 1, figs D-E). Due to the limited number of specimens and their preservation as well as the complexity of the taxonomy and systematics, the cheilostome bryozoans were not classified any further.

Twenty-seven characteristic, up to *c.* 5 mm (maximum measured = 5.07 mm) diameter gastrochaenid bivalve borings with associated carbonate secretions (Pl. 1, figs F-I) were found in otoliths, some examples preserving partial valves of *Gastrochaena mississippiensis* Harris, 1946 *in situ* (D. Dockery, pers. comm.). Gastrochaenids have long been reported from the Paleogene of the southern United States (Palmer & Brann, 1965; Dockery, 1977; Toulmin, 1977) and *Gastrochaena mississippiensis* is reported from several Moodys Branch Formation localities by Dockery (1977). Dockery (1977; pl. 28, figs 3-5, 8) stated that its smooth shell sheath, its large size, and the occurrence of incurrent and excurrent siphonal canals allowed to distinguish the boreholes of this species. Other remains (*n* = 5) thought to be produced by bivalves consisted of a white carbonate material that was often porcelaneous (Pl. 1, fig. J). The white material displayed no discernible structures like a serpulid worm tube or a bryozoan, and there were no associated borings. However, this material was found in association with a mollusc fragment and may be a secretion (cement).

Thirty-three fossilised tubes of marine serpulid worms were identified on the otoliths. The calcareous tubes are bell-shaped in cross-section with accretionary ridges and ranged from less than 1.0 mm in length up to 15.72 mm on the otoliths. The width of the worm tubes averaged around 1.5 mm. It appears that most of the worm tubes are only partially preserved based on their broken and fragmented nature. Breard (1978; 1986) noted two species of serpulids: *Rotularia* (reported as *Tubulostium*) *leptostoma* (Gabb, 1860) and *Serpula* sp. at this site. *Rotularia* is coiled in a single plane with generally three volutions when adult and a periphery with a tricarinate keel (Hoşgör & Okan, 2006; Vinn, 2008). The worm tubes found on the otoliths did not coil in a single plane and were randomly oriented. Boardman *et al.* (1987) noted that *Serpula* produced long, slender, coiled, or contorted tubes. Also, the tube of *Serpula* has longitudinal keels (ten Hove & Kupriyanova, 2009). Therefore a *Serpula* species is likely to have produced these worm tubes (Pl. 1, figs K-M). In addition to the *Serpula* worm tubes, another type of material that apparently was secreted by a serpulid was also found. This material (*n* = 5) tended

to be gray to grayish-white in color and translucent, and might be a cement of *Rotularia leptostoma* (Pl. 1, fig. N).

Discussion and implications

The number of otoliths with recognisable traces of invertebrate settlement appears to be quite small considering the extremely abundant invertebrate assemblage (including diverse epifaunal elements) present at the site (Breard, 1978; Schiebout, 1986). Otoliths of Sciaenidae, Congridae, Ophidiidae, and Albulidae accounted for 93.6% of otoliths showing invertebrate settlements, while the families Myripristidae, Lactariidae, and Haemulidae represented a much smaller percentage. Factors affecting utilisation of otoliths by invertebrates were size, abundance, shape (stability), durability (easily broken), and surface residence-time, which are similar to the ones observed by Nebelsick *et al.* (1997) governing encrustation. The various marine invertebrates observed on the fish otoliths are summarised in Table 1.

A primary consideration in this study is how the otoliths were used as substrata by the various invertebrates. Otoliths have been observed lying loose in unconsolidated Recent sediments on the sea floor and have been collected in various types of sampling devices (Wigley & Stinton, 1973; Stringer, 1992). Invertebrates, such as ahermatypic scleractinian corals that can attach to mollusc shells and fragments (Veron, 2000; Slingsby, 2003; Cairns, 2009), could have affected otoliths that were part of the unconsolidated sediment on the sea bottom. The greatest percentage of affected otoliths (67%) was actually not that large in size (ranging from 2-5.99 mm length). However, this size range includes the most common lengths of the most abundant forms (ophidiids, congrids, and juvenile sciaenids).

Although the percentage of otoliths with traces of invertebrates at Montgomery Landing is relatively small, they provide excellent evidence as to biotic activities that were occurring during the taphonomic process. The most common remains on the otoliths were scleractinian corals, predominantly *Discotrochus orbignianus*, reported as the most abundant cnidarian (Breard, 1986). Many of the corals found on the otoliths appeared to represent rather freshly settled larval juvenile forms based on their sizes (Slingsby, 2003). Bak & Engel (1979) in a study of juvenile corals in the Caribbean, in water depths believed to be similar to the site, recorded that coral recruits immediately after settling were 1-2 mm in diameter. Wallace (1985), in a study of modern scleractinian corals, found a mean size of 0.98 mm for recruits with a maximum size of 4.0 mm. Other studies also indicated a small settlement size (Babcock *et al.*, 2003; Traçon *et al.*, 2013). Most of the corals on the otoliths were 2 mm or less in diameter. Only a few coral specimens exceeded 3.5 mm in diameter. The large number and small size of *Discotrochus* coupled with the abundance of otoliths in the 2-5.99 mm range explains why this size range is the most predominant (67%). Breard (1986) reported nine hermatypic (zooxanthellate or reef-building) and ahermatypic (azooxanthellate and

fish taxon	otolith total	corals	Bryozoa	Gastrochaena	unknown bivalve	Serpula	Rotularia	total remains	ratio
<i>Albula</i> sp.	7	2	2	5	0	3	0	12	1.71
<i>Ariosoma nonsector</i>	13	7	1	3	1	3	2	17	1.31
<i>Paraconger yazoensis</i>	1	0	0	0	0	1	0	1	1.00
" <i>Neobythitina</i> " <i>meyeri</i>	13	10	0	1	0	4	0	15	1.15
" <i>Sirembinus</i> " <i>granus</i>	1	1	0	0	0	0	0	1	1.00
" <i>Myripristina</i> " <i>cajun</i>	3	0	0	1	0	2	0	3	1.00
<i>Lactarius</i> sp.	1	1	0	0	0	0	0	1	1.00
" <i>Haemulida</i> " <i>obliquus</i>	2	2	0	0	0	0	0	2	1.00
" <i>Sciaenida</i> " <i>claybornensis</i>	47	11	1	16	4	18	3	53	1.13
<i>Sciaena pseudoradians</i>	5	2	1	1	0	2	0	6	1.20
Column totals	93	36	5	27	5	33	5	111	1.19 Avg.

Table 1. A synopsis of the fish otoliths showing evidence of marine invertebrates from the Moodys Branch Formation (middle Eocene), Montgomery Landing, Louisiana, U.S.A. (Avg. = average value)

solitary) taxa of scleractinians from the site. Yet, only a few taxa are reported as being present on the otoliths, but several factors probably contribute to this. One of the nine scleractinians is extremely rare, two of the species are colonial, and one is extremely small. Examination of the bases of the remaining five coral taxa indicated that *Discotrochus* best matched the circular shape of the encrustings.

Fossilised tubes of marine serpulid worms (*Serpula*), the second most abundant remains on otoliths, are commonly found on hard structures such as mollusc shells but are abundant on corals and even reported on soft material such as seagrass (Ivany *et al.*, 1990). All serpulids build tubes of crystalline calcium carbonate (calcite, aragonite, or a combination of the two) and a mucopolysaccharide matrix (Simkiss & Wilbur, 1989; ten Hove & Kupriyana, 2009). Serpulid tubes up to approximately 2 cm in length are reported in Recent forms (Glumac *et al.*, 2004). It is presumed that annelids were quite common in the Tertiary as they are in the present marine environment, but few of the annelids secreted structures that were fossilised (Toulmin, 1977; Breard, 1986).

Bosence (1979) noted a monthly length growth rate of 9 mm in his research on *Serpula vermicularis* Linnaeus, 1758. However, Behrens (1968) provided a more detailed and complex formula for serpulid growth, which may provide an approximation of the growth of the Eocene form. Behrens observed a growth of 1.5-2.5 mm/day for the first three days and followed by a decrease in rate to 0.8-1.3 mm/day for the next two to four weeks. After two to four weeks, the rate decreases further to 0.1-0.2 mm/day. Although growth differences probably existed in different habitats, and many of the serpulid tubes on the otoliths are probably not complete, their measurements

can provide a minimum time that the worms were present alive on the otoliths.

Applying Behrens' observations and presuming that all of the tube was fossilised and preserved, a serpulid would be between 4.5 mm and 7.5 mm after three days. After two additional weeks (17 days total), the total length would be between 15.7 mm and 18.7 mm (minimum growth rate of 0.8 mm/day) or between 22.7 mm and 25.7 mm (maximum rate of 1.3 mm/day). The length of the serpulid tubes on the otoliths ranged from as small as 0.26 mm to 15.72 mm. The lengths of the Montgomery Landing serpulid tubes generally fall into one of three categories. Many of the tubes are less than 2.5 mm in length (indicating a presence on the otoliths for only 1 to 1.5 days or less upon their death or movement to another substratum). A smaller group (4 mm to 8 mm) were probably present on the otoliths for approximately three days. The final and smallest group (10 mm to 16 mm) would indicate a residency from 5 to 12 days (maximum growth) or 6 to 17 days (minimum growth). Given that most of the serpulid tubes do not appear to be complete (*i.e.*, broken to some extent), the durations should be considered minimum, and longer durations were certainly possible. However, the dimensions of the otoliths could have been a limiting factor in the length of the serpulid worm tubes.

The two most abundant invertebrate remains or traces on the teleostean otoliths are cnidarians and serpulids, which have paleoenvironmental and taphonomic ramifications. Nebelsick *et al.* (1997) found initial encrustation by cnidarians and serpulids followed by other and more numerous types of epifaunal organisms. While the Montgomery Landing otoliths demonstrated encrustation by cnidarians and serpulids, they do not show later significant coverage by other epifaunal organisms. Bryozoans

represented less than 5% of the remains observed on otoliths. However, cheilostome bryozoans are quite abundant and diverse (20 species) at the site (Martin, 1986). This may be another indication of surface residence-time for the otoliths (*i.e.*, did not remain on the surface for an extended period).

The third most common evidence of invertebrates on the otoliths, the bivalve *Gastrochaena mississippiensis* was found primarily in shallow, tropical marine waters and produced clavate-shaped borings (Edinger, 2003). Although gastrochaenid bivalves bore into lithified material, their shells are actually quite delicate. Recent gastrochaenids are reported as boring into coral, soft rock (especially carbonate rocks), and hardened mud, but they show a preference for bivalves lying on the surface of sands and muds (Edinger, 2003; Tunnell *et al.*, 2010). Gastrochaenids appear to produce boreholes by both mechanical and chemical means and seem to be restricted to boring in calcareous materials (Kleeman, 1996; Tunnell *et al.*, 2010; Belaústegui *et al.*, 2013). Gastrochaenids, unlike most endolithic bivalves, secrete boring linings of aragonite (McDowell & Carter, 1995; Valentich-Scott & Dinesen, 2004; Belaústegui *et al.*, 2013). These aragonitic linings form distinctive internal borehole shapes and often display considerable detail in sculpture and ornamentation (Kleeman, 2008). Studies by Robertson (1963) and Carter (1978) on three common Florida Keys gastrochaenids found borings with a well-defined posterior siphonal burrow and an anterior shell chamber that was circular to slightly elliptical in cross section. Carter (1978), who extensively investigated the ecology and evolution of the gastrochaenids, found an almost linear relationship between the age of several Recent species of *Gastrochaena* and the length of the boreholes, which ranged from less

than 10 mm to greater than 60 mm. It was very difficult to ascertain the length of the gastrochaenid borings in the fossil otoliths. Since the borings vary in depth in the otoliths, thin sections provide partial boreholes, and the technique destroys the otolith. However, a few otoliths had layers of aragonite eroded, and borings of *Gastrochaena* were visible. For example, there were several segments of a *Gastrochaena* boring exposed on an *Ariosoma nonsector* otolith which indicated a minimum length of only 1.56 mm.

Among the less common invertebrates on the otoliths were cheilostome bryozoans, and all appear to be constructed of a simple encrusting sheet (Boardman *et al.*, 1987; Taylor, 1999). Bryozoans can be composed of calcium carbonate as calcite, aragonite, or a combination of both polymorphs. Only two of the specimens have preserved calcium carbonate, while the other three are less distinct impressions of the zooids on the otolith. The specimens probably represent more than one cheilostome species since the pattern arrangement and the size of the zooids are quite variable (Knight *et al.*, 2011).

Another, less common, evidence of invertebrate settlement on the otoliths was a white carbonate secretion that was often porcelainous. It had no recognisable structures or associated borings. However on one of the otoliths, the white carbonate material was associated with a bivalve fragment and could represent oyster spat. It appeared that the white secretory material was used to attach the bivalve to the otolith. The fragmentary bivalve was not identifiable.

A final less common invertebrate recognised on the otoliths was a gray to grayish-white material found on the otolith's surface. The material gives the impression of being biological in origin rather than sedimentological and

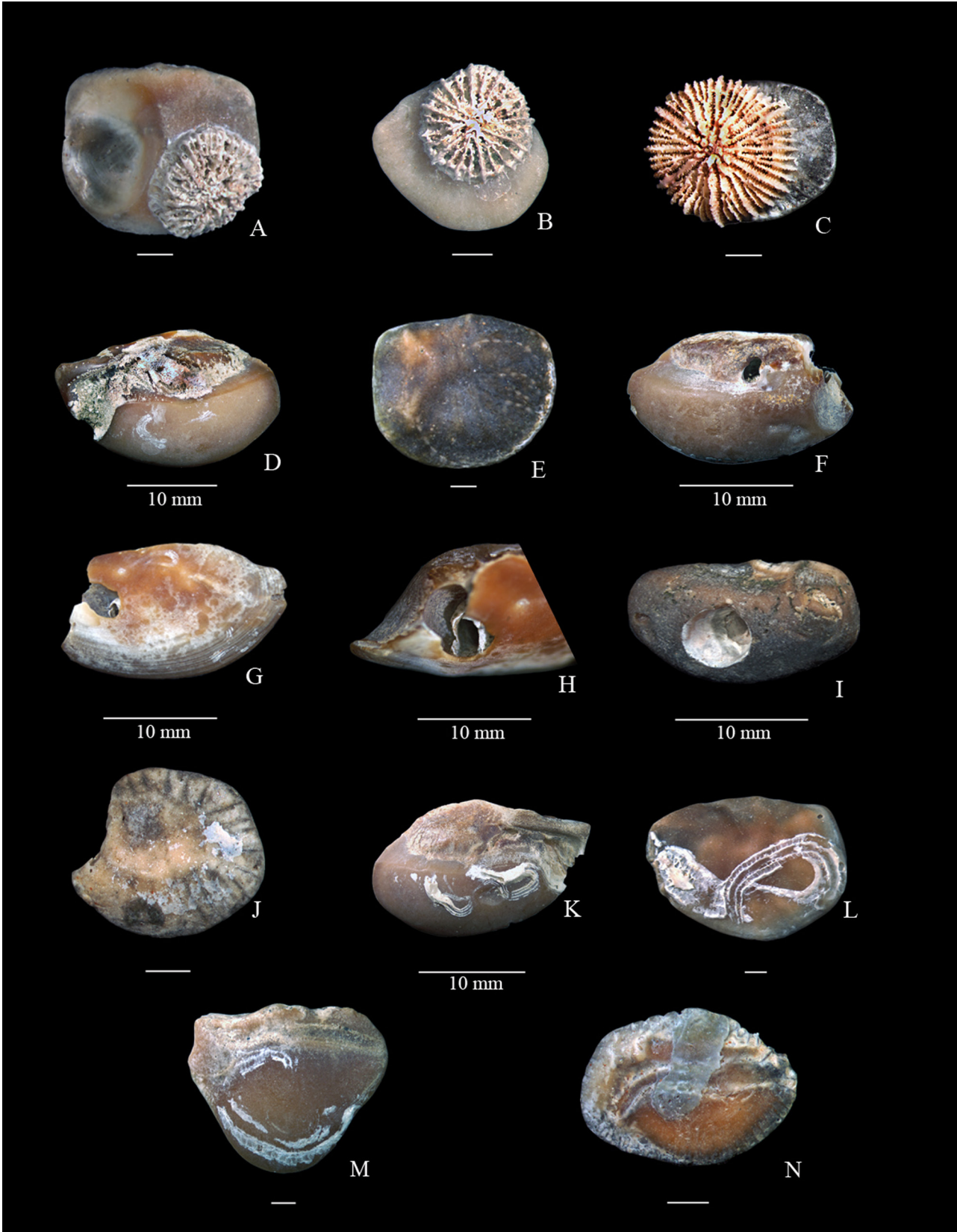
Plate 1.

The taxonomic identification of all invertebrate remains or evidence is provided as well as the taxonomic identification of the otolith, location of otolith in the labyrinth (right or left side), type of otolith (sagitta), and inner or outer face. Scale bar represents 1 mm unless otherwise noted.

- A. *Discotrochus orbignianus* Milne Edwards & Haime, 1848 on *Sciaena pseudoradians* (Frizzell & Dante, 1965), left sagitta (inner face).
- B. *Discotrochus orbignianus* Milne Edwards & Haime, 1848 on *Ariosoma nonsector* Nolf & Stringer, 2003, right sagitta (outer face).
- C. *Discotrochus orbignianus* Milne Edwards & Haime, 1848 on "*Sciaenida*" *claybornensis* Koken, 1888, left sagitta (outer face).
- D. Cheilostome bryozoan on *Albula* sp., left sagitta (inner face).
- E. Cheilostome bryozoan on *Sciaena pseudoradians* (Frizzell & Dante, 1965), right sagitta (outer face).
- F. *Gastrochaena mississippiensis* Harris, 1946 on *Albula* sp., right sagitta (inner face with borehole).
- G. *Gastrochaena mississippiensis* Harris, 1946 on *Albula* sp., right sagitta (outer face of F with shell of *Gastrochaena mississippiensis*).
- H. *Gastrochaena mississippiensis* Harris, 1946 on *Albula* sp., right sagitta ((close-up view of inner and outer face of posterior of F showing shell of *Gastrochaena mississippiensis*).
- I. *Gastrochaena mississippiensis* Harris, 1946 on *Albula* sp. (very worn specimen), right sagitta (inner face with aragonitic-lined borehole).
- J. Unknown bivalve cement on "*Sciaenida*" *claybornensis* Koken, 1888, left sagitta (outer face).
- K. *Serpula* sp. on *Albula* sp., right sagitta (inner face).
- L. *Serpula* sp. on "*Sciaenida*" *claybornensis* Koken, 1888, left sagitta (outer face).
- M. *Serpula* sp. on "*Myripristina*" *cajun* (Frizzell and Lamber, 1961), right sagitta (inner face).
- N. Cement of *Rotularia* sp. on "*Sciaenida*" *claybornensis* Koken, 1888, left sagitta (inner face).

is believed to represent some kind of secretion by an organism. The structures tend to be translucent, generally featureless, and are probably calcareous in composition. All of the secretions are extremely similar in their physical characteristics. Examination of invertebrate compar-

ative material from the site indicated that the secretion is very similar to the cement used by *Rotularia leptostoma* to attach to the substrate. All rotularians cement to the substrate during their earliest growth state and become detached shortly after the first whorl formation (Uppsala,



1995; Vinn, 2008). The remains on the otoliths are interpreted to be the cement used by *Rotularia* for initial attachment. Breard (1978; 1986) cited *Rotularia leptostoma* as very common at the locality.

Conclusions

Microscopic analysis of 3,256 otoliths produced 93 specimens (2.86% of total) with signs of invertebrate settlements during fossilisation. Boreholes and encrustations were indentified on the outer and inner faces fairly equally, but such traces on the margins were quite rare. Factors affecting the utilisation of otoliths by invertebrates were determined to be size, abundance, shape (stability), durability, and surface residence-time, but abundance, size, and surface time were the most limiting factors. The greatest percentage of impacted otoliths (67%) ranged from 2.00–5.99 mm in length, which corresponds to the most common lengths of the most abundant forms (ophidiids, congrid, and juvenile sciaenids).

Representatives of at least four phyla of invertebrates (Cnidaria, Bryozoa, Mollusca, and Annelida) were recognised on the otoliths. The most common invertebrates were the scleractinian solitary coral *Discotrochus orbignianus*. Much less abundant were cheilostome bryozoans. Borings, aragonitic-lined boreholes, and carbonate secretions of *Gastrochaena mississippiensis* were common. Five additional traces (a white secretion or cement) were identified as belonging to an unknown bivalve. Almost as common as the cnidarians were the fossilised tubes of marine serpulid worms attributed to *Serpula*. In addition to the *Serpula* tubes, another type of polychaete material was recognised as a cement of *Rotularia leptostoma*.

Most of the corals attached to the otoliths were 2 mm or less in diameter and obviously represented freshly attached larval forms. The preponderance of larval and juvenile scleractinian corals indicates that the surface residence-time was not long enough for growth into adults, but the restricted size of their substrate might have hampered further growth. Research on Recent serpulid worms provided an estimate of surface residence-time that may be comparable for the fossil otoliths based on the lengths of the *Serpula* tubes. If a similar growth rate for the fossil serpulids is assumed for the fossils, tube lengths indicated that the serpulids were present on the otoliths from as little as 1 day to a maximum of 17 days. This is the best estimate of surface residence-time for the otoliths at the site, reinforced by modern study of Nebelsick *et al.* (1997), which found that initial encrustation was by cnidarians and serpulids followed by other and more numerous types of epifaunal organisms. While the otoliths demonstrated encrustation by cnidarians and serpulids, they do not show later significant coverage by other epifaunal organisms. Bryozoans represented less than 5% of the invertebrates on the otoliths although bryozoans are quite numerous at the site and 20 species are known to occur (Martin, 1986). A limited number of otoliths provided measurements of the lengths of *Gastrochaena* borings. As otoliths are small objects, the borehole

lengths were substantially less than measurements of Recent *Gastrochaena* borings. The bore lengths indicate the presence of *Gastrochaena* for a short period of time. Therefore, the size of the scleractinian corals, the time duration of the serpulids, the encrustation by cnidarians and serpulids, but paucity of other epifauna, and the length of the *Gastrochaena* borings may all contribute to the idea that the otoliths did not remain on the surface for an extended period. The restricted surface residence-time may also explain why the abundant, diverse invertebrate assemblage at the site affected only less than 3% of the available otoliths. The evidence indicates that otoliths were used as substrata during the taphonomic process for various processes by invertebrates, but the actions of invertebrates appear to have been limited by surface-residence duration.

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