








Black Mantle Tissue of Endolithic Mussels (*Leiosolenus* spp.) Is Cloaking Borehole Orifices in Caribbean Reef Corals

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Abstract: Bioerosion caused by boring mussels (Mytilidae: Lithophaginae) can negatively impact coral reef health. During biodiversity surveys of coral-associated fauna in Curaçao (southern Caribbean), morphological variation in mussel boreholes was studied. Borings were found in 22 coral species, 12 of which represented new host records. Dead corals usually showed twin siphon openings, for each mussel shaped like a figure of eight, which were lined with a calcareous sheath and protruded as tubes from the substrate surface. Most openings surrounded by live coral tissue were deeper and funnel-shaped, with outlines resembling dumbbells, keyholes, ovals or irregular ink blotches. The boreholes appeared to contain black siphon and mantle tissue of the mussel. Because of the black color and the hidden borehole opening in live host corals, the mantle tissue appeared to mimic dark, empty holes, while they were actually cloaking live coral tissue around the hole, which is a new discovery. By illustrating the morphological range of borehole orifices, we aim to facilitate the easy detection of boring mussels for future research.

Keywords: bioerosion; boring; coral health; Curaçao; host records; Lithophaginae; Mytilidae



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Boring mussels (Mytilidae: Lithophaginae) are notorious for their bioerosion of limestone rock, bivalve shells, reef corals and various manmade calcareous substrates [1–9]. Most of these boring mussels (also called date mussels) belong to the genera *Leiosolenus* Carpenter, 1857 and *Lithophaga* Röding, 1798 [10]. In addition to causing damage to the structure of reef corals [11–15], these animals are suspected to make host corals more susceptible to diseases [16].

In order to detect the presence of boring mussels inside corals, it is important to recognize the orifices of their boreholes. For their feeding and respiration, boring mussels inhale and exhale seawater through a pair of siphons at the posterior edge of their mantle tissue [17–19]. The siphons use openings in the substrate surface for contact with the surrounding seawater [20]. The outline of such openings is described as “figure-of-eight” or “dumbbell” [3–5,8,20–23] shape, not to be confused with the twin openings of U-shaped excavations of *Polydora* worms (Polychaeta) [24–28] and the perforations made by boring clionaid sponges (Porifera) [25,29].

In mussels of the genus *Leiosolenus*, the borehole and its openings are lined with an aragonite (calcareous) sheath that is excreted by the bivalve [16,20,30,31]. At the substrate surface, such sheaths may appear as chimney-like tubes that provide protection to the siphons [21,22,32,33]. However, these sheaths are not always visible, and the openings of

some borings are described as being oval in shape, which may perhaps be influenced by the host coral or by overgrowing algae [20,32,33]. Oval orifices of mussel borings can be irregular in shape [32,34] and should not be confused with the crescent-shaped openings of some coral-dwelling gall-crab species [35–37]. Owing to their morphological variability, the openings of mussel holes may not always be recognized; it is possible that they therefore become classified as “unknown holes” [38]. Because boring mussels can have a negative impact on the health of reef corals [12,16], it is important that their presence can be detected through the easy recognition of their orifices. In this study, we provide information on how these openings can be spotted in the field.

During biodiversity surveys of coral-associated fauna along the leeward side of Curaçao (southern Caribbean) in October–December 2021 and April 2022 [39,40] a number of live and dead corals were checked for boreholes of lithophagine mussels. To verify the presence of mussels underneath openings, two corals were broken to reveal the position of the mussels (Figure 1).

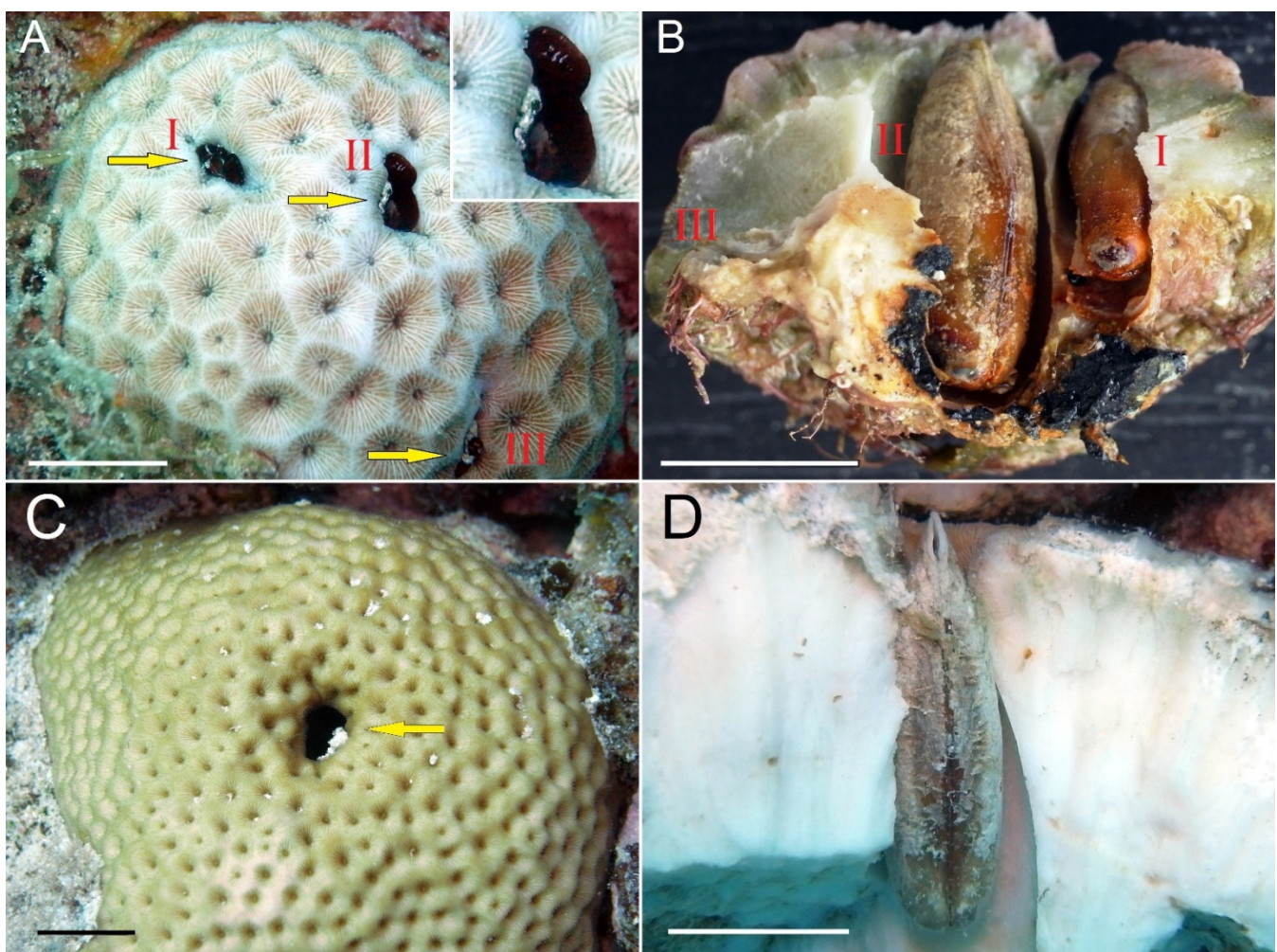


Figure 1. Coral colonies of *Siderastrea siderea* at Curaçao, showing the position of borehole openings (A,C: arrows) and *Leiosolenus* mussels underneath them (B,D). One coral contains three mussels (A,B: I–III) and the other only one (C,D). Each exposed mussel has the posterior side upward, showing either a lateral side (B) or the dorsal side (D). The dark color of each hole (A,C) indicates the presence of the mussel’s mantle tissue; in some individuals approaching dark Bordeaux red (A: insert 2× enlargement). The mantle tissue may be covered by some detritus particles (B,D). In exposed mussels, the mantle tissue is retracted inside the shell (B,D). Scale bars: 1 cm.

The morphological variety in the orifices appeared to be more extensive than previously reported. Many corals, mostly dead but also live ones, showed two calcareous tubes (sheaths), protruding from the substrate surface, described as aragonite chimney-like structures [21,32]. In addition to showing a figure-of-eight shape consisting of two connected tubes (Figure 2A–E), some twin openings appeared to be separate (Figure 2F). A slit was seen in the calcareous margin where twin tubes were merged, varying in width (Figure 2A–E). The tubes did not protrude as high as those made by boring bivalves of the family Gastrochaenidae, which excavate in dead coral [22,32]. Most orifices in live corals showed a so-called “dumbbell shape”, although “keyhole shape” appears to be more appropriate (Figure 2G–I). Other openings surrounded by live coral tissue appeared to have an oval outline (Figure 2J–L) or one resembling an irregular ink blotch (Figure 2M,N). A few boreholes showed an empty *Leiosolenus* shell inside (Figure 2O).

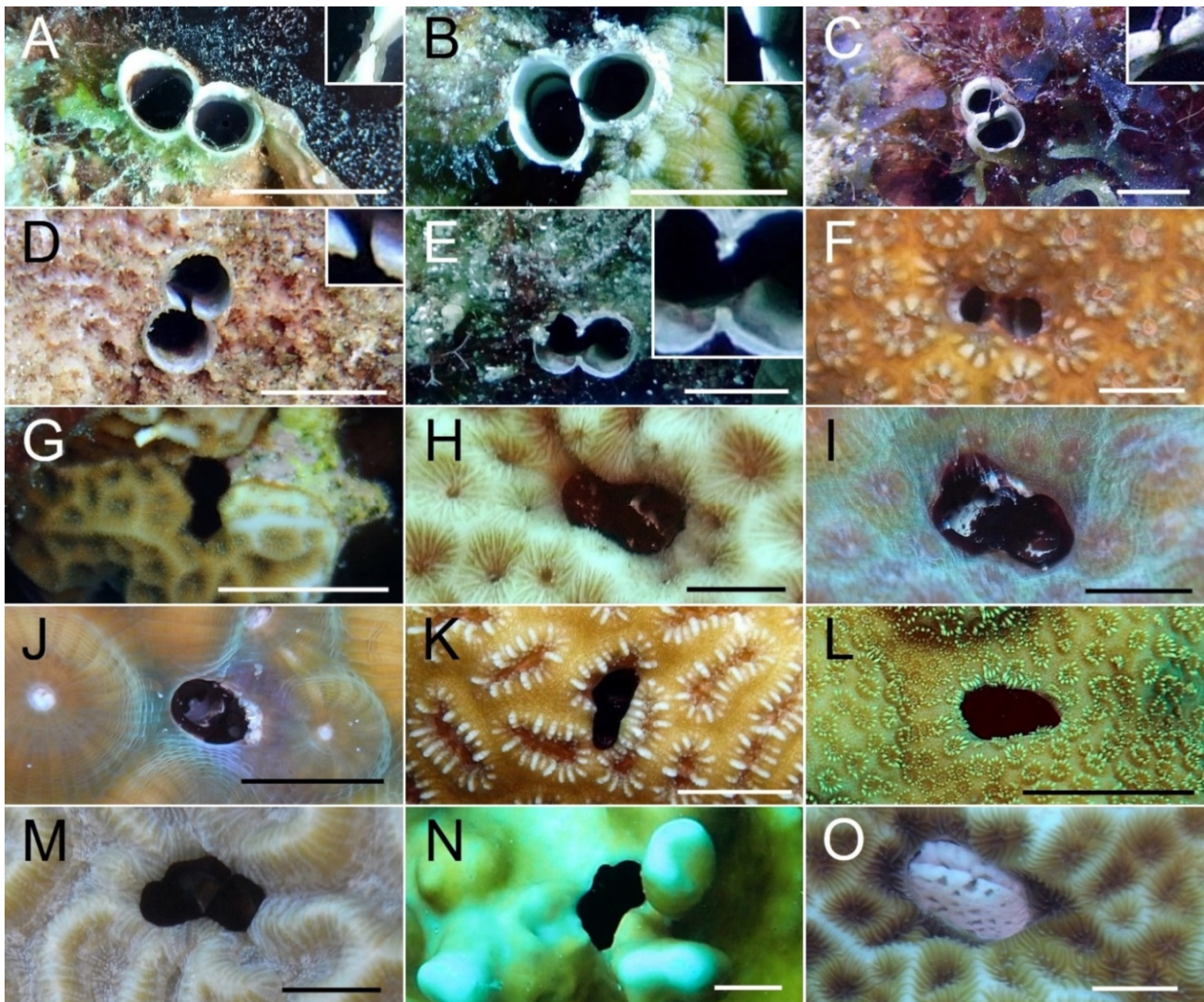


Figure 2. Morphological variation of orifices in corals containing *Leiosolenus* mussels at Curaçao. (A–E) Figure-of-eight shape with two calcareous tubes showing black siphon tissue inside; the tubes are connected apart from a slit (inserts: 2.5× enlargement). (F) The siphon tubes are separated by the host coral. Black mantle tissue is cloaking holes that are shaped like a dumbbell or keyhole (G–I), an oval (J–L), or an irregular ink blotch (M,N). (O) A hole containing valves of a dead mussel. Substrate: dead coral (A,C,D); live corals of *Orbicella franksi* (B,I), *Montastraea cavernosa* (E,J), *Madracis senaria* (F), *Agaricia humilis* (G,O), *Siderastrea siderea* (H), *Favia fragum* (K), *Porites astreoides* (L), *Pseudodiploria strigosa* (M), *Millepora alcicornis* (N). Scale bars: 1 cm.

The inner surface of the tubes was lined with black siphon tissue (Figure 2A–F). The tubes were not visible in the larger holes (Figure 2G–N), which appeared to be pitch black, making them appear to be empty. Closer inspection showed that they were filled with the mussel's black mantle and siphon tissue. Disturbance evoked the retraction of the tissue, revealing that the orifice was funnel-shaped (Figure 3) and that the mantle originally covered live polyps around the hole, masking its true outline. Since the boring activity of the mussels is in posterior and lateral directions [22,41] and the host coral expands, the mussels are forced to move their holes upward in order to remain close to the host's surface [22], as illustrated by Gohar and Soliman (1983: Figure 11B) [23] and by Yahel et al. (2009: Figure 1B) [42]. It is notable that boring mussels of some genera have anterior boring glands [20], suggesting that they can indeed bore in an upward direction. When the calcareous tubes fail in keeping track of the expanding coral and stop reaching the host's surface, the mussel's mantle sustains an open orifice surrounded by growing coral tissue, forcing the host to form a funnel-shaped entrance (Figures 1C, 2H,I, and 3). Such openings may resemble crevices formed by *Pedum* clams that live inside massive corals [11,43,44] or incavations formed by some coral-gall crabs [35].

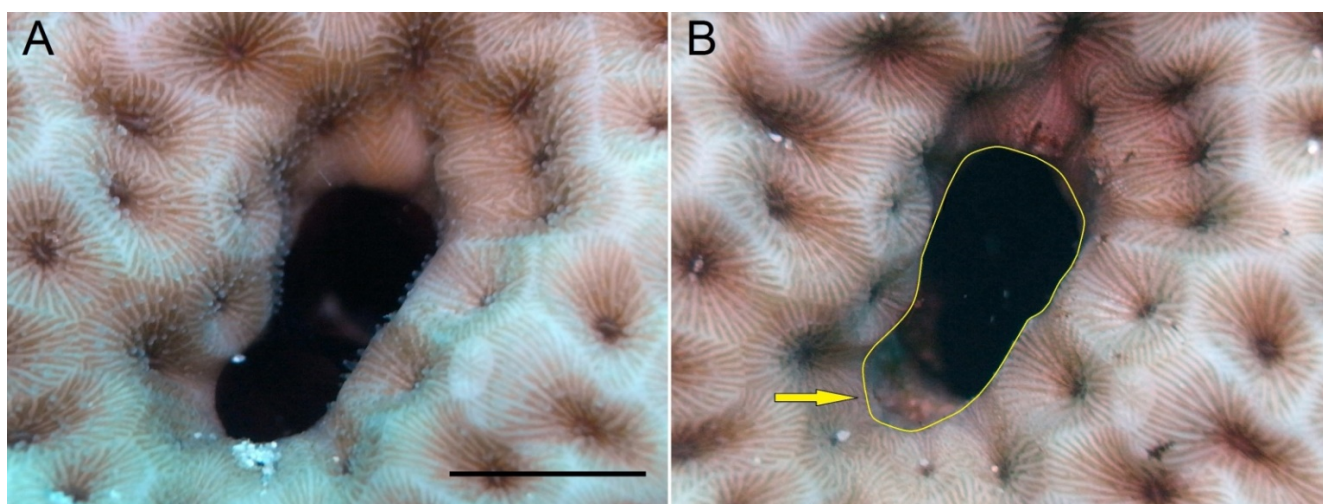


Figure 3. *Leiosolenus* boring in a colony of *Siderastrea siderea* in Curaçao with a funnel-shaped entrance. (A) The mussel's black mantle tissue expanded with a keyhole-shaped outline. (B) The same borehole (from a slightly different angle) with part of the mantle tissue withdrawn (arrow and contour line showing the previous position as depicted in (A)). Retraction of the mantle tissue reveals even more that the opening is funnel shaped. Scale bar: 0.5 cm.

Close up, the color of the mantle tissue appeared to be dark red (Bordeaux) in some mussel individuals, which is slightly visible in Figure 1A. An examination of black holes in corals for the presence of mantle tissue inside makes it easier to see whether boring mussels are present, distinguishing them from dark empty holes without mussels. Previous studies on boring mussels did not pay attention to how mantle coloration may cause lithophagine holes to become less discernible. This finding may help to study whether coral-dwelling date mussels are more abundant than previously thought.

Mussel boreholes were found in 20 scleractinian species and two milleporids (Table 1). Twenty species had large holes (oval and other shapes), and only nine showed figure-of-eight twin openings (Table 1). There were twelve new Caribbean host records, including those of the two *Millepora* species. Three extant *Leiosolenus* species have been described from Caribbean corals [45–49]: *L. aristatus* (Dillwyn, 1817), *L. bisulcatus* (d'Orbigny, 1853) and *L. dixonae* (Scott, 1986). The latter has only been recorded from three *Madracis* species: *M. auretenra* (misidentified as *M. mirabilis*), *M. decactis* (Lyman, 1859) and *M. formosa* Wells, 1973 [45].

Table 1. Coral species at Curaçao observed as hosts for *Leiosolenus*; * = new host record. Shape of orifices observed: T = figure of eight; O = other (oval, dumbbell, keyhole and ink blotch).

Host Taxon	Orifice Shape
Cnidaria: Anthozoa: Scleractinia	
Agariciidae	
<i>Agaricia agaricites</i> (Linnaeus, 1758)	O
<i>Agaricia humilis</i> (Verrill, 1901) *	T O
<i>Agaricia lamarcki</i> Milne Edwards & Haime, 1851 *	O
Astrocoeniidae	
<i>Stephanocoenia intersepta</i> (Esper, 1795)	O
Faviidae: Faviinae	
<i>Colpophyllia natans</i> (Houttuyn, 1772) *	T O
<i>Diploria labyrinthiformis</i> (Linnaeus, 1758) *	
<i>Favia fragum</i> (Esper, 1793)	O
<i>Pseudodiploria strigosa</i> (Dana, 1846)	T O
Meandrinidae	
<i>Eusmilia fastigiata</i> (Pallas, 1766) *	O
<i>Meandrina meandrites</i> (Linnaeus, 1758) *	O
Merulinidae	
<i>Orbicella annularis</i> (Ellis & Solander, 1786)	O
<i>Orbicella faveolata</i> (Ellis & Solander, 1786) *	T O
<i>Orbicella franksi</i> (Gregory, 1895) *	T O
Montastraeidae	
<i>Montastraea cavernosa</i> (Linnaeus, 1767)	O
Pocilloporidae	
<i>Madracis auretenra</i> Locke, Weil & Coates, 2007	O
<i>Madracis decactis</i> (Lyman, 1859)	T O
<i>Madracis pharensis</i> (Heller, 1868) *	T
<i>Madracis senaria</i> Wells, 1973 *	T O
Poritidae	
<i>Porites astreoides</i> Lamarck, 1816	O
Siderastreidae	
<i>Siderastrea siderea</i> (Ellis & Solander, 1768)	O
Cnidaria: Hydrozoa: Anthoathecata	
Milleporidae	
<i>Millepora alcicornis</i> Linnaeus, 1758 *	O
<i>Millepora complanata</i> Lamarck, 1816 *	T O
Dead coral	T

Leiosolenus aristatus has been recorded from Brazil as an introduced species in invasive *Tubastraea* corals [50] and also from Southeast Florida but without a host record [51]. *Leiosolenus bisulcatus* was previously recorded from *Agaricia agaricites*, *Favia fragum*, *Pseudodiploria strigosa*, *Siderastrea radians*, *Siderastrea siderea* and *Stephanocoenia intersepta* (as *S. michelini*) [45,47,52]. *Leiosolenus bisulcatus* has also been recorded from *Oculina arbuscula* Agassiz, 1880 in North Carolina, USA [53] and from *Mussismilia hispida* (Verrill, 1902) and *Siderastrea stellata* Verrill, 1868 in Brazil [54]. In the present study, the mussels were not identified at the species level, but considering previous host records, *L. bisulcatus* is the most likely an associate for most host coral species, with the exception of *L. aristatus* for *Madracis*.

By presenting the host range of boring mussels and by showing the morphological range of their borehole orifices, we aim to facilitate the easy detection of these bioeroding organisms in future research. Our findings may also help in the interpretation of fossil holes of boring mussels, recognized as trace fossils of the ichnogenus *Gastrochaenolites*, and may tell us more about the condition and habitat of their host corals or other substrates when these were still alive [4,55–59].

For a better understanding of the host specificity of coral-associated boring mussels, more research is needed on the host selection during settlement of their larvae, like in earlier studies on Indo-Pacific Lithophaginae [31,60,61], some coral barnacles [62,63], and

Christmas tree worms [64,65]. The present findings may stimulate future studies on borehole orifices in the Indo-Pacific, where more species of coral-dwelling Lithophaginae and host-coral species occur than in the Atlantic [32,66–75]. Molecular techniques are available [2,18,73,76] to study the host specificity of coral-dwelling Lithophaginae on coral reefs in both the Atlantic and the Indo-Pacific.

Coral-dwelling mussels are not the only invertebrates participating in the coral-associated biodiversity of reef corals [77–81]. It is noteworthy that Lithophaginae may also contribute to this fauna indirectly by acting as hosts for symbiotic species themselves, such as pea crabs [82,83]. It is evident that more research is needed on the ecology and evolution of coral-dwelling mussels.

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