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MYTILIDAE

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THE GENUS LITHOPHAGA IN THE WESTERN ATLANTIC

BY

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The lithophages are a specialized group of marine bivalves belonging to the family Mytilidae which are adapted for boring into calcareous rocks, coral, and shells. They are often referred to as datte-de-mer, date shells, or sea dates, because the common species found in the Mediterranean is smooth, dark brown in color, and the shape of a date.

Though the lithophages are not of great economic importance they do occasionally cause damage to jetties, intake tunnels, and similar structures constructed of a poor grade of cement having a high calcareous content. Occasionally, man in his pursuit of the

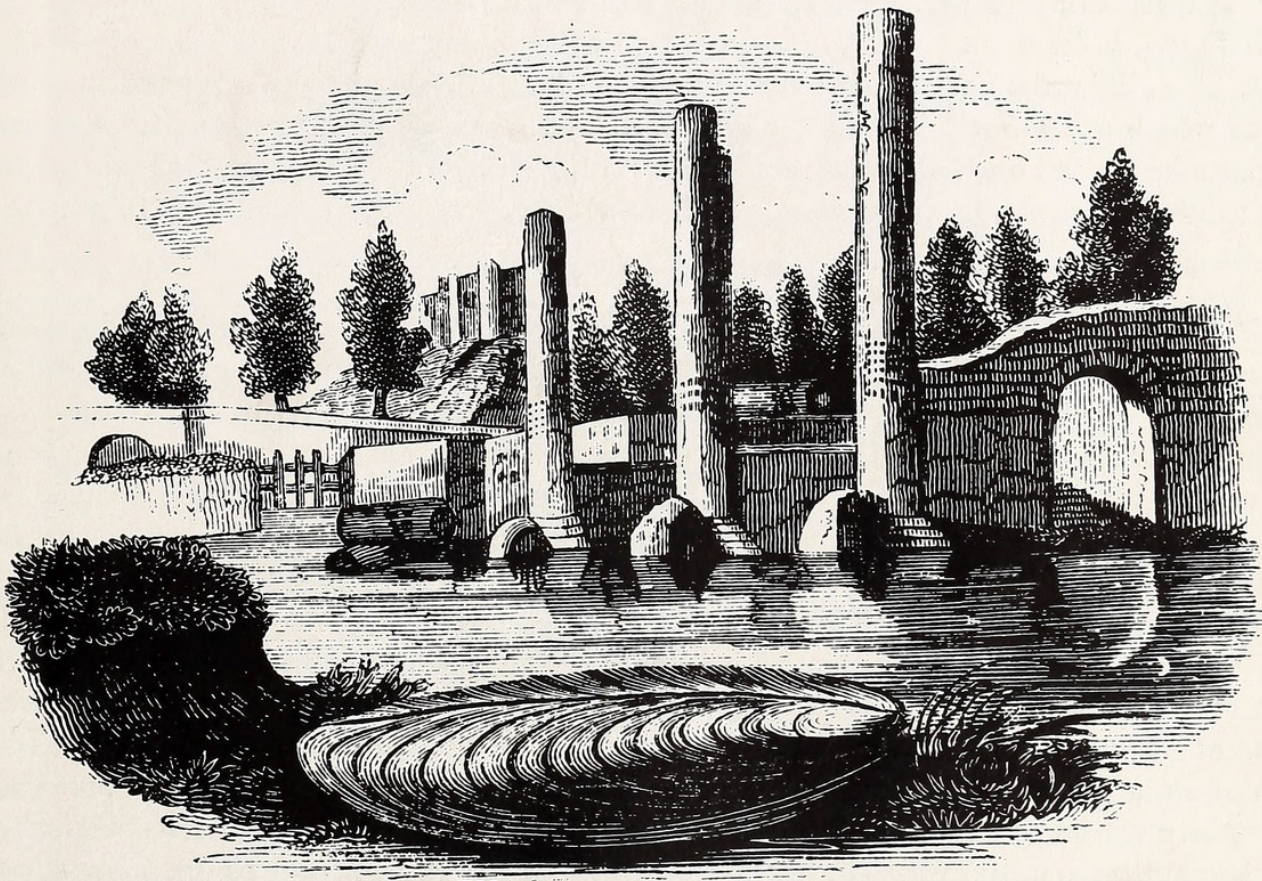


Plate 57. The Temple of Jupiter Serapis, near Pozzuolo, Bay of Naples, Italy, showing the three columns which were bored by *Lithophaga lithophaga* Linné when the temple was submerged. (From Johnston 1850, p. 150, fig. 26.)

datte-de-mer, which in Algiers is considered the most delicious of the many types of sea food, has been more destructive than the clam he sought. Dr. J. C. Bequaert informs us that when he was in Algiers in 1910, the local authorities had to prohibit the collecting and sale of the datte-de-mer lest the breakwater of the port be demolished by the collectors. [See also Remarks under *Lithophaga lithophaga* Linné.]

The boring of *Lithophaga lithophaga* Linné into the pillars of the so-called Temple of Jupiter Serapis¹ has afforded the geologists, notably Lyell, with an example of diastrophism. This ancient Roman ruin (Plate 57), situated in the Bay of Naples near the village of Pozzuolo, Italy has had an interesting history. The exact date of its construction is not known, but sometime during the early centuries of the first millenium, the site was inundated by the sea. Evidence for the eustatic change of the sea level but mainly the sinking and subsequent elevation of the land and the deposition of sediments is seen in the three remaining columns. Lyell has discussed exhaustively the geological events which were necessary to give us this example of the activity of *Lithophaga*. At the height of ten feet above the presently exposed plinths of these pillars, and in a position exactly corresponding in all, is a zone six feet in height where the marble has been penetrated by the Mediterranean species, *Lithophaga lithophaga*. Bodhatch (1761) and Spallanzani (1809) were among the earliest to detect and describe the occurrence of the lithophagous animals in these pillars. The holes made by the *Lithophaga* penetrate to a depth of nearly four inches, and according to Johnston (1850, p. 150) objects of a noncalcareous nature, such as quartz or feldspar, were by-passed and not penetrated at all.

In Japan, holes made by *Lithophaga nasuta* Philippi are used as indicators of old beach lines. The cliff walls near Misaki are studded with hundreds of holes arranged in parallel bands which are about a half meter in width and spaced a few meters apart. A series of earthquakes raised one band after another from the tide level well above high water mark, and the holes remain as evidence of the borers' former activity (Imamura, 1926).

Methods of Boring

Unlike other boring bivalves such as members of the specialized families Pholadidae, Teredinidae, and Petricolidae which use their shells as 'tools' in boring, the lithophages penetrate into the substrate by means of a chemical process. The exact nature of the chemical mechanisms behind this process is unknown. As early as 1846, Osler had made a study of boring bivalves and had concluded that either a chemical, a mechanical, or a combination of the two methods were employed by the various groups of boring mollusks. With a special interest in the method of boring of *Lithophaga*, numerous workers have attempted to adduce concrete evidence to support the hypothesis that acid secretion is the process behind the successful adaptation of *Lithophaga* to its peculiar habitat. List (1902), Carazzi (1903), and Pelseneer (1911) have suggested that particular glands, some of which are located along the margin of the mantle, are responsible for the secretion of an acid mucus. Following the procedure of Carazzi, Kühnelt (1930) in an exhaustive study tested the tissues of the animal with litmus paper. Though the presence of acidic conditions were detected, nothing concerning the concentrations of free acid could be discovered.

¹ Recent archeological investigations have proved that these ruins were not the remains of a temple, called by numerous authors, the Temple of Jupiter Serapis. It has been shown conclusively that the building was actually a market place (Longwell, 1951).

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Kühnelt and, more recently, Hodgkin (1961) have presented excellent inferential evidence in support of the chemical method hypothesis. Using the Eastern Pacific subspecies, *Lithophaga plumula kelseyi* H. and S., Hodgkin experimented with argillaceous and calcareous substrates and showed that this species is unable to bore in noncalcareous media. Observing living animals of the same species, Yonge (1955) found that the fused anterior margins of the inner muscular lobe of the mantle can be protruded for some distance around the anterior end of the valves (see Plate 58). This extensible tissue, he observed, was applied to the anterior end of the burrow and when withdrawn had very fine granular particles embedded in the mucus covering it. Yonge also showed that this area of the mantle was ciliated and that the material was carried by currents in mucus strings ventrally into the mantle cavity and thence posteriorly to be expelled through the incurrent siphon as pseudofaeces.¹ According to Yonge, during the boring process it is necessary that the protruded mantle tissue be closely appressed against the anterior end of the burrow. The byssal threads attach the animal firmly to the substrate, and by the contraction of the posterior byssal retractor muscle, the valves are forced anteriorly. The contraction of the anterior byssal retractor moves the valves posteriorly when the animal is not actively boring. This action lengthens the burrow. The diameter is increased by the relaxation of the adductor muscles and the resulting forceful opening of the valves by the strong ligament. The posterior end of the burrow is probably enlarged by the secretions from the posterior gland and the action of the ligament.

Berry (1907), Amemiya (1923), and Haas (1942) have reported the occurrence of lithophages in noncalcareous substrates. We have seen specimens collected by J. Q. Burch off Monterey in 40 fathoms which were embedded in a rock substrate resembling shale, but a simple acid test revealed the presence of calcium carbonate. We assume that the 'blue hard clay' from Monterey mentioned by Berry (1907) may be of a similar chemical constitution. Through the kindness of Dr. Haas, we have had the opportunity to study the specimen upon which were based the remarks in his paper of 1942. A simple acid did not indicate the presence of calcium carbonate, but the material was shown to be a firm silt, composed largely of silt-sized particles of feldspar, quartz, and mica. Dr. Marlin Billings of the Department of Geology of Harvard referred to it as a dried mud, which when wet would be of a soft consistency. A small piece removed from the specimen completely disintegrated when placed in water. It would therefore appear that, though this firm mud is an unusual habitat for *Lithophaga*, there is no great problem concerned with the method of boring.

Unfortunately, it was after Dr. Haas' material had been returned that we received from

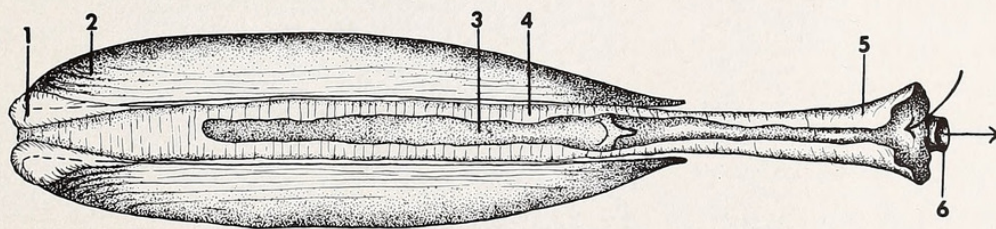


Plate 58. Ventral view of *Lithophaga plumula* Hanley showing the mantle extended over the anterior end of the valves. 1. Extension of the mantle over the shell. 2. Shell. 3. Mantle cavity. 4. Velum fold of the inner lobe of the mantle. 5. Incurrent siphon. 6. Excurrent siphon. (After Yonge, 1955.)

¹This process of cleaning the mantle cavity found in most bivalves is accomplished by a reverse muscle action of the incurrent siphon.

John Fitch a piece of hard rock from near Rocky Point, Lunada Bay, Palos Verdes, Los Angeles County, California from which we extracted five young specimens of *Lithophaga plumula* Hanley. Also boring into the rock were specimens of *Penitella penita* Conrad. When a drop of hydrochloric acid was applied to the rock, it appeared to have no effect; however, when the specimen was viewed microscopically, minute bubbles could be seen. A microscopic thin-section examination and an X-ray analysis of the rock by Professors Billings and Siever of the Geology Department showed it to be a rock dolomite which was 90% lime magnesium carbonate with a grain size of 0.04 mm. According to the engineer's scale this was a hard rock, 'solid with a ringing sound when struck with a hammer.' It was interesting to note that the rock around the opening of the *Lithophaga* burrows was sufficiently softened so that the aperture could be enlarged by picking with a dental tool while that around the aperture of the *Penitella* was not so affected and could not be enlarged. It is possible that Haas' specimen if examined microscopically would have also shown bubbles when acid was applied. Various reports have indicated that lithophages occur in sandstone, but invariably upon chemical testing the particles of sand have been found to be cemented together by calcium carbonate. As stated by Hodgkin (1961), the exact nature of the chemical process is unknown, but future experimental endeavors should indicate that either a free acid secretion or some ionic exchange mechanism is the responsible factor in the remarkable adaptation of *Lithophaga* to the rock-boring habit. It should be remembered that given time and constant application even a weak acid is capable of corroding a hard calcareous substrate, and such appears to be the case with *Lithophaga*.

The experimental results of Kühnelt, Hodgkin, and Yonge show that the method of boring is chemical and the records of lithophages in firm muds or clays show that at times they invade unusual substrates. *Lithophaga* have a free swimming veliger and a diligent search of various substrates would probably reveal young *Lithophaga* in a wide variety of places, most of them being unsuitable, so that the animal, unable to bore or to have some kind of protection, dies at a young stage. In fact, we have received specimens which were nestling among the fouling organisms on a buoy. The largest specimen had reached 11 mm. in length and was sufficiently well developed to be determined without question as *L. bisulcata* d'Orbigny.

Shell Structure

The structure of the shell of *Lithophaga* has been observed and discussed by Carpenter (1847) and List (1902). It is composed of three distinct layers. The outer non-calcareous, horny periostracum which is secreted by the mantle edge is subdivided into two layers: a thin outer, finely granulated portion which is generally brown or black in color and a thicker, lighter colored portion which is characterized by the presence of dorso-ventral lirations. The nacreous or mother of pearl layer is directly beneath the periostracum, a position unlike that of other mytilids and the majority of bivalves where this nacreous layer, if present at all, is innermost. The third and innermost layer of the shell is prismatic with each prism perpendicular to the nacreous layer, appearing polygonal in cross section, and surrounded by supporting conchiolin. Since the prismatic layer covers all the nacreous layer except for a small marginal area, the internal surface of *Lithophaga* normally appears dull and lustreless with iridescence showing only on the marginal or peripheral areas. Carpenter (1847) was the first to report the presence of peculiar tubules

which penetrate both the prismatic and nacreous layers; List (1902) corroborated this finding and elaborated further on their structure, presenting excellent evidence in microscopic sections of the shell. The tubules which are extremely small, as Carpenter noted, about $1/20,000$ of an inch in diameter, appear to begin in the prismatic layer and extend

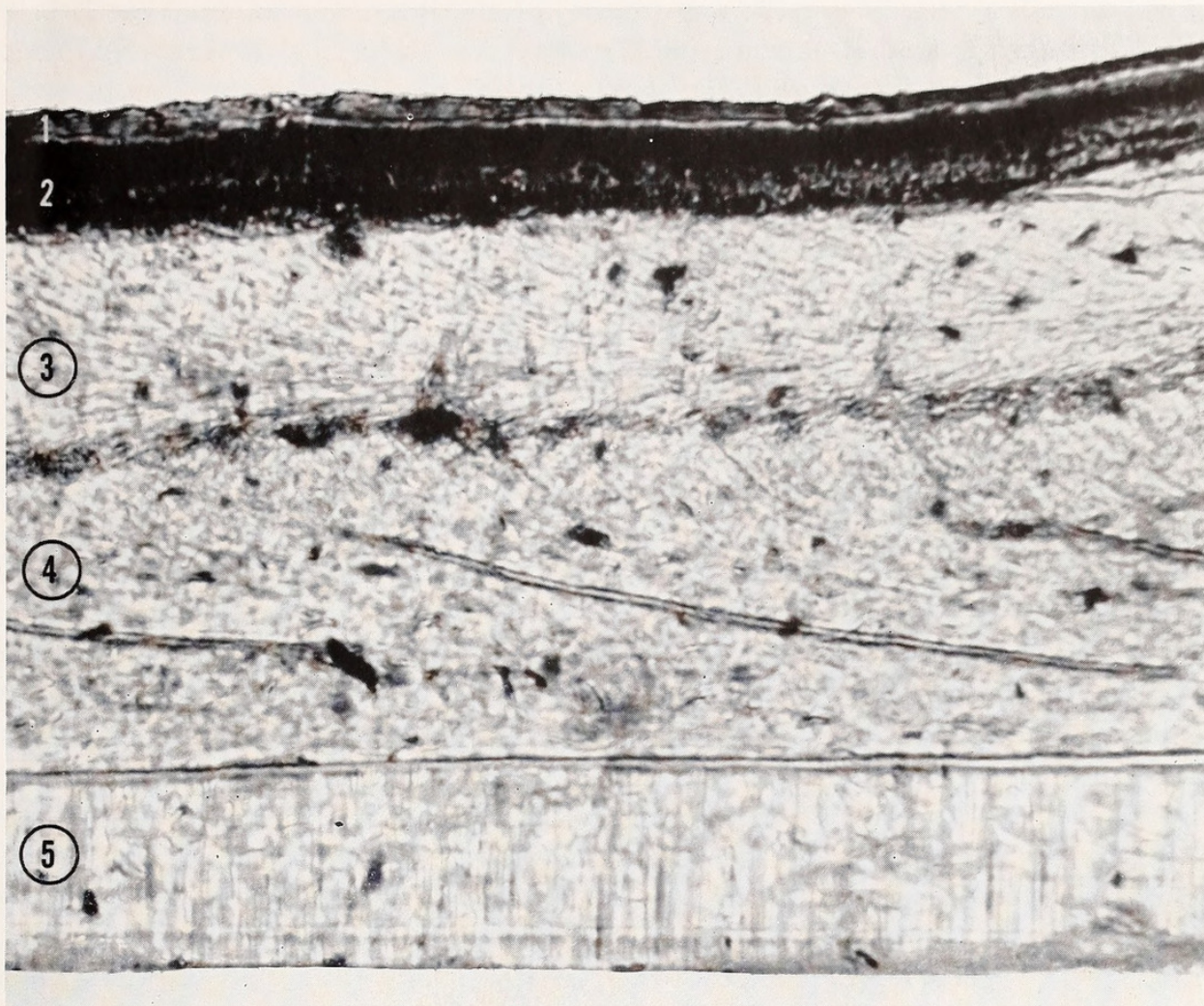


Plate 59. Cross section of the shell of *Lithophaga nigra* d'Orbigny from Soldier's Key, Florida. The various layers are indicated by numbers. 1. Outer layer of the periostracum. 2. Inner layer of the periostracum. 3. Outer layer of the laminated layer. 4. Inner layer of the laminated layer. 5. Prismatic layer. Section taken near the dorsal margin in the mid portion of the valve. ($665\times$.)

into the nearby lamellae of the nacreous layer but not into the outermost lamellae. Unlike the tubules which have been found in *Anomia* and *Lima*, those of *Lithophaga* appear to be straight and parallel to one another; rarely do they anastomose or branch. Another peculiarity of the calcareous layers of the shell of *Lithophaga* has been cited by List (1902). He reported the presence of parasitic algae which occupy the special tubular spaces in both the prismatic and nacreous layers.

Plate 59 shows the position and relationship of the various layers of the shell of *Lithophaga nigra*. For the general external morphology of the shell, see the generic description of *Lithophaga* and Plate 63.

Notes on the Anatomy and Biology

The earliest work done on the anatomy of *Lithophaga* was that of Poli (1795) who described and figured the gross morphology of *Lithophaga lithophaga* Linné. Menegaux

(1890) described in some detail the circulatory system of the same species, and Pelseneer (1911) made some observations on the anatomy of *L. gracilis* Philippi from the Indo-Pacific. List (1902) did the anatomy and histology of the Mytilidae of the Mediterranean including *Lithophaga lithophaga* Linné. Working with living animals, Yonge (1955) described the ciliary tracts and the functioning of the mantle of *L. plumula* Hanley of the California coast, and Ridewood (1903) described the gill structure of *Lithodomus dactylus* Sowerby [= *Lithophaga lithophaga*].

The general morphology of the soft parts of *Lithophaga* is similar to that of *Mytilus*; the differences arise mainly from the transformations made necessary to accommodate the animal to a narrow and elongate shell, as well as those resulting from the use of the byssus and the byssal retractor muscles in boring. The most striking of these is the compact arrangement of the posterior adductor and posterior pedal-byssal retractor muscles and the reduction of the pedal retractors. In addition, the anterior adductor muscle is much larger in *Lithophaga* and is located ventrally.

The mantle in all species of *Lithophaga* examined is thin and transparent except at the margin where it is thickened and a mahogany-brown in color. Many of the organs can be identified through the thin mantle as shown in Plate 61, fig. 1, but the mantle becomes opaque in specimens preserved for a long period of time. The mantle is firmly attached to the shell along its thickened margin which is composed of three lobes. The thin outer lobe, which secretes the shell, is covered by the thick periostracum secreted by cells located between the outer and middle lobes. The middle lobe is evident only as a fine ridge following the edge of the valve. The inner muscular lobe forms a wide ventral fold or velum. Anteriorly the two halves of the inner lobe fuse and in *L. antillarum* this area is thickened and appears glandular. It can be extended out over the anterior surface of the valves where it functions in the boring process (see also under section on Boring). Posteriorly the inner lobe of the mantle produces the relatively short and mahogany-brown siphons. The dorsal or excurrent siphon is complete and has a simple margin which lacks papillae. The incurrent siphon is open ventrally. The margin is firmly attached to the surface of the animal at the base of the siphons and at the dorsal margin of the inner demibranch of the gills.

The arrangement of the major muscles is similar in all species of *Lithophaga* but in the size and shape of the muscles the species appear to be divided into two groups. Though we have seen preserved material of only limited series of five species it would appear that, in those species having a posterior prolongation on the shell, the anterior adductor mus-

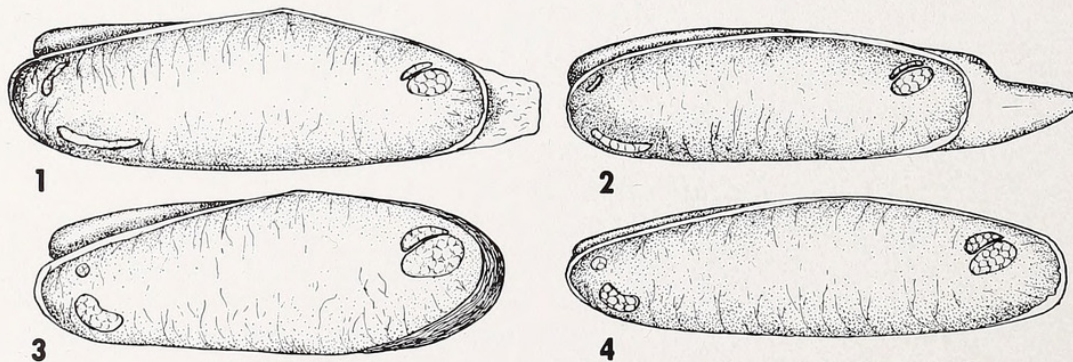


Plate 60. Figures of four species of *Lithophaga* with the left valve removed to show the surface of the mantle and the location of the muscles. Fig. 1. *L. bisulcata*. Fig. 2. *L. aristata*. Fig. 3. *L. nigra*. Fig. 4. *L. antillarum*. Note the resemblance between Figs. 1 and 2 and between Figs. 3 and 4. (About natural size.)

cle at the point of contact with the shell is long, thin and arcuate in cross-section while in those lacking the projection it is kidney-shaped. There appear also to be consistent differences in the shape of the pedal and byssal retractor muscles as shown in Plate 60. The small, digitiform, and extensible foot has rather weak retractor muscles and is apparently used only for the attachment of the byssal threads. The byssal gland is located posterior to the foot, and the threads, though few in number, are heavy and strong. The byssal retractor muscles are well developed and, with the attached byssus, function in moving the shell when boring (see section on Boring). The anterior byssal retractor divides just posterior to the stomach into right and left branches which attach to the valves just beneath the umbos. In Plate 61, fig. 2 the left half of this muscle has been deflected downward to show the large mouth, the funnel-shaped esophagus, and the labial palps. In Plate 61, fig. 1 the labial palps are in their normal position. The stomach is surrounded by the rather large, green digestive gland to which it is connected by means of several ducts so that it is difficult to remove the gland without breaking the walls of the stomach. The gastric shield is easily seen when the stomach is open, but the crystalline style, which lies in the mid-gut, just posterior to the stomach, quickly disintegrates and must be studied in well fed living specimens. Purchon (1957) has described in detail the internal structure of the stomach of *Lithophaga nasuta* Philippi from Singapore. The intestine which is imbedded in the gonads, extends posteriorly from the stomach almost to the posterior pedal-byssal retractor muscles where it turns dorsally, then anteriorly, passing beneath the pericardium and continuing forward nearly to the digestive gland. At this point it reverses, passes through the pericardium and the ventricle of the heart, then extends posteriorly over the dorsal surface of the posterior adductor muscle and opens in the normal position at the base of the excurrent siphon.

The open circulatory system is similar to that of other bivalves. The large ventricle of the heart occupies most of the pericardium while the two lateral, thin-walled auricles are located just ventral to it. There is a single aorta which opens from the anterior end of the ventricle and passes forward just beneath the thickened midline of the mantle. Just anterior to the heart a large trunk branches off which turns posteriorly and passes beneath the pericardium to supply the posterior portion of the animal. Continuing anteriorly the aorta again divides to send paired trunks into the viscera. A third pair of vessels branches off in the region of the esophagus and extends ventrally and then posteriorly along the anterior byssal retractor muscle to the foot. This third pair also sends branches into the labial palps, the anterior adductor muscle, the gonads, the foot, and the byssal retractor muscles. The pallial arteries run from the umbonal area ventrally and posteriorly along the margin of the mantle. These major vessels are illustrated by the dashed lines in Plate 61, fig. 2.

The main ganglia and trunks of the nervous system in freshly preserved specimens are a light salmon color and rather easy to observe. The circumesophageal nerve ring and the paired cerebral ganglia are connected by large commissures which extend posteriorly to the large visceral ganglion located on the anterior surface of the posterior adductor muscle. The paired pedal ganglia are located on the dorsal surface of the anterior byssal retractor muscle near the foot.

The reno-pericardial gland occupies the base of the pericardium and spreads over the surface of the auricles. It connects ventrally with the paired nephridia which are dark brown in color and which extend nearly the length of the animal. Waste products from

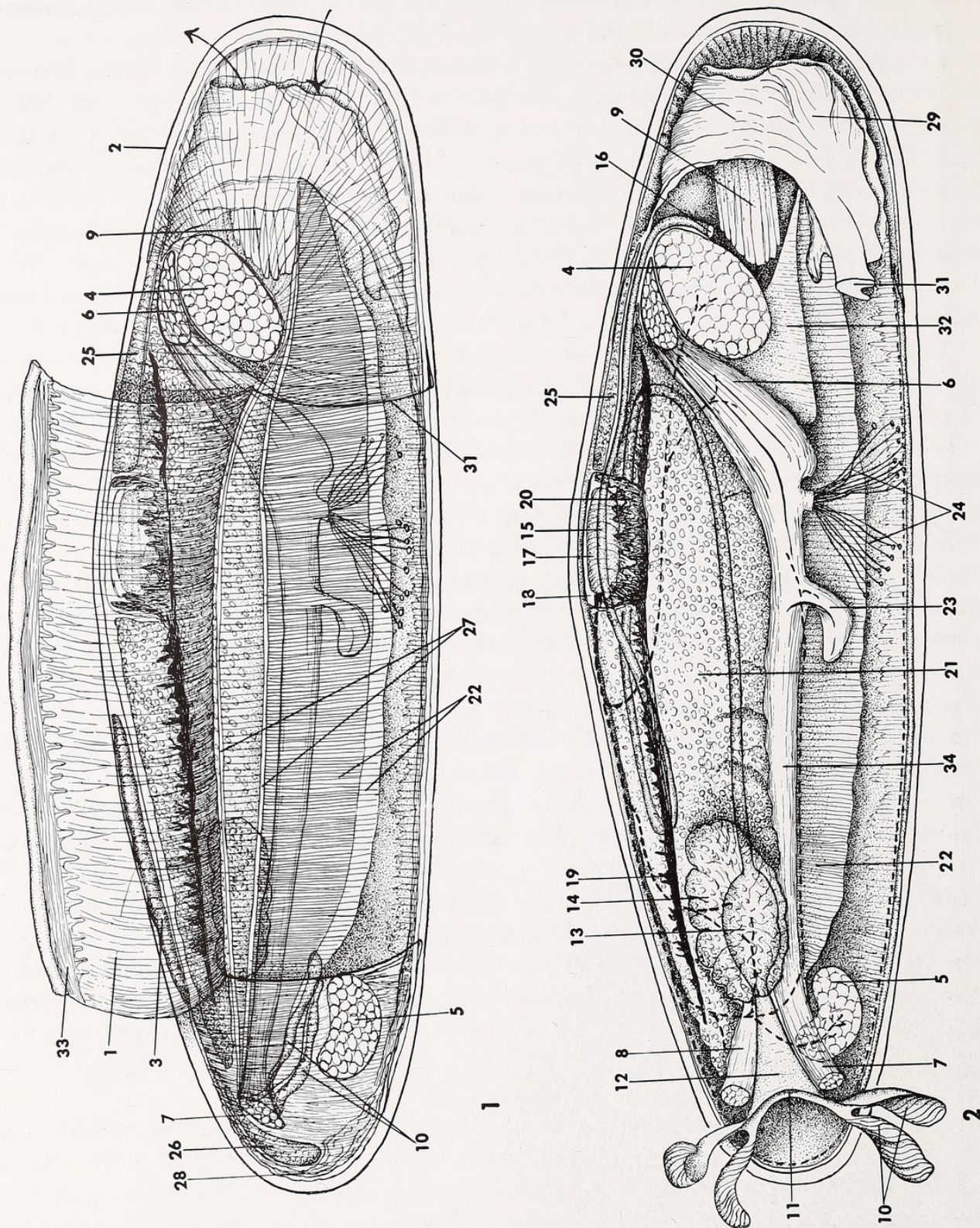


Plate 61

the nephridia and the reproductive products from the gonads empty into the supra-branchial chamber of the mantle cavity via separate orifices in a common uro-genital papilla-like projection. The gonads are large, extending nearly the length of the animal, and occupy most of the space dorsal to the pedal-byssal retractor muscles.

Though *Lithophaga lithophaga* has been well known in the Mediterranean area since very early times and was sufficiently common to be sold in the market, very little is known of its biology and life history. In fact, as far as we can determine nothing has been published on the life history of any species of *Lithophaga* other than the statement of MacGinitie (1935) that *Lithophaga plumula* Hanley spawned in January and February at Monterey Bay, California. He also stated that the larvae metamorphosed to the bi-valve stage in ten days. Dr. G. Thorson, who has made a bibliography of marine invertebrate larvae, writes that he knows of nothing published on the breeding of *Lithophaga*. We have received from A. Merrill a lot of young *Lithophaga bisulcata* taken from St. Mary's buoy which is anchored 7 miles off the mouth of the St. Mary's River, Georgia. On the smaller specimens the embryonic valves were still visible and these are figured in Plate 62, figs. 1-2. On the anterior end of the valves, these young specimens have a fine pustule-like sculpture which is produced until the shells reach 4-6 mm. in length; this roughened surface may aid the animal during its initial settling into the crevices of a substrate. Figure 3 of Plate 62 illustrates changes in the outline of the shell during early growth. Since the depth of the water at the buoy is about five fathoms, it is evident that the veliger larvae of *L. bisulcata* are free swimming and come close to the surface. As previously mentioned, these specimens were not boring but nestling. Since the buoy was removed from its mooring for cleaning in November and since these specimens were very young, ranging in size from about 1.85 to 11 mm. in length, it would appear that at this locality *L. bisulcata* probably has a spawning period in the late summer or fall. The nestling of *Lithophaga* among fouling organisms on shipbottoms is a possible means of dispersal.

Copepod parasites are common in many bivalves and Ummerkutty (1960) reported the first species known to be parasitic on *Lithophaga*. He described it as a new genus and species of archinotodelphyid copepod, *Nearchinotodelphys indicus* Ummerkutty. The specimens were obtained from the mantle cavity of *Lithophaga straminea* Reeve [= *L. antillarum* d'Orb.] collected on the southeast coast of India.

Though Fischer (1886, p. 969), Allen (1950, p. 295), and others have reported simply that some date mussels are phosphorescent, this appears to need verification. *Lithophaga* is not mentioned by Mangold (1910) or Harvey (1957) in their comprehensive works on

Plate 61. Semidiagrammatic illustrations of the anatomy of *Lithophaga antillarum* d'Orbigny. Fig. 1. Specimen with the left valve removed and with the mantle cut just posterior to the anterior adductor muscle and just anterior to the posterior adductor muscle, and turned back to the line of attachment above the gills. Labial palps in their normal position. Fig. 2. Specimen with the mantle and gills removed. Labial palps turned to show position of the mouth.

1. Mantle. 2. Shell. 3. Ligament. 4. Posterior adductor muscle. 5. Anterior adductor muscle. 6. Posterior pedal-byssal retractor muscle. 7. Left anterior byssal retractor muscle. 8. Right anterior byssal retractor muscle. 9. Siphonal retractor muscle. 10. Labial palps. 11. Mouth. 12. Esophagus. 13. Stomach. 14. Digestive gland. 15. Intestine. 16. Anus. 17. Ventricle. 18. Pericardium. 19. Nephridium. 20. Renopericardial gland. 21. Gonads. 22. Ctenidium (gill). 23. Foot. 24. Byssus. 25. Posterior acid gland. 26. Anterior acid gland. 27. Branchial vessels. 28. Fused edge of mantle lobes. 29. Incurrent siphon. 30. Excurrent siphon. 31. Cut edge of mantle. 32. Branchial septum. 33. Pallial muscles. 34. Anterior pedal-byssal retractor muscle.

bioluminescence. It perhaps stems from Fougeroux de Bondaroy (1768) who seems at times to have confused *Pholas dactylus* Linné and *Lithophaga lithophaga* Linné.

Though the Mytilidae are known to have existed as far back as the beginning of the Silurian (Schrock and Twenhofel, 1953, p. 394), the genus *Lithophaga* first appeared in the Pennsylvanian of North America. According to Shimer and Shrock (1944, p. 413), *Lithophaga carolinensis* Conrad is an index fossil of the Upper Cretaceous sediments of

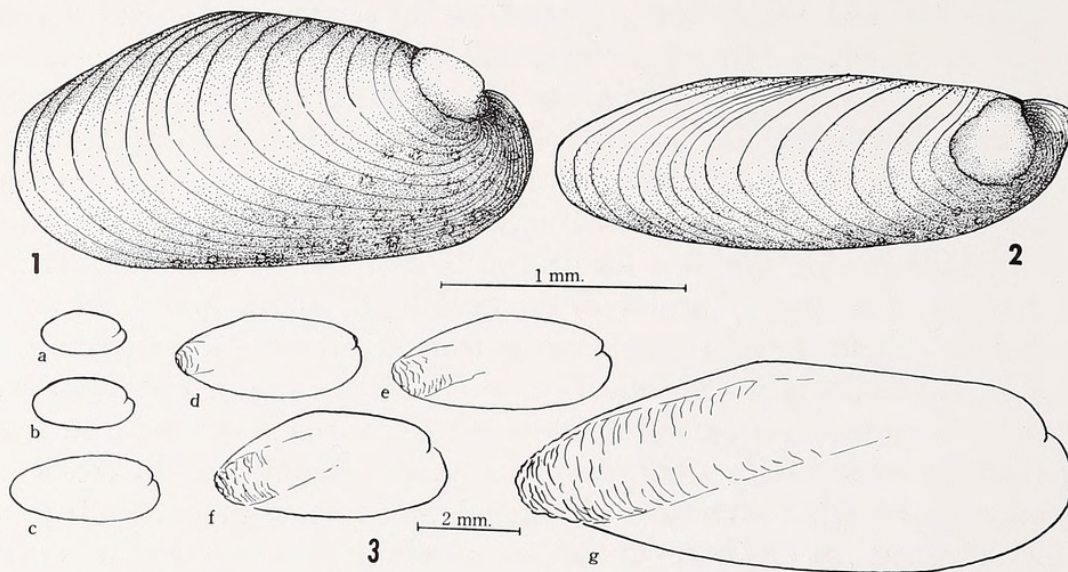


Plate 62. Figs. 1 and 2. Young specimens of *Lithophaga bisulcata* d'Orbigny showing the nepionic valves. Fig. 1. Lateral view of the right valve. Fig. 2. Dorsal view of same. Figs. 3a-g. Stages in the growth of young specimens showing the change in shape and the beginning of the development of the sulci and the calcareous incrustation. Specimens from St. Mary's Buoy off St. Mary's River, Georgia.

the Atlantic and Gulf Coastal plain. *Lithophaga claibornensis* Conrad is found in the Eocene. According to Dall, all four recent species of West Indian *Lithophaga* occur in the Oligocene Silex Beds of Ballast Point, Tampa Bay, Florida. In addition, Dall described as new *L. nuda* which is said to be very similar to *L. nigra*. Maury (1917) has recorded *L. nigra* and *L. antillarum* from the lower Miocene of Santo Domingo. Conrad (1866) described a *L. subalveata* from the lowest Miocene of Shiloh, New Jersey. This appears, however, to be a *Botula*. On the basis of the literature, *Lithophaga* appears to be rather common in the Tertiary of Europe and *Lithophaga lithophaga* Linné is known from the Miocene of Western Europe. According to Dall, because of the thin and fragile nature of the shell, most of the fossil specimens in North America are represented either by casts of burrows or by silicious pseudomorphs.

Notes on Classification

The family Mytilidae is a large and important family of filibranch, anisomyarian bivalves which are equivalve but generally very inequilateral. The umbos are anterior or even terminal, the ligament is long and internal or nearly so, and the periostracum is heavy. The foot is small, digitiform, and there is usually a well developed byssus. The mantle lobes are joined only at the base of the excurrent siphon; the incurrent siphonal opening is continuous ventrally with the pedal opening.

Thiele (1935) groups the many species belonging in this family into eight genera while Soot-Ryen (1955) recognizes twenty seven. Undoubtedly the actual number lies some-

where between these two. Perhaps the most important genus is *Mytilus*, not only because it contains the largest number of species, but also because some members of this genus are important as items of food or as fouling organisms in nearly every maritime country in the world.

The genus *Lithophaga*, the most specialized of the mytilids, includes a relatively uniform group of species which are adapted for boring into calcareous rocks, coral, and shells. Thiele has considered *Botula* Mörch and *Adula* H. and A. Adams as subgenera of *Lithophaga*, but we agree with Soot-Ryen and others that these are distinct genera.

A total of at least 11 subgenera, including the nominate subgenus, has been proposed for the genus *Lithophaga* (the subgenus *Lithophaga* as understood by Thiele). We have seen type specimens of the type species of most of the described subgenera and we believe that there are far more subgenera than necessary for this small compact group. A monotypic subgenus has little meaning unless the species for which it is proposed is truly different. Therefore, we have attempted to group the species according to the basic characters given in the description of the genus, namely: 1) the sculpture, 2) the presence or absence of an incrustation, 3) the presence or absence of sulci dividing the valves, and 4) the type of the posterior prolongation if present. As a result, we have recognized four subgenera in the Western Atlantic and synonymized four. Of the remaining three subgeneric names, *Leiosolenus* Carpenter 1856 with the type species, *Lithophaga* (*Leiosolenus*) *spatiosa* Carpenter 1856 and *Myopalmula* Iredale 1939 with the type species *Litho-*

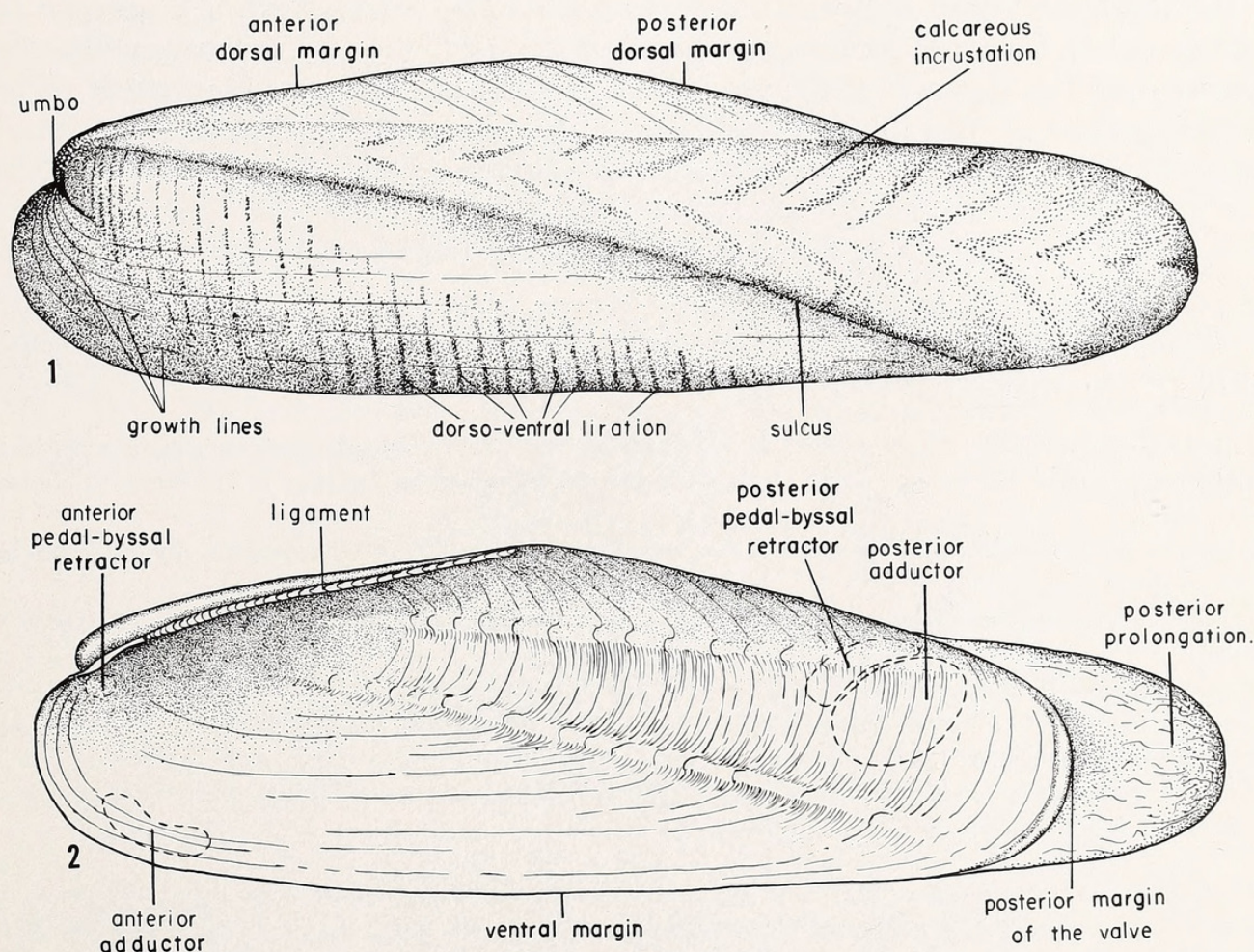


Plate 63. Composite diagrammatic illustrations of the parts of the shell. Fig. 1. External lateral view of left valve. Fig. 2. Internal lateral view of right valve.

phaga (*Myopalmula*) *dichroa* Iredale 1939 are both characterized by having a thin uniform incrustation covering the valve and by lacking any posterior prolongation beyond the valves; therefore, we consider these subgeneric names to be synonymous. Species belonging to *Leiosolenus* are found in the Eastern Pacific and the Indo-Pacific. It is possible that, when further material is available for study, only two subgenera will be recognized: one including those species having posterior prolongations on the shell and narrow arcuate anterior adductor muscle scars and the other including those species that lack the prolongations and have kidney-shaped anterior adductor muscle scars (see Plate 60).

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Genus *Lithophaga* Röding

Lithophaga Röding 1798, Museum Boltenianum, p. 156.

Lithophagus Megerle von Mühlfeld 1811, Magazin der Gesellschaft Naturforschender Freunde, Berlin 5: 69 (type species, *Lithophagus communis* Megerle von Mühlfeld [= *M. lithophagus* Linné] monotypic; non Berthold 1827.

Lithodomus Cuvier 1817, Règne Animal 2: 471 (type species, *Mytilus lithophagus* Linné, monotypic).

Lithotornus 'Cuvier' Schweigger 1820, Handbuch der Naturgeschichte, Leipzig, p. 712 [error for *Lithodomus* Cuvier].

Lithodoma de Blainville 1823, Dictionnaire des Sciences Naturelles 27: 66 (type species, *Mytilus lithophagus* Linné, original designation).

Lithotomus Nitzsch 1825 [in] Ersch und Gruber, Allgemeine Encyclopädie 14: 175 [error for *Lithodomus* Cuvier].

Tamarindiformis Herrmannsen 1849, Indicis Generum Malacozoorum 2: 528.¹

Dactylus Mörch 1861, Malakozoologische Blätter 7: 206 (type species, *Dactylus attenuatus* Deshayes, here selected); non Schumacher 1817.

Dactylus 'Lang' Jousseaume 1894, Le Naturaliste 16 (2): 201 (type species, *Dactylus tripartitus* Jousseaume, monotypic); non Schumacher 1817.

¹ Neave credited this genus to Herrmannsen, but in reality Herrmannsen was only listing the genus and credited it to Meuschen 1787, Museum Geversianum, p. 412, a work which should be placed on the Official Index of Rejected and Invalid Works in Zoological Nomenclature by the International Commission because all generic names, at least in the mollusca, are in the plural form.

Type species, *Lithophaga mytuloides* Röding [= *Mytilus lithophagus* Linné], monotypic.

Shell edentulous, elongate, subcylindrical, but generally becoming laterally compressed posteriorly. Umbos terminal or nearly so. Valves in some species divided by two radial sulci. Shell generally smooth with a heavy periostracum, and, in some species, with an incrustation of calcareous material which may be produced posteriorly beyond the valves. Color of the periostracum ranging from a light golden brown to nearly black. Ventral margin nearly straight; dorsal margin obtusely angled, the highest point of the shell being just posterior to the ligament. The ligament is long, narrow and internal. Anterior adductor muscle scar small and located near the anterior ventral margin. The anterior byssal retractor scar located just beneath the umbos. Posterior adductor and posterior pedal-byssal retractor scars large, adjacent, and located in the posterior quarter of the valve as shown in Plate 63.

Certain mytilid genera may be confused with the genus *Lithophaga* as it is presently defined. Thiele (1935) included within *Lithophaga* the subgenera *Adula* H. and A. Adams and *Botula* Mörch which have, since that time, been elevated to full generic rank by numerous workers. *Adula* may be distinguished from *Lithophaga* by its elongate, thickened, anterior dorsal margin and its short, obliquely truncated, posterior dorsal margin. Furthermore, in *Adula* the siphonal retractor muscle scars are well defined, the dorsal margin of the valves is sometimes crenulate, and the umbos are not terminal but are slightly removed from the anterior position. *Botula*, on the other hand, may be differentiated by the relatively shorter and higher proportions of the valves, the inflated umbos and the convex anterior and posterior dorsal margins which are thickened and crenulate. Unlike *Lithophaga* and *Adula*, the anterior byssal retractor muscles of *Botula* are inserted beneath or behind the inflated and incurved umbos. All three genera are members of the family Mytilidae and may be separated from the coral boring *Coralliophaga* de Blainville of the family Trapeziidae by the lack of cardinal and lateral hinge dentition.

The genus *Lithophaga* is world-wide in distribution mainly in tropical and subtropical waters but a few species extend into the temperate zone.

The genus has been divided into subgenera on the basis of shell ornamentation, as shown in the following key.

Key to the subgenera of the genus *Lithophaga*

1. Shell with calcareous incrustations 2
 Shell without calcareous incrustations *Lithophaga* s.s.
2. Valves divided by sulci *Diberus*
 Valves not divided by sulci 3
3. Shell with calcareous posterior prolongations crossed . . . *Myqforceps*
 Shell with calcareous posterior prolongations not crossed . . . *Labis*

* * * *

Key to the species of *Lithophaga* of the Western Atlantic

1. Shell with posterior prolongations 2
 Shell without posterior prolongations 3
2. Posterior prolongations of valves crossed *aristata*
 Posterior prolongations not crossed *patagonica*
3. Valves divided by two sulci *bisulcata*
 Valves not divided by sulci 4
4. Sculpture consisting of strong dorso-ventral lirations on the
 disc only *nigra*
 Sculpture consisting of weak dorso-ventral lirations on the
 disc, becoming chevroned on the posterior slope *antillarum*

Subgenus *Lithophaga* Röding

This subgenus is characterized by the lack of any calcareous incrustations or prolongations on the valves and by having a glabrous, medium to dark brown periostracum and fine dorso-ventral lirations on the disc.

***Lithophaga (Lithophaga) lithophaga* Linné**

Plate 64, figs. 1-2

Mytilus lithophagus Linné 1758, Systema Naturae, ed. 10, p. 705 [in part, reference to Bonnani 1684, Recreation, p. 102, fig. 28 and d'Argenville 1742, Hist. Nat., p. 365, pl. 30, fig. L].

Callitricoderma lithophagum Poli 1795, Testacea Utriusque Siciliae 2: 260.

Lithophaga mytuloides Röding 1798, Museum Boltenianum, p. 156 [refers to Gmelin 1791, *Mytilus lithophagus* Linné].

Lithophagus communis Megerle von Mühlfeld 1811, Magazin der Gesellschaft Naturforschender Freunde, Berlin 5: 69 [refers to Gmelin 1791, *Mytilus lithophagus* Linné].

Lithodomus lithophagus Linné. Cuvier 1817, Règne Animal 2: 471.

Modiola lithophaga Linné. Lamarck 1819, Histoire Naturelle des Animaux sans Vertèbres (1) 6: 115.

Lithodomus dactylus Sowerby 1824, The Genera of Recent and Fossil Shells, **Lithodomus**, no. 23, figs. 1-2 (no locality given).

Lithodomus inflatus Requier 1848, Catalogue des Coquilles de l'Ile de Corse, p. 30 (Ile de Corse).

Lithophaga lithoglypha 'Meuschen' Mörch 1853, Catalogus Conchyliorum Comes de Yoldi 2: 55 [error for *L. lithoglypha*].

Lithophaga lithoglypha 'Meuschen' Dunker 1882, Conchylien-Cabinet (2) 8 Abt. 3a, **Lithophaga**, p. 3, pl. 4, figs. 5-6 (Zara, Dalmatia).

Lithophagus lithophagus Linné. List 1902, Fauna und Flora des Golfes von Neapel. Monograph, no. 27, p. 11, pl. 3, figs. 1-9; pl. 4, figs. 19-22.

Lithophaga lithophaga Linné. Lamy 1937, Journal de Conchyliologie 81: 106.

Description. Shell elongate-elliptical in outline, reaching 91 mm. (about 3½ inches) in length and 27 mm. (about 1 inch) in height, thin and with anterior umbos. Umbos small but conspicuous and located very close to the anterior end of the shell, the anterior slope extending only slightly beyond the umbos. Color a medium golden brown to dark mahogany. Periostracum thin, smooth and shining. Sculpture consisting of low, irregularly spaced concentric ridges and growth lines. In addition, the area of the disc is sculptured with fine, more or less parallel but slightly wavy lirations which extend dorso-ventrally and cross the growth lines, giving a finely reticulate appearance. Interior of shell a bluish

gray and shining, often quite iridescent near the posterior end. Hinge line nearly straight, extending from the umbo to about midway on the dorsal margin. Muscle scars only slightly impressed, the anterior adductor scar kidney-shaped and located near the anterior ventral margin. The anterior byssal retractor scars nearly circular and located just beneath the umbos. Posterior adductor scar about midway between the end of the ligament and the posterior margin of the shell and confluent with those of the pedal and byssal retractors. Ligament internal, long and narrow.

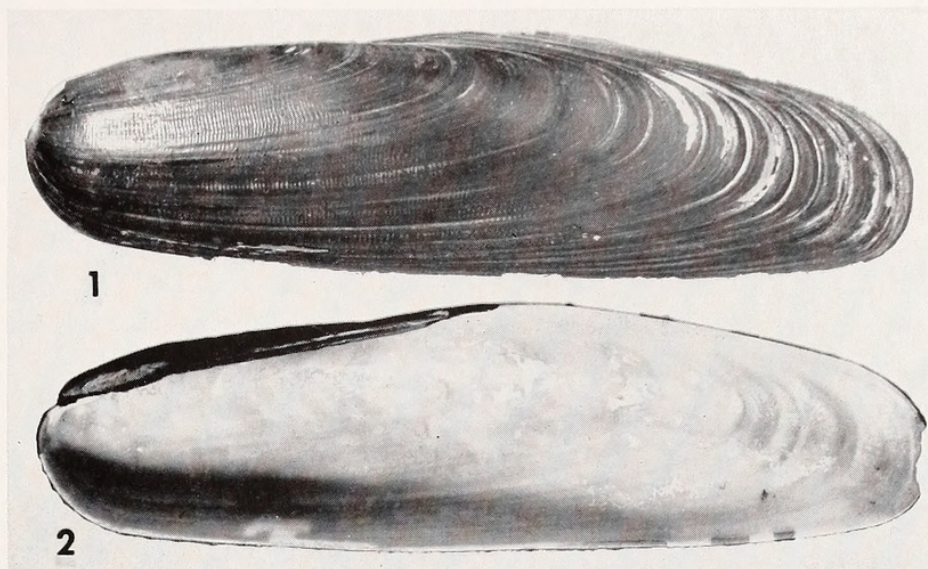


Plate 64. *Lithophaga lithophaga* Linné. Fig. 1. External lateral view of left valve showing lirations on the disc. Fig. 2. Internal lateral view of right valve. Island of Malta, Mediterranean Sea. (Natural size.)

length	height	
91.0 mm.	24.0 mm.	Malta Island
90.0	26.5	“ “
90.0	26.0	Mahon, Minorca Id., Balearic Islands
84.0	24.5	“ “ “ “ “
67.5	24.5	Minorca Id.
18.0	6.0	Spezzia, Italy

Types. The holotype of *Mytilus lithophagus* Linné is in the collection of the Linnean Society of London. The type locality is here restricted to Ancona, Italy, the locality mentioned by D'Argenville 1743, p. 365, to which Linné referred. The type figure of *Lithophaga mytuloides* Röding is in the Conchylien-Cabinet (1) 8: pl. 82, figs. 729 and 730. The type of *Lithodomus dactylus* Sowerby is probably in the British Museum (Natural History). The locations of the type specimens of *Lithodomus inflatus* Requien and *Lithophaga lithoglypha* Dunker are unknown to us.

Remarks. A complete account of *L. lithophaga* is included in this report because it is the type species of the genus *Lithophaga*. Apparently it is a fairly common species though series in collections are not large. Johnston (1850) stated that in the Mediterranean the rocks were broken with large hammers in order to obtain them for food. They were considered a great delicacy throughout the Mediterranean countries and particularly in Italy where they were known as the 'dattolo di pietra' or 'dattolo di mar.' It was this species that bored into the columns of the so-called temple of Jupiter Serapis (see

also the Introduction). Bucquoy, Dautzenberg and Dollfus (1890, p. 163) record this species as fossil in the Miocene of Western Europe.

Lithophaga lithophaga is variable in both color and shape as attested by the measurements given above and reflected in the lengthy synonymy. It is perhaps most closely related to *L. nigra* of the Western Atlantic, from which it differs by having the anterior margin of the shell protruding slightly beyond the umbos. *Lithophaga nigra* is definitely darker in color, its posterior slope is higher, and the dorso-ventral lirations do not extend as far posteriorly on the disc. The thickening on the posterior end of *L. nigra* never occurs in *L. lithophaga*. In the latter species the posterior end of the shell is usually higher than the anterior end, whereas in *L. nigra* the dorsal and ventral margins are nearly parallel. Young specimens of these two species are difficult and often impossible to distinguish. See also Remarks under *L. nigra*.

Range. *Lithophaga lithophaga* occurs throughout the Mediterranean Sea and in the Red Sea near Tor, Sinai Peninsula, Egypt, according to Dunker (1882). According to Nickles (1950) it occurs on the west coast of Africa from Morocco to Sénégal. We have seen a lot from ballast taken at Cardiff, Wales in the collection of the United States National Museum. Such specimens may explain certain erroneous records.

Specimens examined. EUROPE. FRANCE: Nice (MCZ); Toulon (USNM). SPAIN: Cadiz; Malaga (both BMNH). ITALY: Spezzia (MCZ); Livorno (USNM); Viareggio (MCZ); Naples (MCZ; USNM). JUGOSLAVIA: Zara, Dalmatia (USNM). MEDITERRANEAN ISLANDS: Port Mahan, Minorca Id., Balearic Islands (MCZ; USNM); Malta Island (MCZ; USNM; BMNH). ASIA: Aden (BMNH).

***Lithophaga (Lithophaga) nigra* d'Orbigny**

Plate 65, figs. 1-5; Plate 66, figs. 1-3; Plate 75, figs. 2-3

Lithodomus niger d'Orbigny 1842 [in] Sagra, Hist. Nat. L'Ile de Cuba, Mollusques, Atlas, pl. 28, figs. 10-11; ibid 1853 Mollusques 2: 331 (Cuba).

Modiola (Lithophagus) antillarum Philippi 1847, Zeitschrift für Malakozoologie 4: 116; Philippi 1847, Abbildungen und Beschreibungen Conchylien 3: 20, pl. 2, fig. 4 (St. Thomas, Virgin Islands), *non* d'Orbigny 1842.

Modiola (Lithophagus) caribaea Philippi 1847, Zeitschrift für Malakozoologie 4: 116 (Antillae); 1847, Abbildungen und Beschreibungen Conchylien 3: 20, pl. 2, fig. 5.

Lithophaga nigra d'Orbigny. Mörch 1853, Catalogus Conchyliorum Comes de Yoldi 2: 56.

Lithodomus antillarum Philippi. Reeve 1857, Conchologia Iconica 10: **Lithodomus**, pl. 2, fig. 7, *non* d'Orbigny 1842.

Lithophaga crenulata Dunker 1848, Zeitschrift für Malakozoologie 5: 180 (Porto Cabello, Venezuela); Dunker 1883, Conchylien-Cabinet (2) 8 Abt. 3a, **Lithophaga**, p. 11, pl. 3, figs. 7-9.

Description. Shell elongate-elliptical in outline, reaching 65.5 mm. (about 2½ inches) in length and 20 mm. (about ¾ inch) in height, thin, fragile and with anterior umbos. Umbos small but conspicuous and located very close to the anterior end of the shell; anterior margin not extending beyond the umbos. Color a deep chestnut brown to nearly black. In many adult specimens the posterior margin of the shell is thickened and diverged, resulting in a labiate, or lip-like appearance as shown in Plate 65, figs. 3-4. Often at successive increments in the length of the shell a series of lip-like structures are formed which remain as pronounced ridges on the surface of the valves. Periostracum nearly

black, rather smooth and shining. Sculpture consisting of low, irregularly spaced, concentric growth lines and ridges. The area of the disc is sculptured with pronounced parallel lirations which extend dorso-ventrally and cross the growth lines, giving a reticulate appearance. Interior of the shell bluish gray, shining, with iridescence generally slight and limited to the area of the muscle scars. Hinge line nearly straight and extending from just posterior of the umbo to about midway along the dorsal margin. Ligament internal, narrowing anteriorly. Posteriorly the nacreous portion is smoothly rounded and the posterior area beyond this is somewhat angled and covered with periostracum. Muscle scars faintly impressed. Anterior adductor scar kidney-shaped and located near the anterior ventral margin; anterior byssal retractor scar nearly circular and located just beneath the umbos; posterior muscle scar, including the posterior adductor, the posterior pedal and byssal retractors is located just posterior to the arcuation of the posterior dorsal margin.

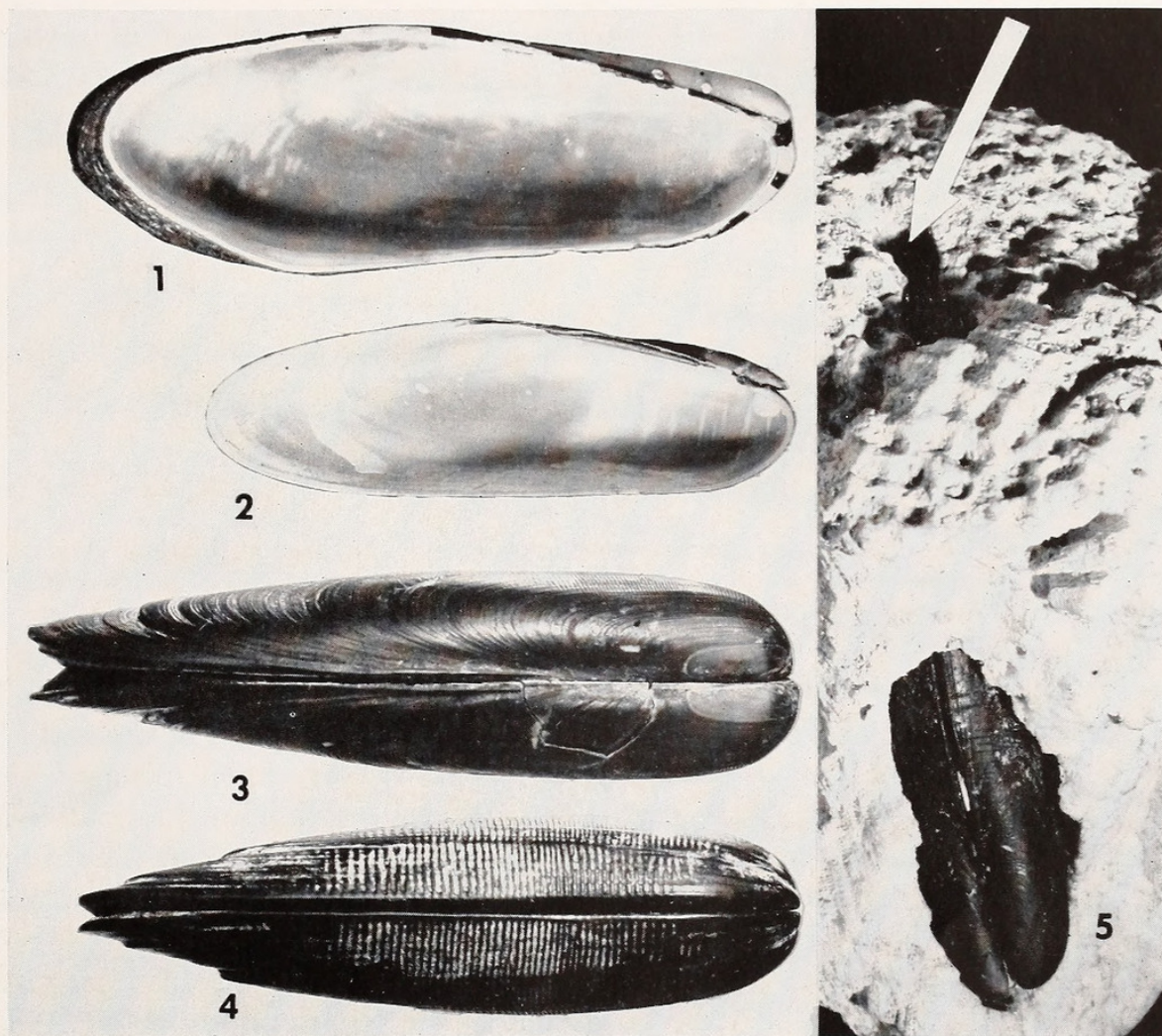


Plate 65. *Lithophaga nigra* d'Orbigny. Fig. 1. Internal view of the left valve showing the thickened posterior. St. John, Virgin Islands. Fig. 2. Internal view of the left valve of a young specimen from Cuba. Fig. 3. Dorsal view of opposed valves. Fig. 4. Ventral view of opposed valves. Figs. 3 and 4 from Bonefish Key, Florida. Fig. 5. Specimen imbedded in rock (arrow indicates the entrance of the burrow). Lower Florida Keys. (All $2\times$.)

length	height	
65.5 mm.	20.5 mm.	Bermuda
51.5	16.0	10 miles N of Hamilton, Bermuda
40.5	13.5	St. John, Virgin Islands
45.5	14.5	Bonefish Key, Florida
21.5	8.0	" " "

Types. The types of *Lithodomus niger* d'Orbigny are in the British Museum (Natural History) no. 54.10.4.604; the type locality Cuba, is here restricted to Guantánamo, Oriente, Cuba. The locations of the type specimens of *Modiola* (*Lithophagus*) *antillarum* Philippi from St. Thomas, Virgin Islands and *Modiola* (*Lithophagus*) *caribaea* Philippi from the Antilles are unknown to us. The type specimen of *Lithophaga crenulata* Dunker from Porto Cabello, Venezuela is probably in the Natural History Museum in Berlin, Germany.

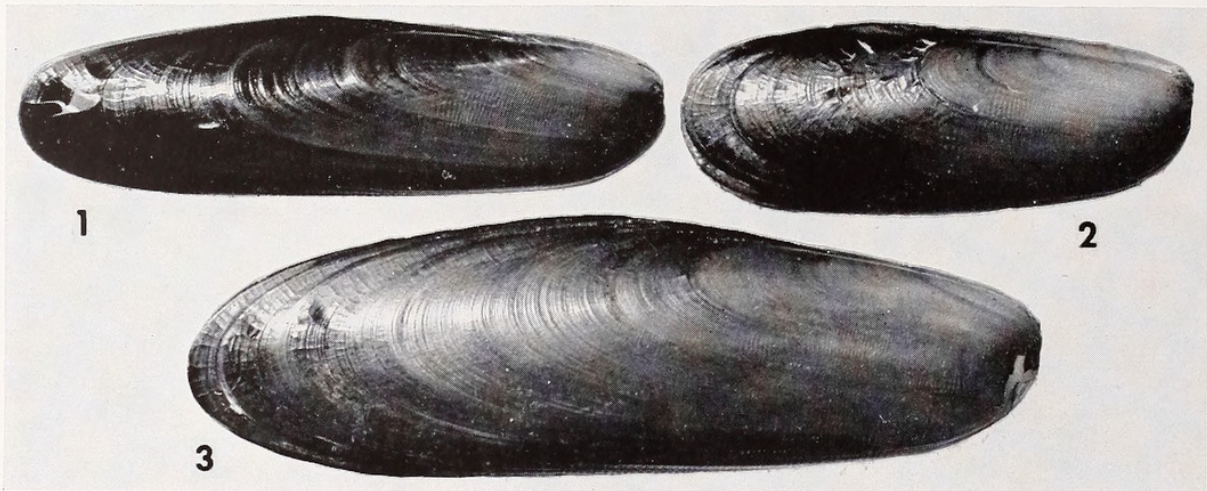


Plate 66. *Lithophaga nigra* d'Orbigny. A series showing variation in the shape of the shell. Fig. 1. A long thin specimen with an angled dorsal margin. Fig. 2. A short broad specimen with a nearly straight dorsal margin. Fig. 3. A typical specimen. All from Hamilton, Bermuda. (All about 2×.)

Remarks. This species is very close in its relationship to *Lithophaga lithophaga* Linné of the Eastern Atlantic and the Mediterranean, and in fact, in much of the early literature on the West Indies, it was referred to under this name. Such misidentifications have not been included in the synonymy. For further discussion on the relationship of these species see remarks under *Lithophaga lithophaga*. *Lithophaga nigra* is also closely related to *L. teres* Philippi 1846 of the Indo-Pacific; we have been unable to find any distinguishing characters to separate specimens of *nigra* and *teres* which are of equal size. However, since *L. teres* reaches a size more than twice that of the largest known specimens of *nigra*, we hesitate at this time to place it in the synonymy of *nigra*. As a matter of fact, the *L. lithophaga* of Europe, the *L. teres* of the Indo-Pacific region, and the *L. nigra* of the Western Atlantic form a complex whose precise interrelationships remain unknown due to a lack of ample material in research collections. It may well be that this complex represents a single cosmopolitan species with at least three subspecies. Furthermore, the three named species, *gracilis* Philippi 1847, *malayana* Philippi 1847, and *cylindrica* Krauss 1848, which are recorded from the Indo-Pacific region are probably *teres*, but more material is needed before this can be definitely stated.

Lithophaga nigra is a tropical and warm water subtropical species occurring in cal-

careous rock, corals and shells from the intertidal zone to depths of at least four fathoms. Specimens taken by the *Albatross* from 130 fathoms are based on shells only and it is doubtful that the species lives at that depth. Dall (1898) reports *L. nigra* as occurring in the Oligocene Silex beds of Ballast Point, Tampa Bay, Florida, a locality rather considerably north of its known distribution in Florida today.

For a discussion of the anatomy of this species see the Introduction.

Range. From Pompano, Florida south through the Florida Keys, Bermuda, the Bahama Islands and south through the West Indies to Trinidad; from British Honduras to Curaçao, Dutch West Indies and south to Abrolhos, Brasil. This species has been recorded by Dall (1898) and Johnson (1934) from South Carolina but this is open to question.

Specimens examined. FLORIDA: Pompano; Miami; Soldier's Key; off The Elbow, Key Largo; Carysfort Reef, off Key Largo; Bonefish Key; Ohio Key (all MCZ); Key West; Eastern Dry Rocks; Bird Key, Tortugas (all USNM); Fort Jefferson, Dry Tortugas (MCZ; USNM). BERMUDA: Castle Harbour; Harrington Sound; Hamilton; Pembroke (all MCZ); St. Georges (MCZ; USNM). BAHAMA ISLANDS: North Point, Elbow Cay and Turtle Cay, Abaco Island (both MCZ); New Providence (MCZ); Long Bay Cay District, Andros Island; Lisbon Point, Mangrove Cay, Andros (both USNM). CUBA: *Albatross*, station 2320, off Habana ($23^{\circ}10'39''$ N; $82^{\circ}18'48''$ W) in 130 fathoms; *Tomas Barrera*, station 231, off Cayo Levisa, in 2–3 fathoms and *Tomas Barrera*, station 218, off Cayo Hutia Reef, Pinar del Río (USNM); east of Farallone de Arena, Oriente (ANSP); Guantánamo, Oriente (MCZ). JAMAICA: Montego Bay (MCZ). HISPANIOLA: Santa Bárbara de Samaná, Santo Domingo (MCZ). VIRGIN ISLANDS: 1 mile south of settlement, Anegada (MCZ); Tortola (USNM; MCZ); St. John (MCZ); St. Thomas (MCZ; USNM; BMNH); Drift Bay, Water Island (USNM); St. Croix (MCZ). LESSER ANTILLES: Port Castries, St. Lucia; off Lord's Castle, Barbados in 3–4 fathoms (both USNM); Barbados (MCZ; USNM); Oistin Bay, Barbados in 4 fathoms (R. Gooding); Pelican Island, Barbados (USNM); Union Island, The Grenadines; Bucco Reef, Tobago; Carenage, Trinidad (all MCZ). BRITISH HONDURAS: Triangles ($17^{\circ}19'55''$ N; $88^{\circ}09'25''$ W) in 1–10 feet; Glory Cay ($17^{\circ}06'00''$ N; $88^{\circ}00'55''$ W) in 2–4 feet; north of Tarpum Cay ($16^{\circ}37'05''$ N; $88^{\circ}09'05''$ W) in 2–5 feet (all ANSP); coral reef near St. George's Cay, Belize (USNM). CARIBBEAN ISLANDS: Curaçao, Dutch West Indies (USNM). BRASIL: off Abrolhos in 30 fathoms [dead] (MCZ).

***Lithophaga (Lithophaga) antillarum* d'Orbigny**

Plate 67, figs. 1–3; Plate 75, fig. 1

Lithodomus antillarum d'Orbigny 1842 [in] Sagra, Hist. Nat. l'Île de Cuba, Atlas, pl. 28, figs. 12–13; *ibid.* 1853, Mollusques 2: 332 (Cuba; Guadeloupe; Martinique), *non* Philippi 1847.

Modiola corrugata Philippi 1846, Abbildungen und Beschreibungen Conchylien 2: 147, **Modiola**, pl. 1, fig. 1 (locality unknown).

Lithodomus stramineus 'Dunker' Reeve 1857, Conchologia Iconica 10, **Lithodomus**, pl. 2, fig. 11 (West Indies).

Lithophagus dactylus 'Sowerby' Mörch 1859, Catalogus Conchyliorum Comes de Yoldi 2: 55 [refers to *L. antillarum* d'Orbigny and *L. corrugata* Philippi], *non* Sowerby 1824.

Lithophaga straminea Dunker 1882, Conchylien-Cabinet (2) 8: abt. 3a, **Lithophaga**, p. 6, pl. 2, figs. 1-2 (*Antillae insulae*).

Lithophaga antillarum d'Orbigny. Dall 1898, Trans. Wagner Free Institute of Science, Philadelphia 3: 799.

Description. Shell lanceolate in outline, reaching 109 mm. (about $4\frac{3}{8}$ inches) in length with the anterior end being about one half the height of the posterior end. Broadly oval in cross section at the anterior end, becoming compressed laterally at the posterior end. Thin, fragile with inconspicuous anterior umbos, the anterior margin of the shell extending slightly beyond the umbos. Color a light straw-yellow to medium brown. Posterior margin simple and smoothly rounded. Periostracum thin and marked with exceedingly fine longitudinal lines when viewed under $30\times$ magnification. In adult specimens the

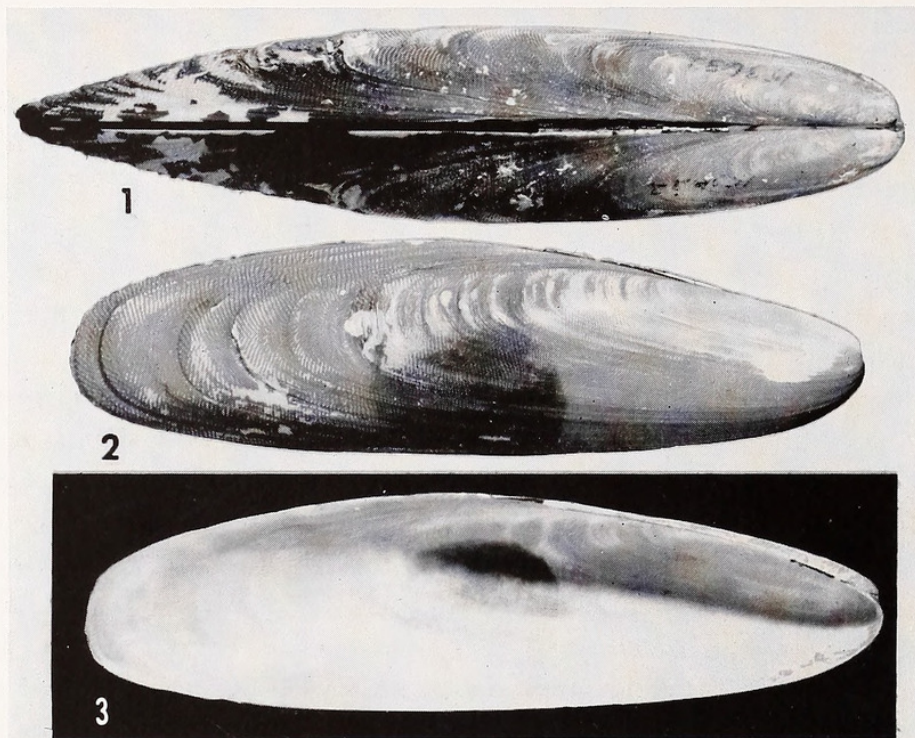


Plate 67. *Lithophaga antillarum* d'Orbigny. Fig. 1. Dorsal view of opposed valves. One mile S.W. of Soldier's Key, Florida. Fig. 2. External view of the right valve. Fig. 3. Internal view of the left valve (both from St. Thomas, Virgin Islands. (All natural size.)

periostracum is often worn away. Sculpture consisting of low, irregularly spaced, rather broad, concentric growth ridges. The area of the disc is sculptured with fine irregular lirae, which are more or less parallel anteriorly, becoming curved about midway and somewhat irregularly radiating or chevron-shaped at the posterior end. Interior of the shell grayish white to brownish purple, becoming whiter as the shell increases in age and thickness. Posterior half of the valves usually iridescent and the lirae are often evident. Muscle scars faintly impressed; anterior adductor scar kidney-shaped and located near the anterior ventral margin. Anterior byssal retractor scar located in the concavity of the umbos. Posterior muscle scar, including the posterior adductor, the byssal and pedal retractors, located about midway between the end of the ligament and the posterior end of the shell.

length	height	
109.5 mm.	25.0 mm.	Key West, Florida
101.0	26.5	Soldier's Key, Florida
83.5	23.5	Looe Key, Florida
44.0	12.5	Santa Bárbara de Samaná, Santo Domingo

Types. The types of *Lithodomus antillarum* d'Orbigny are in the British Museum (Natural History), no. 54.10.4.605. The type locality as given by d'Orbigny, which included Cuba, Guadeloupe and Martinique, is here restricted to Guantánamo, Oriente, Cuba. The location of the type specimens of *Modiola corrugata* Philippi and *Lithophagus dactylus* 'Sowerby' Mörch is unknown to us. The type of *Lithodomus stramineus* 'Dunker' Reeve is probably in the British Museum (Natural History); the type locality is the West Indies. The type of *Lithophaga straminea* Dunker is probably in the Natural History Museum in Berlin; the type locality is West Indies.

Remarks. This species, the largest of the lithophages found in the Western Atlantic, is readily distinguished by its light brown color, lanceolate shape, and lack of calcareous incrustations or posterior prolongations on the shell. In addition, it is differentiated by the chevron-shaped sculptural ridges on the posterior slope. The closest relative of *L. antillarum* in the Western Atlantic is *L. nigra* from which it may be distinguished by its light coloration and the sculpturing on the posterior end of the shell. *Lithophaga antillarum* is found boring into living or dead coral from the intertidal zone to depths of at least 6 fathoms. We have been unable to find a record of this species boring into shells but this is probably only a reflection of the fact that notes concerning the substrata into which the shells were boring are seldom added to the labels in collections.

The name *Lithophaga straminea* was first applied in manuscript to a shell in the Cuming collection by Dunker. It was labeled as from the West Indies. Reeve (1857) described and figured this specimen giving credit to Dunker with the type locality as the West Indies. Dunker (1882) later published a description and figures of the species and gave the locality as Antillae insulae. He compared his species to *L. corrugata* Philippi [= *antillarum* d'Orbigny] and suggested that more material might prove them to be the same. When Hedley (1906) first discovered what he called *L. straminea* Reeve, he recorded its occurrence as new to Australia. Later Lynge (1909) used *L. straminea*, considering it as an Indo-Pacific species, and stated that the locality "West Indies" given by Reeve was in error. Lamy (1937) followed Hedley and Lynge, and the name has attained wide usage in the Indian, Australian, and Japanese literature (i.e. Okada, 1960). Nevertheless, it is evident that the name *straminea* is not available since it is a synonym of *antillarum*. Furthermore, we are in agreement with Hedley and consider that only a single species with a discontinuous distribution is involved. We have not found any sufficiently distinguishing characteristics which will separate Western Atlantic specimens from Indo-Pacific specimens, and all series which we have seen from the Pacific fit well within the range of variation exhibited by the Atlantic specimens. When more material is available for study some consistent conchological or anatomical differences may be found, but at the moment this seems unlikely. Should the Indo-Pacific populations eventually prove to be a distinct subspecies or species, a new name will have to be proposed.

At the present time, it is difficult to explain the occurrence and distribution of this species in the Indo-Pacific, for it does not occur in the Eastern Atlantic or the Eastern

Pacific. It is possible that these two are relict areas remaining from a widespread Tethyan distribution. *Cymatium pileare* Linné has a similar distribution (see *Johnsonia*, 1957, no. 36, p. 216). It is also possible that *antillarum* was introduced into the Pacific during the early days of explorations in fouling on ships.

Range. WESTERN ATLANTIC: The known range of this species extends from Miami, Florida south through the West Indies and in Central America from Veracruz, Mexico south to British Honduras. INDO-PACIFIC: From Japan south to New Caledonia and Australia and west through the Gulf of Siam (Lynge, 1909) to India (Ummerkutty, 1960).

Specimens examined. WESTERN ATLANTIC. FLORIDA: Miami Beach; Soldier's Key; 1 mile SW of Soldier's Key in 2 fathoms; Carysfort Light, in 2 fathoms; Western Dry Rocks (all MCZ); Bonefish Key (MCZ; USNM); Looe Key, off Marathon (MCZ); Key West, in 6 fathoms (MCZ; USNM). BAHAMA ISLANDS: Abaco Island (USNM). CUBA: Guantánamo, Oriente (MCZ; USNM). HISPANIOLA: Santa Bárbara de Samaná, Santo Domingo (MCZ). VIRGIN ISLANDS: Tortola (USNM); St. Thomas (MCZ; USNM; BMNH). MEXICO: Veracruz (MCZ); *Albatross*, station 2365, about 46 miles off Cabo Catoche (22°18' N; 87°04' W) in 24 fathoms (USNM). BRITISH HONDURAS: Glory Cay (17°06'00" N; 88°00'55" W) in 2–4 feet; N of Tarpum Cay (16°37'05" N; 88°19'05" W) in 2–5 feet (both ANSP). INDO-PACIFIC. JAPAN: Osima Osumi (MCZ). NEW CALEDONIA. AUSTRALIA. QUEENSLAND: Lindeman Id.; Cape York (all Australian Mus.).

Subgenus *Labis* Dall

Labis Dall 1916, Proc. United States National Museum 52: 405.

Type species, *Lithophaga attenuata* Deshayes, original designation.

Species in this subgenus are characterized by having a smooth shell with a very thin calcareous incrustation which becomes thicker posteriorly and extends beyond the valves as smooth projections, which may be rounded or triangular. The outer surface of these projections is convex and the inner surface may be flattened or slightly concave.

Lithophaga (Labis) patagonica d'Orbigny

Plate 68, figs. 1–4

Lithodomus patagonicus d'Orbigny 1847, Voyage dans l'Amérique Méridionale 5: 650, pl. 82, fig. 24; pl. 85, figs. 19–20 (l'Ensenada de Ros, sud du Rio Negro, Patagonie).

Lithodomus platensis Philippi 1893, Anales del Museo Nacional de Chile, Santiago, no. 10, p. 12, pl. 3, fig. 3 (late Miocene, La Bajada, Rio Parana, Corrientes, Argentina).

Lithodomus patagonicus dalli von Ihering 1907, Anales Museo Nacional, Buenos Aires 7(3): 275. (Golfo de San Jorge, Rada Tilly [6 miles south of Comodoro Rivadavia], formation Patagonienne moyenne [late Oligocene]).

Lithophaga (Diberus) patagonica d'Orbigny. Carcelles 1944, Revista del Museo de la Plata (n.s.) Sec. Zoolo-gia 3: 272, pl. 6, figs. 58–63.

Description. Shell elliptical in outline, reaching 41 mm. (about 1 $\frac{3}{4}$ inches) in length and 14 mm. (about $\frac{1}{2}$ inch) in height, thin, fragile, usually covered with irregular patches of gray-white calcareous material and with inconspicuous anterior umbos. Anterior

end of shell smoothly rounded. Periostracum moderately heavy and medium golden brown in color. Sculpture consisting of irregular concentric ridges and fine growth lines which are often partially to completely covered by the calcareous deposit. This deposit thickens towards the posterior end of the shell and generally extends beyond the posterior margin of the valves as a triangular prolongation, which is often broken, so that specimens appear truncated. The outer surface of the prolongation is convex and smooth except



Plate 68. *Lithophaga patagonica* d'Orbigny. Fig. 1. External view of the left valve. Fig. 2. Internal view of the right valve. Fig. 3. Ventral view of opposed valves. Fig. 4. Dorsal view of opposed valves showing the cup-shaped cavity between the posterior prolongations. From off Mar de la Plata, Argentina. (All about 2 $\times$.)

for fine growth lines; its inner surface has a slight concavity. Interior of the valves is a medium purplish brown, smooth and shining, often highly iridescent at the posterior margin. Anterior and posterior ends of the valves smoothly rounded, the anterior end being considerably higher and with a broader curvature. Ventral margin nearly straight, dorsal margin of two subequal portions, both the anterior and posterior portions of the dorsal margin slope at an angle of about 20° to a high point just posterior to the mid point of the dorsal margin. Ligament internal, strong, heavy, and extending from the umbos to the high point of the dorsal margin. Muscle scars lightly impressed, the posterior adductor with the adjacent posterior pedal and byssal retractor scars broadly oval and located about midway between the dorso-ventral margins in the posterior quarter of the shell. Anterior byssal retractor scar narrowly elliptical and located just beneath the umbos; the anterior adductor scar long, thin and arcuate, and located near the anterior ventral margin.

length	height	
41.0 mm.	14.0 mm.	Off Río de la Plata, Argentina
33.5	12.5	" " " " "
23.5	9.5	Mar del Plata, Argentina

Types. The holotype of *Lithodomus patagonicus* d'Orbigny is in the British Museum (Natural History) according to Gray (1854); the type locality is l'Ensenada de Ros, Río Negro, Argentina. The holotype of *Lithodomus platensis* Philippi is probably in the National Museum in Santiago, Chile; the type locality is the Tertiary Formation at La Bajada, Río Paraná, Corrientes, Argentina. The holotype of *Lithodomus patagonicus dalli* von Ihering is probably in the museum in São Paulo, Brasil. It is a Oligocene fossil from the Golfo de San Jorge, Argentina.

Remarks. *Lithophaga patagonica* appears to be a rather rare species to judge by the very few specimens found in museum collections. It is not closely related to any other species in the Western Atlantic. From *L. aristata*, the only other non-sulcate species in the Western Atlantic which has a posterior prolongation on the shell, *L. patagonica* differs by having the projection straight rather than crossed. It is most closely related to *Lithophaga attenuata* Deshayes from the Eastern Pacific from which it differs in being generally smaller and much less attenuate. In addition, the posterior dorsal margin of *patagonica* is straight while that of *attenuata* is concave.

Nothing is known of the life history of *Lithophaga patagonica* or the substrata into which it bores. Our records show that it occurs from the intertidal zone to depths of about 30 fathoms. The records would also indicate that this species prefers temperate waters rather than those of the tropics or subtropics as do most *Lithophaga*. It has been recorded by von Ihering under the subspecies name *dalli* from the Oligocene of Patagonia.

Range. So far as known, *Lithophaga patagonica* has a very restricted range. It occurs from Rio Grande do Sul, Brasil south, according to Carcelles and Williamson (1951, p. 328), as far as Comodoro Rivadavia, Golfo San Jorge, Argentina and in the Falkland [Malvinas] Islands.

Specimens examined. BRASIL: Sarita, Rio Grande do Sul (ANSP). URUGUAY: La Paloma, Roche (E. Duarte). ARGENTINA: Mar del Plata (USNM); *Albatross*, station 2765, about 18 miles NE of Punta Médanos, Buenos Aires (36°43' S; 56°23' W) in 10.5 fathoms (USNM); *Hassler* voyage, about 35 miles E of Querandi (37°40' S; 56°25' W) in 30 fathoms (MCZ; USNM).

Subgenus *Myoforceps* Fischer

Myoforceps Fischer 1886, Manuel de Conchyliologie, p. 969.

Type species, *Lithodomus caudigerus* Lamarck (= *Lithophaga aristata* Dillwyn), monotypic.

Species in this subgenus are characterized by having the smooth calcareous incrustation extending beyond the valves posteriorly and forming pointed projections which are crossed.

Lithophaga (Myoforceps) aristata Dillwyn

Plate 69, figs. 1–5; Plate 70, figs. 1–3; Plate 71, figs. 1–2; Plate 72, figs. 1–3

Mytilus curviroster Schröter 1787, Neue Litteratur 4: 268, pl. 3, fig. 12 (no locality given) [nomen oblitum¹].*Mytilus lithophagus striatus* Sowerby 1807, Trans. Linnean Soc. London 8: 274, pl. 6, fig. 2 (ballast stones, Tothill-fields, London, England) [nomen oblitum²].*Mytilus aristatus* 'Solander' Dillwyn 1817, Descriptive Catalogue of Recent Shells 1: 303 (Senegal).*Modiola caudigera* Lamarck 1819, Animaux sans Vertèbres 6: 116 (mers australes, les côtes d'Afrique).*Lithodomus caudigerus* Lamarck. Sowerby 1824, Genera of Recent and Fossil Shells, **Lithodomus** fig. 4 only.*Lithophagus caudatus* Gray 1827 [in] King, Narrative of a Survey of the Coast of Australia 2: 477 (refers to *Modiola caudigera* Lamarck 1819).*Mytilus ropan* Deshayes 1836 [in] Lamarck, Animaux sans Vertèbres (2) 7: 27 (l'Isle de Gorée du Cap Verd).*Modiola caudigera* Lamarck. Philippi 1846, Abbildungen und Beschreibungen Conchylien 2: 149, pl. 1, fig. 5.*Mytilus caudigera* Lamarck. Gibbs 1848, Catalogue of the Fauna of South Carolina, p. xxii.*Lithophagus aristatus gracilior* Carpenter 1856, Catalogue of the Reigen Collection of Mazatlan Mollusca, p. 129 (Mazatlan, Mexico).*Lithophagus aristatus tumidior* Carpenter 1856, Catalogue of the Reigen Collection of Mazatlan Mollusca, p. 129 (Mazatlan, Mexico).*Lithodomus forficatus* Ravenel 1861, Proc. Acad. Nat. Sciences Philadelphia, p. 44 (in coral from Blackfish Banks off Charleston bar, South Carolina).*Dactylus carpenteri* Mörch 1861, Malakozologische Blätter 7: 206 (Puntarenas, Costa Rica).*Lithodomus bipenniferus* Guppy 1877, Proc. Sci. Association, Trinidad, p. 154; Guppy 1879, Journal of Conchology 2: 169 (Gulf of Trinidad).*Lithodomus (Myoforceps) caudigerus* Lamarck. Fischer 1886, Manuel de Conchyliologie, p. 969.*Lithophaga (Myoforceps) aristata* Dillwyn. Dall 1898, Trans. Wagner Free Institute of Science 3: pt. 4, p. 800.*Lithophaga arista* (Solander). Buchanan 1854, Journal of the West African Science Association 1: 40 [error for *aristata* 'Solander' Dillwyn].

Description. Shell reaching 52 mm. (about 2 inches) in length and 16.5 mm. (about $\frac{2}{3}$ inch) in height, thin, fragile, covered with a thin, gray-white, calcareous deposit and with anterior umbos. Anterior end of the shell smoothly rounded, the umbos only evident in very young specimens. Periostracum relatively thin and a golden brown in color. Sculpture consisting of concentric growth lines only and these are usually obliterated by the calcareous deposit. This deposit thickens toward the posterior end of the shell and extends beyond the posterior margin of the valves as more or less triangular prolongations which cross each other. The prolongation of either the right or left valve may be dorsal, both forms occurring in the same population (see under *Remarks*). Interior of the shell medium purplish brown, smooth, shining, and highly iridescent, particularly on the ventral posterior margin. Anterior and posterior ends of the valves smoothly and similarly rounded. Ventral margin straight, the dorsal margin angled and composed of two nearly equal portions. Both the anterior and posterior portions of the dorsal margin slope

¹To our knowledge, this name has never been used for this species though the description and figure are both good. This name has a priority of twenty-seven years, but we are compelled under Article 28, Section B of the International Code of Zoological Nomenclature (1961) to consider this a forgotten name (nomen oblitum) which is no longer available.

²There is considerable confusion concerning this name. In the text of the original description Sowerby definitely refers to some species in the subgenus *Lithophaga*, but the plate caption refers to a figure of *L. aristata*. In the plate caption there is confusion for it refers to figures 2 to 5 whereas on the plate the figures are numbered 1 to 4. The name may also be considered a nomen oblitum.

upward at an angle of about 20° to a central high point. The ligament extends from the umbo nearly to the high point on the dorsal margin. Muscle scars not impressed. The posterior muscle scar, including the posterior adductor, the byssal and pedal retractors broadly oval and located just posterior to the midpoint between the end of the ligament and the posterior margin of the valve. Anterior byssal retractor scar located in the concavity of the umbo. The anterior adductor scar long, thin, arcuate and located near the anterior ventral margin.

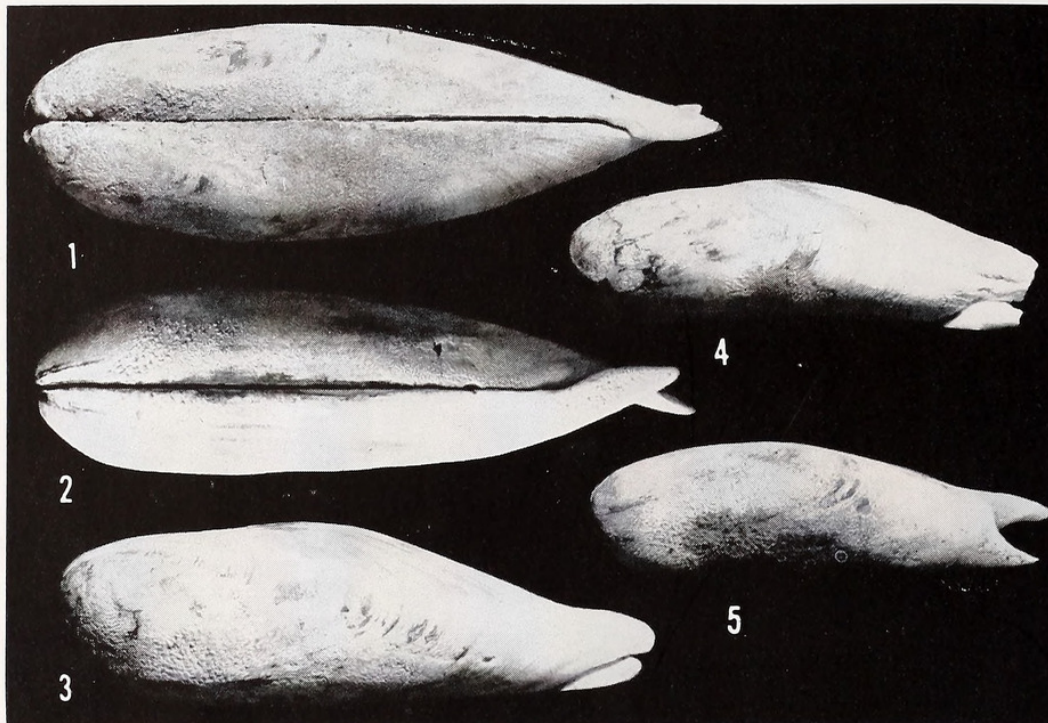


Plate 69. *Lithophaga aristata* Dillwyn. Fig. 1. Dorsal view of opposed valves. South Inlet, Lake Worth, Florida. Fig. 2. Ventral view of opposed valves. From off Sanibel Island, Florida. Figs. 3-5. Lateral views of shells to show variation in shape and in the direction of the crossing of the posterior prolongations. Fig. 3. From South Inlet, Lake Worth, Florida. Fig. 4. From Acapulco, Mexico. Fig. 5. From Faro, Algarve, Portugal. (All $2\times$).

length	height	
44 mm.	14 mm.	South Inlet, Lake Worth, Florida
37	12	" " " " "
28	11	" " " " "
25	10	Off Sanibel Island, Florida

Types. In his original description of *Mytilus aristata*, Dillwyn referred to Adanson 1757, pl. 19, fig. 20, and we here designate this to be the type figure. The specimen on which this figure was based is in the Adanson collection at the Museum National d'Histoire Naturelle, Paris. The type locality is Sénégal. According to Lamy (1937) the types of *Modiola caudigera* Lamarck are in the Museum National d'Histoire Naturelle, Paris and the locality given on Lamarck's label is Nouvelle-Hollande. Through the cooperation of J. Gaillard of the Laboratoire de Malacologie, we are able to figure Lamarck's specimens. The locality Nouvelle-Hollande [Australia] given on the label is apparently in error. The type specimens of *Lithophaga aristatus gracilior* and *L. a. tumidior* Carpenter are in the British Museum (Natural History). The type locality for both of these forms is Mazatlan, Mexico. The type of *Lithodomus forficatus* Ravenel is in the Charles-

ton Museum, Charleston, South Carolina. The type locality is Blackfish Banks, off Charleston, South Carolina in 14 fathoms. The type of *Dactylus carpeni* Mörch from Puntarenas, Costa Rica is probably in the University Museum, Copenhagen, Denmark. The type of *Lithodomus bipenniferus* Guppy from the Gulf of Paria, Trinidad was lost in the fire that destroyed the Victoria Institute.



Plate 70. *Lithophaga aristata* Dillwyn. Fig. 1. External view of the right valve. Fig. 2. Internal view of the left valve showing the ligament. Both from off Sanibel Island, Florida. Fig. 3. Lateral view showing the crossed posterior prolongations. South Inlet, Lake Worth, Florida. (All 2 $\times$.)

Remarks. *Lithophaga aristata* is a common, easily recognized species not closely related to any other. It is the only species belonging to the subgenus *Myoforceps* and is one of the most widely distributed of all lithophages. It bores into a wide variety of shells including *Spondylus*, *Chama*, *Haliotis*, *Patella*, *Strombus*, *Lambis*, and *Ostrea*, as well as calcareous rocks. We have seen a series which was taken from a large intake water pipe of a refining company in Amuay, Venezuela. A single specimen in the collection of the Academy of Natural Sciences of Philadelphia was labeled as having been taken from "the Barque Santee arriving in Boston after 3 years on the west coast of Africa." This was a young specimen and may have been taken from an oyster or other mollusk which was fouling the bottom of the ship or may possibly have been a nestler attached by its byssus threads in a small crevice among the fouling organisms. The wide range of *L. aristata* may well be the result of the variety of substrata into which it will bore. Certainly ships badly fouled with oysters are a perfect means of transport for these mollusks. Specimens in the United States National Museum from west Africa are in an *Ostrea*.

There is considerable variation in the size, shape and direction of crossing of the posterior prolongations of the valves of *L. aristata* and this is reflected in the rather lengthy synonymy given above. The prolongations may be broad, nearly equal in width and with only the tips crossed or they may be long, narrow and crossed near the posterior margin of the valves. In some populations nearly all specimens have the prolongation of the left

valve crossing dorsally, while in others that of the right valve is in the dorsal position and in still others the direction of crossing may be equally divided.

Though *L. aristata* is basically a littoral species, Soot-Ryen (1955) reports a living specimen taken from a depth of 165 fathoms.

Geologically, this species probably goes back to the Oligocene, as Dall (1898, p. 800) reports fragments from the Silex beds of Ballast Point, Tampa Bay, Florida, and Hertlein and Strong (1946) record it from the Pleistocene of the Galapagos Islands. See also *Remarks* under *L. patagonica* d'Orbigny.

Range. Though *Lithophaga aristata* has been reported from the Red Sea (Lamy 1937), Australia (Gray 1827) and Japan (Lischke 1871) these records need confirmation. We have not seen specimens nor have there been any recent reports of this species from these areas. The localities given by the above authors are all very general which adds doubt to the records. It is possible that these specimens could have come from ballast. To our knowledge this species has not been found living except in the tropical, subtropical and warm temperate areas of the Eastern Atlantic, the Western Atlantic, and the Eastern Pacific. In the Eastern Pacific it is distributed from the Gulf of California to Peru and in the Western Atlantic from North Carolina to Venezuela.

EASTERN ATLANTIC. PORTUGAL: Faro, Algarve (MCZ). MEDITERRANEAN ISLANDS: Malta (BMNH). CAPE VERDE ISLANDS: São Vincent (USNM). SENEGAL: Gorée (BMNH); Cap Vert, Dakar (MCZ; BMNH).

WESTERN ATLANTIC. NORTH CAROLINA: Shackleford Id.; 25 miles SE of Cape Fear (both USNM). SOUTH CAROLINA: Sullivans Id.; Blackfish Banks, off Charleston Bar, Charleston in 14 fathoms (both Charleston Mus.). FLORIDA: *Pelican*, station 167-5, 8 miles NE of Indian River Inlet, St. Lucie Co. in 16 fathoms (USNM); South Inlet, Lake Worth; Hillsboro Light, Pompano; American Shoal, off Cudjoe Key in 45 fathoms (all MCZ); *Eolis*, station 34, off Tortugas in 15 fathoms; Bird Key, Tortugas (both USNM); off Sanibel Island (MCZ); 3½ miles SW of Longboat Key, Manatee Co. in 6 fathoms (USNM); about 30 miles off Anclote Key, near Tarpon Springs (D. Moore); 15-20 miles ESE of Destin (MCZ). TEXAS: 107 miles SE of Galveston in 10 fathoms; Port Isabel (both MCZ). JAMAICA: Kingston Harbour (USNM). VIRGIN ISLANDS: St. Thomas (MCZ; USNM). LESSER ANTILLES: Grenada; Milford Bay, Tobago; Trinidad; Casper Grande Island, Trinidad (all MCZ). MEXICO: Veracruz; Contoy Island in 12-18 fathoms; Isla Mujeres, Yucatan (all MCZ). VENEZUELA: Amuay, Paraguana Peninsula (ANSP); Cumaná; Gulf of Paria (both MCZ).

EASTERN PACIFIC: CALIFORNIA: La Jolla (ANSP); San Diego (USNM). MEXICO: Conception Bay (ANSP); Santa Margarita (USNM); San Luis Bonzaga (J. Fitch); ½ mile NE of La Paz; *Albatross*, station 2826, Gulf of California, E of La Paz (24°12' N; 109°55' W) in 9½ fathoms; and Cape San Lucas, all Baja California (all USNM); Punta Penasco, Sonora (MCZ; ANSP); Porto Libertad, Sonora (USNM); Mazatlan, Sinaloa (USNM); Manzanilla, Colima (ANSP); Acapulco, Guerrero (MCZ; ANSP; USNM). COSTA RICA: Bahia de Chatham, Isla del Coco (USNM). PANAMA: Perico Island; Balboa, Canal Zone (both USNM); Bay of Panama (MCZ). GALÁPAGOS ISLANDS: Tagus Cove, Albermarle Island (ANSP).

Subgenus *Diberus* Dall

Diberus Dall 1898, Trans. Wagner Free Institute of Science, Philadelphia 3: 799.

Doliolabis Iredale 1939, Great Barrier Reef Expedition 5: no. 6, Mollusca, pt. 1, p. 417 (type species, *Lithophaga laevigata instigans* Iredale, original designation).

Exodiberus Iredale 1939, Great Barrier Reef Expedition 5: no. 6, Mollusca, pt. 1, p. 417 (type species, *Lithophaga calcifer* Iredale, original designation).

Salebrolabis Iredale 1939, Great Barrier Reef Expedition 5: no. 6, Mollusca, pt. 1, p. 417 (type species, *Lithophaga divaricalx* Iredale, original designation).

Stumpiella Soot-Ryen 1955, Allan Hancock Pacific Expeditions 20: 93 (type species, *Lithophagus calyculatus* Carpenter, original designation).

Type species, *Lithophaga plumula* Hanley, original designation.

Species belonging to this subgenus are characterized by having the valves divided by two radial sulci extending from the umbos to the posterior margin of the valves. The wedge-shaped area between the sulci is heavily incrustated with a calcareous deposit. This incrustation may be nearly smooth, deeply pitted or sculptured with plumulose or diverging ridges. The extension of the incrustation beyond the valves varies in length, the outer surface is convex, the inner surface concave. In forms with short projections, a cup-shaped cavity may be formed when the valves are opposed.

A study of the paratypes of *Lithophaga calcifer* Iredale, *Lithophaga divaricalx* Iredale and *Lithophaga instigans* Iredale has indicated that these species, which are the type species of the subgenera of Iredale given in the synonymy above, fit well within the scope of the subgenus *Diberus*. The outstanding characteristic of the subgenus *Diberus* is the division of the valves by the radial sulci extending posteriorly from the umbos. At the time Dall described the subgenus, only *plumula* Hanley and *bisulcata* d'Orbigny were included. The former species generally has a very plumulose incrustation, but *bisulcata* varies from those which are plumulose to those which are slightly pitted or nearly smooth. Iredale's subgenera were based upon differences in the sculpturing of the incrustations which can be found within the range of variation of the sculpturing of *bisulcata* alone.

The subgenus *Stumpiella* Soot-Ryen has for its type species *Lithophaga calyculatus* Carpenter, a bisulcate species which by definition would place it in the subgenus *Diberus*;



Plate 71. *Lithodomus forficatus* Ravenel [= *Lithophaga aristata* Dillwyn]. Fig. 1. External view of the left valve of the lectotype. Fig. 2. Internal view of the left valve of the paratype. From Blackfish Bank, off Charleston Bar, Charleston, South Carolina in 14 fathoms. (About 2×.)

the other characters mentioned by Soot-Ryen do not appear to be sufficient for the creation of another subgenus. It is probable that the subgenus *Rupiphaga* Olsson (1961) based on another bisulcate species *Lithophaga (Rupiphaga) hastasia* Olsson, also belongs with *Diberus*, but more material is needed for study before a definite decision can be made.

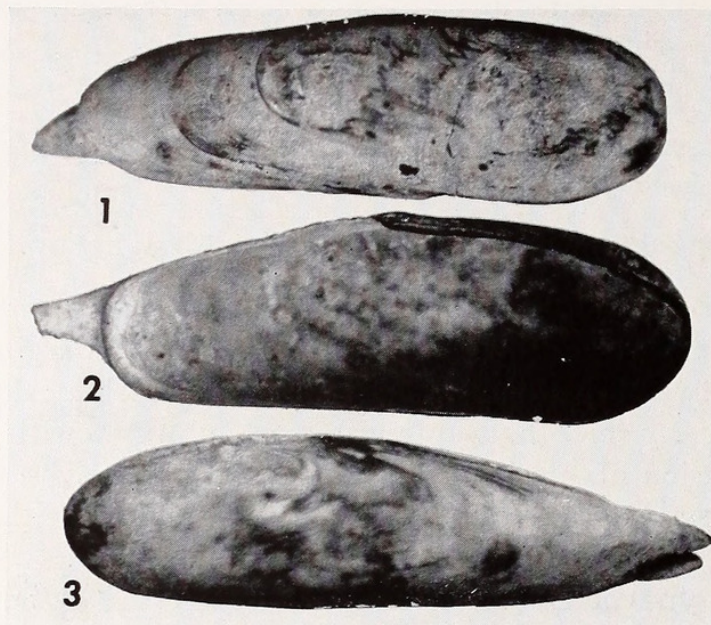


Plate 72. *Modiola caudigera* Lamarck [= *Lithophaga aristata* Dillwyn]. Specimens in the Muséum National d'Histoire Naturelle, Paris, considered by Lamy as the type specimens.

***Lithophaga (Diberus) bisulcata* d'Orbigny**

Plate 73, figs. 1-4; Plate 74, figs. 1-3; Plate 75, figs. 4-5

Lithodomus bisulcatus d'Orbigny 1842 [in] Sagra, Histoire Naturelle de l'Île de Cuba, Mollusques 2: 333, pl. 28, figs. 14-16 (Cuba, Jamaica, Martinique, Santo Domingo and Guadeloupe).

Modiola appendiculata Philippi 1846, Abbildungen und Beschreibungen Conchylien 2: 150, *Modiola*, pl. 1, fig. 4 (Insula Cuba).

Lithophaga appendiculata Philippi. Mörch 1853, Catalogus Conchyliorum Comes de Yoldi 2: 56.

Lithodomus biexcavatus Reeve 1857, Conchologia Iconica 10, *Lithodomus*, pl. 4, figs. 22a-b (St. Thomas, West Indies).

Lithophaga (Diberus) bisulcata d'Orbigny. Dall 1898, Trans. Wagner Free Institute of Science, Philadelphia 3: 801.

Description. Shell elliptical in outline, reaching 41 mm. (about $1\frac{2}{3}$ inches) in length, the anterior end considerably higher than the posterior end, the dorsal margin with a slight alation, and the anterior margin extending slightly beyond the umbos. Valves thin, fragile and covered with a golden brown periostracum which is generally overlain by a gray-brown calcareous incrustation. Sculpture on the anterior slope and disc consists of rather regular and fine growth lines. The disc is sharply separated from the posterior slope by a rather deep sulcus extending from the umbo to the ventral margin near the posterior end of the valve. Posterior slope divided into two areas by a second sulcus which extends from the umbo to the dorsal margin of the posterior end of the shell. The wedge-shaped area between these two sulci has a heavy calcareous incrustation which is irregularly pitted. The pitting becomes more pronounced toward the posterior margin of the shell. The incrustation extends beyond the end of the valve, and its posterior mar-

gin is smoothly rounded. The area dorsal to the sulci is somewhat wedge-shaped or alate. Ventral margin of the valves slightly arcuate; the anterior and posterior margins rounded. The anterior dorsal margin is slightly concave and parallels the ventral margin; it is about $1\frac{1}{4}$ times the length of the posterior dorsal margin, which is slightly convex and descends rapidly to the narrow posterior margin. Interior of the shell a mottled grayish purple, usually somewhat iridescent at the posterior end. The sulci evident internally as low rounded ridges. Muscle scars slightly impressed, the anterior adductor scar long, thin and arcuate and located near the anterior ventral margin. The anterior byssal retractor scar small, irregularly elongate and located just beneath the umbos. The posterior muscle scar, including the posterior adductor and posterior pedal-byssal retractor scars, broadly elliptical and located on the dorsal ridge of the sulcus very close to the posterior end of the valve.

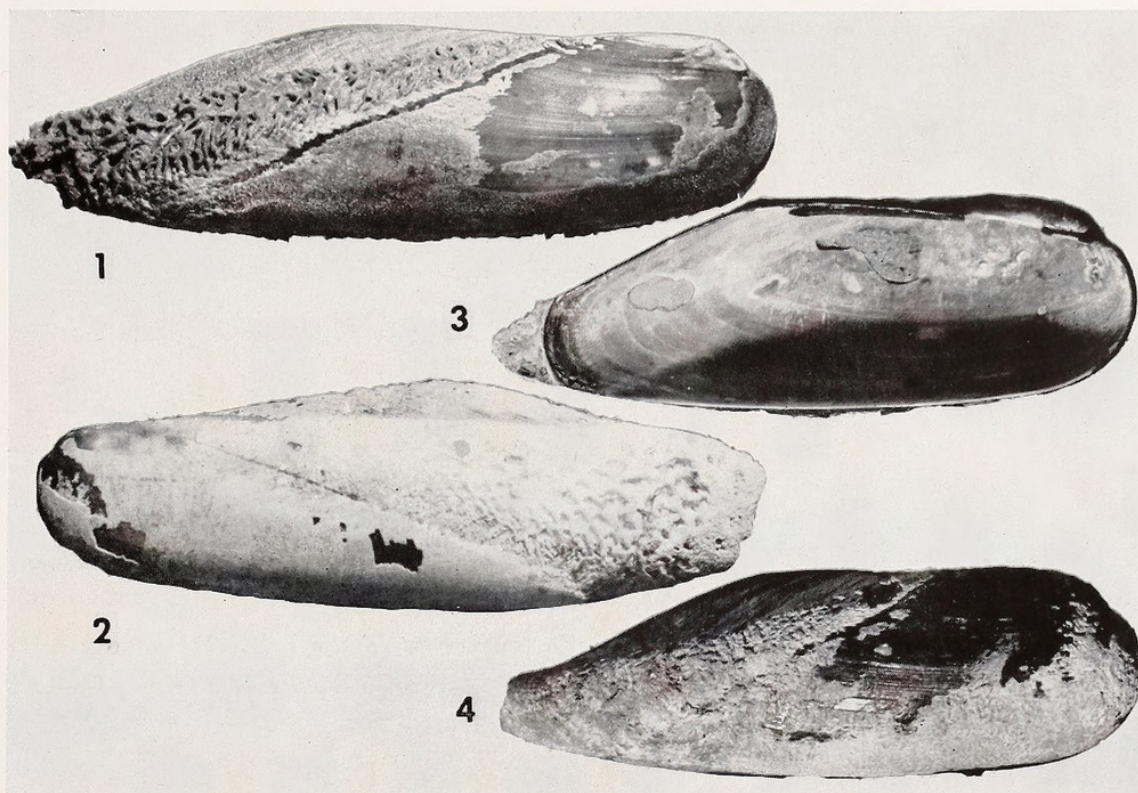


Plate 73. *Lithophaga bisulcata* d'Orbigny. Fig. 1. External view of the right valve. St. Augustine, Florida (about $2\times$). Fig. 2. External view of the left valve. From off Port Everglades, Florida ($2.2\times$). Fig. 3. Internal view of the left valve. Fig. 4. External view of the right valve. Figs. 3 and 4 from Daytona Beach, Florida (both $2.1\times$).

length *	height	
34.5 mm.	12.0 mm.	Off Port Everglades, Florida in 7 to 9 fathoms
22.0	9.0	" " " " " "
42.0	14.0	" " " " " "
40.5	13.0	Bonefish Key, Florida
34.5	12.5	Beaufort, North Carolina
25.5	9.5	" " "
41.0	14.0	St. Thomas, Virgin Islands
36.0	13.0	Vitoria, Brasil
25.0	13.5	" "

* Not including the protruding calcareous incrustation.

Types. The types of *Lithodomus bisulcatus* d'Orbigny are in the British Museum (Natural History), no. 54.10.4.606. The type locality cannot be further restricted at this time because of insufficient records. The type of *Lithodomus biexcavatus* Reeve is also probably in the British Museum (Natural History); the type locality is St. Thomas, Virgin Islands. The location of the type specimen of *Modiola appendiculata* Philippi from Cuba is unknown to us.

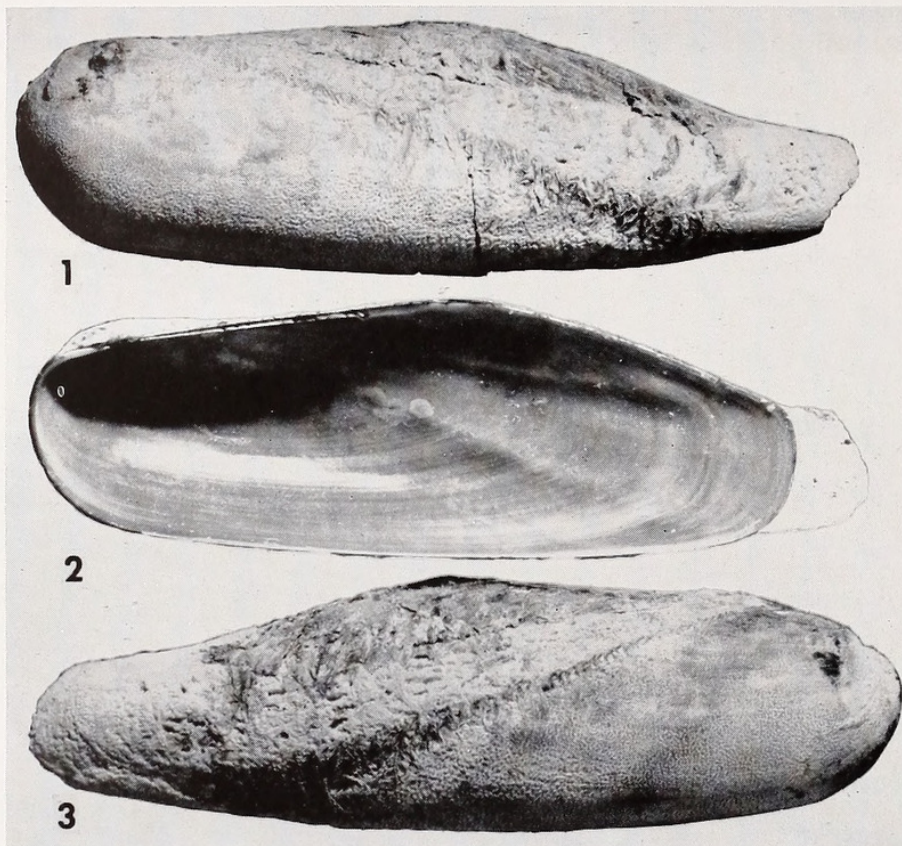


Plate 74. *Lithophagus bisulcata* d'Orbigny. Fig. 1. External view of the left valve with nearly terminal umbos. Fig. 2. Internal view of the right valve showing the straight hinge line and the sulci as internal ridges. Fig. 3. External view of the right valve with the anterior margin extending beyond the umbos. All from Bonefish Key, Florida. (All $2\times$.)

Remarks. This is perhaps the most common species of *Lithophaga* in the Western Atlantic, and it is found boring into living coral. Krebs (1864) described the expanding wedge-shaped holes made in living coral as these lithophages moved outward in order to maintain contact with the surface. This species is also found boring into living shells such as *Strombus* as well as into dead coral and calcareous rock. When boring into coquina or other coarse-grained rocks they line their burrows with a fine, gray, amorphous calcareous deposit.

Lithophaga bisulcata is most closely related to *L. plumula* Hanley from the Eastern Pacific from which it differs in having the incrustation on the posterior slope far less elaborately sculptured. In general, *bisulcata* is a smaller species and has the posterior dorsal margin more nearly equal in length to the anterior dorsal margin, while in *plumula*, the posterior dorsal margin is much shorter than the anterior dorsal margin.

Lamy (1937) under the synonymy of *Lithophaga bisulcata* d'Orbigny lists the name "*Mytilus attenuatus* 'Gibbs' (non Deshayes), Cat. South Carol. pg. XXII." Gibbs

(1848) listed under the genus *Mytilus* the name *attenuata* Deshayes and simply referred to *Lithodomus* in Sowerby's Genera. On the single plate of *Lithodomus* in the Genera, figures 1 and 2 are labelled *dactylus*, and figures 3 and 4 *caudigera*, but figure 5 is unnamed. This may be the figure to which Gibbs was referring but as he did not quote figure numbers it is impossible to say. Therefore *attenuata* 'Deshayes' Gibbs need not be considered as it is a nomen nudum.

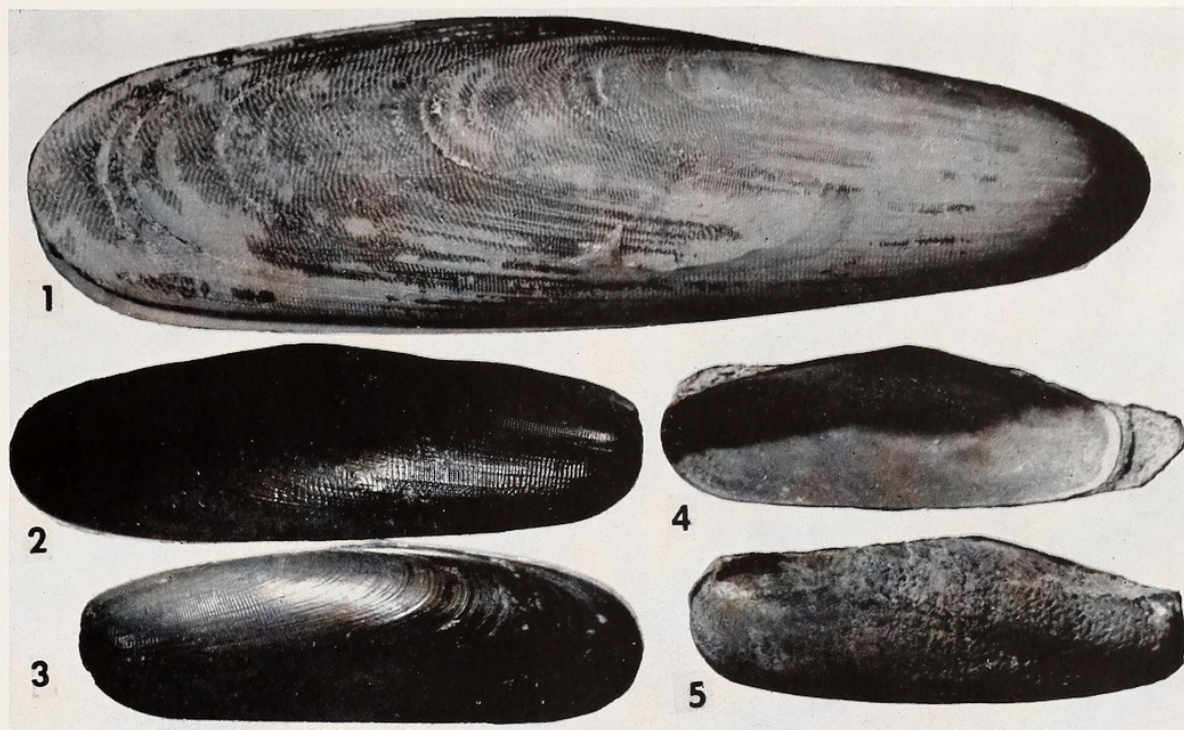


Plate 75. Fig. 1. *Lithodomus antillarum* d'Orbigny. Lectotype ($1\frac{1}{2}\times$). Figs. 2 and 3. *Lithodomus niger* d'Orbigny. Fig. 2. Lectotype. Fig. 3. Paratype ($1\frac{1}{2}\times$). Figs. 4 and 5. *Lithodomus bisulcatus* d'Orbigny. Lectotype ($2\times$). Photographs courtesy of the British Museum (Natural History).

Range. In the Western Atlantic this species extends from Beaufort, North Carolina south through the West Indies and the Gulf of Mexico to Vitoria, Brasil. In the Eastern Atlantic it is known from the island of St. Helena. It is found from the intertidal zone to depths of at least 79 fathoms.

Specimens examined. EASTERN ATLANTIC. St. Helena (USNM).

WESTERN ATLANTIC. NORTH CAROLINA: Beaufort; *Albatross*, station 2280, off Cape Hatteras ($35^{\circ}02' N$; $75^{\circ}21'30'' W$) in 16 fathoms (both USNM). SOUTH CAROLINA: 7 miles off Little River Inlet in $7\frac{1}{2}$ fathoms (USNM); NE of Pilot Boat, off Charleston in 8 fathoms; Pawleys Island (both Charleston Mus.). GEORGIA: from St. Mary's buoy, 7 miles off mouth of St. Marys River (A. Merrill). FLORIDA: St. Augustine (MCZ; USNM); Daytona Beach (MCZ); near Ozone; Lake Worth (both USNM); South Inlet, Lake Worth; Bonefish Key; off Port Everglades in 79 fathoms (all MCZ); *Albatross*, station 2370, about 30 miles SW of Cape San Blas ($29^{\circ}18'15'' N$; $85^{\circ}32' W$) in 25 fathoms (USNM); Sanibel Island (MCZ); $\frac{1}{2}$ mile N. of Whittaker Bayou, Sarasota Bay; $3\frac{3}{4}$ miles SW of Long Boat Pass, off Manatee Co. in 6 fathoms (both USNM); Madeira Beach, St. Petersburg (E. Marcott); Tampa Bay (MCZ; USNM); Apalachi-

cola; Pensacola (both USNM). LOUISIANA: West Rigolets Lighthouse (MCZ). TEXAS: *Atlantis*, station 107 miles SE of Galveston ($27^{\circ}54'05''$ N; $93^{\circ}35'02''$ W) in 10 fathoms; Port Aransas jetty; Cline's Point, Port Aransas; 50 miles off Port Arthur; Padre Island, Port Isabel (all MCZ). BERMUDA: Castle Roads, Castle Harbour, in 4–5 fathoms; $\frac{1}{2}$ mile S of North Rock, 10 miles N of Hamilton, in $1\frac{1}{2}$ fathoms (both MCZ); Harrington Sound (MCZ; USNM); between Trunk Island and south shore of Harrington Sound; Challenger Banks south of Bermuda (both MCZ). BAHAMA ISLANDS: Green Turtle Cay, Abaco Island in 15–25 fathoms (USNM); Clarence Town, Long Island (MCZ). CUBA: Cayo Levisa, Pinar del Río in 3 fathoms (USNM). HISPANIOLA: San Lorenzo Bay, Bahía de Samaná; Cayo Chico, $2\frac{1}{2}$ miles E of Santa Bárbara de Samaná, both Santo Domingo (both MCZ). JAMAICA: Kingston; Palisadoes (both USNM). PUERTO RICO: Port Real (USNM); San Juan (MCZ); Cabo Rojo (USNM). VIRGIN ISLANDS: St. Thomas (MCZ; USNM; BMNH); Mosquito Bay, St. Thomas in 2 fathoms; St. Croix (both USNM). LESSER ANTILLES: Falmouth, Antigua; Pelican Island; off Lord's Castle, Barbados; off Carlisle Bay, Barbados in 2–3 fathoms (all USNM); CARIBBEAN ISLANDS: Cayman Island (BMNH); Curaçao, Dutch West Indies (USNM). MEXICO: *Albatross*, station 2365, off Cabo Catoche, Yucatan ($22^{\circ}18'$ N; $87^{\circ}04'$ W) in 24 fathoms (USNM). BRITISH HONDURAS: Glory Cay ($17^{\circ}06'$ N; $80^{\circ}00'55''$ W) (ANSP). PANAMA: Colón (MCZ). COLOMBIA: Cartagena (USNM). VENEZUELA: Puerto Cabello (BMNH). BRASIL: Parahybat, Pernambuco (MCZ); Maceió (USNM); Rio de Janeiro (USNM); Vitoria (MCZ).

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